Work, R. W. 1981. A comparative study of the supercontraction of major ampullate silk fibers of orb-web-building spiders (Araneae). J. Arachnol., 9:299-308.

A COMPARATIVE STUDY OF THE SUPERCONTRACTION OF MAJOR AMPULLATE SILK FIBERS OF ORB-WEB-BUILDING SPIDERS (ARANEAE)[1]

Robert W. Work

Fiber and Polymer Science Program, David Clark Laboratory
North Carolina State University, Raleigh, North Carolina, 27607 U.S.A.

ABSTRACT

An improved and simple technique is described for determining the magnitude of the recently observed phenomenon of supercontraction of major ampullate silk fibers of orb-web-building spiders. Supercontraction ratios obtained by the use of that method and also from an instrumental method are given. It is seen that only three levels of supercontraction are found among twenty two species of orb-web-building spiders. The data are presented on the basis of taxonomic classification and are subjected to statistical analyses in order to determine which ones may be effectively differentiated from the others. A contribution to the integerity of the wetted web is suggested as a function for the retractive driving force which underlies supercontraction. Mention is made of the possible usefulness of supercontraction as a taxonomic symptom.

INTRODUCTION

This paper is one of a continuing series (Work 1976, 1977a, 1977b, 1978, 1981) which have been concerned with the silks produced by orb-web-building spiders. In the third of these, the discovery was announced of a very large axial shrinkage in water at room temperature of major ampullate silk fibers and its absence in minor ampullate fibers. It had been observed that the former retract to about one half their original lengths when they are wetted in an axially unrestrained condition. In the field of macromolecular chemistry this phenomenon is not unknown, being termed supercontraction. But it was quite unexpected, for although it can be induced in some natural and man-made fibers, it can be produced only under drastic conditions of chemical swelling or elevated temperatures, or both. Thus its existence has encouraged an expanded physico-chemical investigation, having as its objectives the characterization of the phenomenon and the determination of its basis at the molecular level. It is expected that the fruits of this research will be published in future papers of this series. But since orb webs are commonly wetted by dew and rain, arachnological considerations were not disregarded.

[1]Grants from the Research Corporation and the National Science Foundation (currently CPE-79-08905) supported, in part, the research described in this paper.

In the earlier part of the study it was found that the magnitude of supercontraction was remarkably uniform among all of the samples examined, as compared with their other physical properties such as axial force-elongation behavior. When one spider was found to have produced silk having an entirely different level of supercontraction, the observation was brought to the attention of Dr. Herbert W. Levi, who indicated that the property might be found to be a taxonomic symptom. Accordingly, while the study has remained centered upon macromolecular chemistry, increased attention was given to taxonomic aspects. To this end, silk samples from as many species of orb-web-building spiders as became available were examined for supercontraction. Techniques for measuring this property were improved in order to increase precision. The results which have been secured will be found in this paper.

BACKGROUND

The silk of *Bombyx mori* (Linnaeus) has been studied extensively, as is well known. Other silks have received relatively little attention, but workers at the Shirley Institute (Manchester, England) examined a considerable number of them. Lucas, Shaw and Smith (1960a) related the chemical compositions of 68 species of four orders of the class Instecta, and six species of Arachnida, to their taxonomy and also (1955), to a lesser degree, to certain of their physical properties. Associated observations were published by these authors (1958, 1960b) and by Lucas (1964). By their nature, chemical analyses, reported upon as amino acid ratios of the silk polypeptides, are amenable to classification in only the broadest sense. On the other hand, X-ray diffraction measurements of the crystalline domains in most of these same silks allowed Warwicker (1954, 1955, 1960) to classify them. He reported that all had orthorhombic unit cells, which possessed uniform axial and hydrogen bonding dimensions. He placed them in five groups based upon differences in the third, i.e., the side group, dimension. Of the seven arachnid silks, six came from named species. Of the latter, three were from "nests" of species of the family Theraphosidae, and one was a cocoon silk. The remaining two were from orb-web-builders, being "reeled" silk from *Nephila madagascariensis* (Vinson) and silk of undefined origin from *Araneus diadematus* Clerck. It is possible, even probable, that these last two were in whole or in part from the major ampullate glands. In any case, the two were found to be different and the former was placed in group 3 and the latter in group 5.

Other investigators of chemical compositions of spider silks (Braunitzer and Wolff 1955, Fischer and Brander 1960, Peakall 1964, Zemlin 1968, Andersen 1970) have reported their analyses on the basis of species. The same is true of workers (Herzog 1915, DeWilde 1943, Zemlin 1968, Work 1976, 1977b, Denny 1976) who have described physical properties. Since none of these authors has attempted to classify his observations on the basis of taxonomy, it is reasonable to assume that the limitations imposed by the intrinsic natures of such analyses and measurements have precluded this.

MATERIALS

Fibers obtained from the following species of orb-web-building spiders were examined: *Araneus diadematus* Clerck, *Araneus gemma* (McCook), *Araneus marmoreus* Clerck, *Araneus pegnia* (Walckenaer), *Neoscona hentzi* (Keyserling), *Neoscona nautica* (L. Koch), *Verrucosa arenata* (Walckenaer), *Eriophora fuliginea* (C. L. Koch), *Nuctenea cornuta* (Clerck), *Nuctenea sclopetaria* (Clerck), *Argiope argentata* (Fabricius), *Argiope aurantia*

Lucas, *Argiope trifasciata* (Fôrskal), *Micrathena gracilis* (Walckenaer), *Micrathena mitrata* (Hentz), *Nephila clavipes* (Linnaeus), *Nephilengys cruentata* (Fabricius), *Tetragnatha elongata* Walckenaer, *Tetragnatha versicolor* Walckenaer, *Uloborus penicillatus* Simon, *Uloborus glomosus* (Walckenaer), and *Hyptiotes cavatus* (Hentz). In addition, a few other spiders happened along, *Achaearanea tepidariorum* (C. L. Koch), *Metacyrba undata* (DeGeer) and *Lycosa rabida* Walckenaer, and their trailing silks were sampled. With the exception of one *V. arenata*, one *N. hentzi* and the *L. rabida*, all were females. The primary silk samples from *U. penicillatus* were taken from webs (W. G. Eberhard) and sent from Colombia. All others were obtained by the writer or his students.

METHODS

Primary samples of silk fibers have been secured by the forcible silking of large spiders. Where these fibers could be seen exiting from the spiders' bodies, all from major ampullate spigots on the anterior spinnerets supercontracted, but none from the minor ampullate spigots on the median spinnerets has supercontracted. Fibers also were obtained directly from orb webs, either in natural habitat or from caged spiders (Witt 1971). From webs, the loci of sampling were generally the support elements (foundation lines of the first or second order, Kaston 1972: 137: mooring and framework threads, Jackson 1973). A few of the samples were radii or segments of temporary spirals. With captured spiders that did not build webs in cages, samples were secured from the trailing silk left in their movements about the cages, or from induced draglines (Work 1978) or induced trailing silk (Work 1981). The sources of all such silks can only be determined indirectly. In a great many cases, primary samples were found to consist of more than one pair of fibers. Among these, it was often seen that two distinct diameters were represented, their ratio being of the order of two to one. In every such case the larger supercontracted, the smaller did not. Based upon all of this evidence, the criterion for inclusion in the present study has been the presence of axial supercontraction, when wetted at room temperature with distilled water, in an unrestrained condition. It has been inferred that for orb-web-building spiders the sources of these fibers were the major ampullate gland systems. Hereinafter, unless otherwise described, the word "fiber(s)" refers only to those assumed to originate in the major ampullate gland system. Induced trailing silks of the non-orb-building spiders were examined essentially out of curiosity and the results have been included for such interest as they may provoke.

The methods of obtaining samples, examining them for imperfections, manipulating them, and making the measurements, have been described in earlier papers (Work 1976, 1977b and 1981). Added experience has led to modifications that future investigators may find to be useful. In recent stages of the study, all samples have been taken directly onto glass microscope slides (plastic causes problems with static), to which they are fastened by means of small tabs of single faced self-adhesive tape. This provides for easy microscopic examination by transmitted light at 250-430X. For wider study of the physical properties of these silks, it has been necessary to reject many due to the presence of discontinuities or flaws, cemented sections, or because the sample consisted of multiple pairs which could not be easily separated. But when the only objective is to determine the magnitude of supercontraction, a greater incidence of useful samples may be expected. A sample consisting of a single pair is to be preferred; two pairs may be useful; a complex of more than two usually defies manipulation. Experience has shown that when the sample is composed of four fibers of approximately the same diameter, these are more often than

not in line contact for their entire lengths. With this situation only rarely can they be separated successfully into two component pairs, with subsequent transfer of one pair to a second glass microscope slide, without incurring the hazard of causing damage which may invalidate measurements. On the other hand, if two of the four are about one half the diameter of the other two, it may be assumed that the sample consists of a pair of major and a pair of minor ampullate fibers. In such a case, it is often seen that the two pairs do not remain entirely in line contact, since the smaller pair tends to loop slightly away from the larger pair. Such loops provide vantage points for the insertion of a micro dissection needle (Clay-Adams) between the pairs for separation, with one pair then being transferred to another slide for individual study.

There is always the possibility that the original sample is other than straight, or more often, in a state of slight strain, similar to the situation in which it existed when it was in the web. To correct either condition, the tab at one end is lifted and while illuminated at a glancing angle, perpendicular to the axis of the sample, it is allowed to form a slight catenary which is then brought to linearity and refastened to the slide. When it is a catenary it is axially unrestrained, and during these moments it is vital that the experimenter, necessarily close to it, should not breathe on it since condensation of moisture on it will initiate supercontraction. Although this investigator has not examined the major ampullate fibers for sensitivity to high relative humidities, it is suggested that these materials should not be manipulated under moist atmospheric conditions.

Subsamples for measurement of supercontraction (if any) are prepared by cementing the sample to the microscope slide at intervals of 5-10 mm. The electrical conducting "paint", commonly used for attaching specimens to studs for scanning electron microscopy is useful for the purpose and is easily applied with a double zero camel's hair brush. This cement is "quick drying," forms a strong adhesive bond to both glass and silk, and being observable by the unaided human eye, makes obvious the location of the subsamples. Also, it has less tendency to run into the sample adjacent to the cemented spot than other equally adhesive cements, such as catalyzed epoxy materials.

Since the original publication of the method of determining supercontraction (Work 1977b: 653) an improvement in the technique has been developed. As before, the length of the subsample is first measured. Instead of then immersing it completely in a droplet of water, followed by cutting it free of the cement at one end, the reverse is done. This makes it possible to place the droplet of water adjacent to the freed end and move it with a camel's hair brush until it touches the end. Capillarity then draws the water progressively along the fibers, which supercontract upon contact. This tends to prevent a snapping back which may occur at the instant of cutting of a completely immersed subsample. With the suggested improvement, the fibers shrink and retract axially without excessive lateral motion. This modification is particularly important when the subsample consists of a pair each of major and minor ampullate fibers. With the original method, the violent retraction of the former fibers usually caused them to entangle the non-shrinking latter pair. With the improved technique, the slowly retracting major pair tends in many instances to draw away from the dimensionally stable minor pair. In the sections to follow, this entire procedure will be referred to as the "slide" method, because the sample is cemented to a microscope slide, and the measurement obtained will be termed as "slide supercontraction," this being the ratio of the supercontracted length to the original length.

The method of producing and measuring supercontraction through the usage of the Instron® tensile tester has been described (Work 1977b: 654) and has continued to be

essential in connection with the broad study of this phenomenon and the force-elongation behavior of the supercontracted fibers. The measurement so secured will be referred to in what follows as "Instron supercontraction," being the ratio of fully retracted length to original length.

The data obtained in this investigation have been subjected to statistical analyses, the results of which are presented in the next section. The methods used and the computer programs for them were developed by the staff of the SAS Institute (1979). Computations were made by means of an IBM® 370/165 computer at the Triangle Universities Computer Center.

RESULTS

Table 1 presents the results obtained for the following groups. (A) The slide and Instron supercontraction of major ampullate fibers from 22 species of orb-web-building spiders. (B) The slide supercontraction of the forcible trailing silk fibers of *A. tepidariorum*, a spider which does not build an orb web. (C) The small shrinkage of forcible trailing silk fibers from *L. rabida* and *M. undata*, which do not build orb webs. The mean values from these two are compared with the mean value of minor ampullate fibers of eight of the species found in group A.

For the samples from each species the data include N, the number of spiders from which samples were secured, N, the number of observations used in making the calculation of the mean value, the mean value, and the coefficient of variation for each such calculation. These data are presented on a taxonomic basis provided by Levi (per. comm.). The cells (species) of group A, within each of the two sets, Slide Supercontraction and Instron Supercontraction, are neither symmetrical from the standpoint of spiders involved, nor uniform in size, as would be desirable for statistical analyses. If Student's *t* tests were to be used to determine whether each mean value in a set differs significantly from every other mean value in it, this would require 231 and 136 comparisons for the set Slide Supercontraction and the set Instron Supercontraction, respectively. Duncan's New Multiple-Range Test, described in many tests, as for example by Steel and Torrie (1980), simplifies the problem of analysis. The raw data upon which the mean values of supercontracting fibers of Table 1 are based were subjected to an analysis of variance to establish overall species differences, ($F = 22.08$, $P < 0.0001$ for set Slide Supercontraction and $F = 9.55$, $P < 0.0001$ for set Instron Supercontraction). The Duncan procedure provides each mean value within a set with one or more alphabetic letters. When the same letter is given to mean values within a set, it is not possible to effectively differentiate between them, using the Duncan analysis. The calculations made for the set Slide Supercontraction are independent of those for the set Instron Supercontraction and the Duncan letters found in one must not be associated with those of the other.

DISCUSSION

It will be seen in Table 1 that the individual mean values of slide supercontraction ratios are generally slightly higher than those for the comparable Instron supercontraction. The means are 0.564 and 0.543 respectively, for all samples from the subfamily Araneinae. In order to further examine this difference, the data on those samples in this set upon which both slide and Instron supercontraction ratios had been determined on

adjacent subsamples (N = 43) were subject to a *t*-test. It was found that the difference between the means of the two variables gave a *t*-value of 2.202 with a significance probability level of 0.030. This suggests that the two means came from different populations, which in turn implies that the two methods of measuring supercontraction provide a small, but real, systematic difference.

It is possible to suggest an explanation of both the difference, as such, and its direction. With the Instron device a sample several centimeters long is wetted, allowed to supercontract to its maximum level, and dried, at which condition it possesses a very high modulus. This being the case, when it is straightened and stretching starts, there is an immediate response by the recording pen. Reversal of the motion of the crosshead drops the strain level to zero. But with the slide technique the supercontracted fiber must be made straight while wetted, at which time it has a very low modulus. Neither the sensitivity of the human eye nor the hand manipulating a camel's hair brush is great enough to differentiate between straightness at zero strain and stretching to a small degree. For example, the difference between the two mean ratios mentioned above, 0.564 and 0.543 is 0.021, which is equivalent to only about 50-100 μm of strain in a sample originally a few mm long. It follows that the Instron provides more accurate data and based upon the lower coefficients of variation in set Instron Supercontraction, seen in Table 1, these are more precise. But when consideration is given to the cost of the Instron device, its general unavailability in biological laboratories, the considerable delicacy of manipulation involved in the preparation of the sample and the comparatively large consumption of time required to secure a single datum, the practical value of the slide supercontraction technique is apparent.

There are similarities in the formation of major ampullate and strong man-made fibers (Work 1977a) and in their properties (Work 1976). (Biologists who are not familiar with the production and properties of the latter materials may wish to refer to Work (1974) for a summary, or to the Encyclopedia of Polymer Science and Technology for more comprehensive information). But supercontraction brings out distinct differences between man-made and major ampullate fibers. The former may supercontract under drastic conditions of chemical treatment or temperature or both. The amount of shrinkage is a function of amount, speed, and temperature of stretching (technically known as drawing) during manufacture, and the conditions of treatment used to produce supercontraction. On the other hand, whether the latter fibers are produced rapidly as draglines or more slowly as trailing silks, or by pulling out with the fourth leg, the level of supercontraction for each species is uniform, and occurs in water at room temperature, a condition commonly encountered.

These differences suggest a function for the driving force which triggers supercontraction, without regard for the three distinct supercontraction ratios, about 0.55, 0.63, and 0.82, which may be of taxonomic significance.

It is, of course, common knowledge that an undisturbed "dry" orb web is in a state of static tension, a condition considered by Denny (1976) and by Wainwright (1976, esp. Fig. 8.2 and associated text). The axial retractive forces of the major ampullate fibers, as radials and supportive elements, are not known, nor are the correlative levels of strain. But it is reasonable to assume that the state of these is within the so-called Hookean, essentially linear and elastic region of the force-elongation response of these fibers, before the yield section is reached. The Hookean region and its attendant yield section disappear when major ampullate fibers are wetted (Work 1977b, Fig. 1), a condition to be expected of fibers which are highly sorbative of and swollen by water. In such a state, the weight of

Table 1.–The shrinkage of certain spider fibers when axially unrestrained and wetted with water at room temperatures. Explanations of the column headings are given in the text. Classifications by Levi (per. comm.).

		Supercontraction								
		Slide				Instron				
Genus Species	N sp.	N obs.	Mean	Cv. %	Duncan	N sp.	N obs.	Mean	Cv. %	Duncan
Araneidae: Araeinae										
Araneus diadematus	18	41	0.552	13.6	A	4	5	0.570	5.1	A
Araneus gemma	1	9	0.578	8.2	ABC	1	3	0.560	1.0	A
Araneus marmoreus	3	8	0.520	12.1	A	2	4	0.492	6.7	A
Araneus pegnia	1	4	0.560	3.1	ABC	1	3	0.553	6.8	A
Neoscona hentzi	6	24	0.545	11.0	A	4	7	0.529	10.3	A
Neoscona nautica	1	2	0.605	1.2	ABC	-	-	-	-	-
Verrucosa arenata	3	6	0.548	14.3	A	2	4	0.500	2.8	A
Eriophora fuliginea	2	2	0.540	0.0	A	2	2	0.595	10.7	AB
Nuctenea cornuta	2	10	0.563	10.2	AB	1	4	0.535	12.4	A
Nuctenea sclopetaria	3	8	0.561	12.8	AB	-	-	-	-	-
Araneidae: Argiopinae										
Argiope argentata	2	5	0.572	11.6	ABC	1	1	0.570	-	AB
Argiope aurantia	5	11	0.548	9.0	A	5	7	0.544	7.3	A
Argiope trifasciata	2	7	0.586	13.0	ABC	1	3	0.553	5.5	A
Araneidae: Gasteracanthinae										
Micrathena gracilis	4	18	0.636	10.4	C	2	5	0.590	15.9	AB
Micrathena mitrata	1	6	0.560	13.2	AB	1	2	0.535	4.0	A
Araneidae: Tetragnathinae										
Tetragnatha elongata	1	3	0.510	22.1	A	1	3	0.553	11.1	A
Tetragnatha versicolor	2	3	0.537	2.2	A	2	3	0.553	12.0	A
Araneidae: Nephilinae										
Nephila clavipes	6	22	0.635	11.5	C	5	7	0.650	11.0	B
Nephilengys cruentata	3	17	0.822	3.6	D	3	5	0.800	12.7	C
Uloboridae										
Uloborus glomosus	3	8	0.832	4.4	D					
Uloborus penicillatus	7	7	0.810	7.4	D					
Hyptiotes cavatus	2	14	0.619	10.9	BC					
Theridiidae										
Achaearanea tepidariorum	1	10	0.583	9.7	ABC					

			Mean ratio, final/orig.	Cv. %
Lycosidae				
Lycosa rabida	1	4	0.960	2.3
Salticidae				
Metacyba undata	1	3	0.987	0.6
Various minor ampullate	8	35	0.956	4.0

droplets of water on the elements of the orb web, place them under greater axial stress than in the unwetted static state. It follows that the increased weight will tend to extend the fibers, but this will be opposed by the newly developed retractive forces, which, if they were to be axially unrestrained, will cause them to supercontract. To what degree this retractive force may support the added load of water cannot be estimated at this time.

It is perhaps fortunate that casual attention was given to three spiders that do not build orb webs, because the trailing silk of *A. tepidariorum* supercontracts to a level which does not allow it to be effectively differentiated from fibers of the subfamilies Araneinae, Argiopinae, and Tetragnathinae of the family Araneidae. It must be concluded that whatever may be the function, it is not limited to contributing only to the integrity of a wetted orb web. This raises the question as to whether the major ampullate silk of species which build orb webs only in extremely dry habitats supercontract and also whether supercontracting fibers are produced only in climates where they may be expected to be exposed to wet conditions. Only one datum can be added in this connection. Fibers taken from the web of a *N. cruentata* in the hot dry climate of the Taita Hills, Kenya, East Africa, in no way differed from those produced by the same spider in the moist climate of North Carolina.

When attempting to secure observations on silks from as many species as possible, recourse was made to samples secured in the very early stages of the overall program, which resulted in a rather interesting peripheral observation. A few samples which originally had been considered to be too complex for manipulation had been stored in closed microscope slide boxes, and thus, most importantly, had not been exposed to light, which may be expected to cause degradation of organic fibers. Two samples from *E. fuliginea* were 197 and 230 weeks old; two from *A. argentata*, 173 weeks; three from *A. aurantia*, 206, 219, and 227 weeks; one from *A. gemma*, 119 weeks. All supercontracted in the same manner as new samples and the data secured from them are included in Table 1. Under the conditions of storage it is apparent that the dormant or potential retractive stresses do not decay during a period of several years. On the other hand, when, as a matter of curiosity, force-elongation measurements were made on these same fibers, it was found that they ruptured at about one third to one half of the values expected for new fibers. Considering the circadian life and ephemeral nature of the orb web, the resistance of one of its component silks to aging is noteworthy.

In taking up the subject of supercontraction as a possible taxonomic symptom, it is well to first examine the data seen in Table 1 for *M. gracilis* and *M. mitrata*. The Duncan letters assigned to them indicate that based upon the slide technique they can be differentiated but the Instron data shows that this is not possible. In an attempt to resolve this uncertainty the raw data were subjected to *t*-tests. In the set Slide Supercontraction a *t* value of 2.222 and a significance probability level of 0.058 were secured; for set Instron Supercontraction the corresponding figures were 1.238 and 0.274. It must be concluded that the two species produce fibers which do not differ significantly. But more importantly, these findings emphasize that additional measurements must be made so as to make definitive conclusions possible. Similarly, it would have been advantageous if a greater number of both spiders and samples had been available for some of the species listed in Table 1. This would have reduced the uncertainties which exist where a species carries more than one Duncan letter. But it is quite clear that fibers from the several species and genera listed in Table 1, of the subfamilies Araneinae, Argiopinae, and Tetragnathinae of the family Araneidae, cannot be effectively differentiated. The two related species (Levi, per. comm.) in the subfamily Nephilinae are differentiated from this group and from each other. In connection with this former situation it is well to be reminded, as earlier noted, that Warwicker (1960) placed *A. diadematus* and *N. madagascariensis* in different groups, based upon X-ray diffraction diagrams. That the supercontraction ratio of about 0.82 for *N. cruentata* is not unique to one species is clear, when it is seen that two uloborids produced the same level. The supercontraction of the fibers from the other

uloborid, *H. cavatus*, resembles that of fibers from *N. clavipes*. There is little that can be said regarding the lack of supercontraction for the trailing silks of *L. rabida* and *M. undata*. The grandular sources of these are unknown. They are dimensionally stable axially when unrestrained in water, as are minor ampullate fibers. The small, reversible, axial, shrinkages exhibited by these fibers are not unexpected among fibers which are highly swollen laterally by water, a property of minor ampullate fibers recorded by Work (1977b, Table 1).

Thus the data seen in Table 1 illustrate that there are three distinct levels of supercontraction. Although I do not have equipment sufficiently sensitive to discriminate between the driving forces which produce these, it is reasonable to assume that corresponding differences exist and are based fundamentally upon molecular structure. Furthermore, it is seen that these are not transient factors. This combination strengthens the suggestion that the entire phenomenon is basic, and as such, may be a taxonomic symptom.

The data summarized in Table 1 may be of interest to students of taxonomy, even as the phenomenon itself has stimulated its study from the standpoint of macromolecular chemistry. The measurement is easily performed through the use of commonly available equipment, on such spider silks as any person may come upon. I wish to emphasize that although I happen to be the first one to observe supercontraction in spider silk, I also urge other investigators, whose imaginations may be aroused by it, to expand upon this very small beginning.

ACKNOWLEDGMENTS

Dr. Herbert W. Levi provided the motivation for this study, gave counsel during its progress, and identified many of the spiders used. Dr. William G. Eberhard supplied primary silk samples. Drs. John F. Andersen, Cesar Edes, Cynthia Grant, Donald Kimmel, Brent Opell (who also identified uloborids), Michael E. Robinson and Messrs. H. H. Newton, W. A. Nattleton and Jesse Perry supplied spiders. Dr. Robert J. Monroe contributed guidance concerning statistical analyses. My wife, Anne, has borne with my research activities since my official retirement several years ago, helped with the forcible silking of spiders, and edited and typed this paper. To all of these, and to others who helped along the way, I express my sincere appreciation.

LITERATURE CITED

Andersen, S. O. 1970. Amino acid composition of spider silks, Comp. Biochem. Physiol., 35: 705-711.

Braunitzer, G. and D. Wolff 1955. Vergleichende chemische Untersuchungen über die Fibroine von *Bombyx mori* and *Nephila madagascariensis*. Zeitschriff für Naturforschung, Series B 10: 404-408.

Denny, M. 1976. The physical properties of spider's silk and their role in the design of orb webs. J. Exp. Biol., 65: 483-506.

DeWilde, J. 1943. Some physical properties of the spinning threads of *Aranea diadema* L., Arach. Néerl. Physiol., 27: 117-132.

Encyclopedia of Polymer Science and Technology. 16 vol. and 2 supp. (N. M. Bikales, exec. ed.) 1964-1977, Interscience Publishers, New York.

Fishcer, F. G. and J. Brander 1960. Eine Analyse der Gespinste der Kreuzspinne. Hoppe-Seyler's Z. Physiol. Chem., 320: 92-102.

Herzog, A. 1915. Zur Kenntnis der Spinnenseide. Kunststoffe, 5: 25-27, 53-55.

Jackson, R. R. 1973. Nomenclature for orb web thread connections. Bull. British Arachnol. Soc., 2(7): 125-126.

Kaston, B. J. 1972. How to know the spiders. 2nd ed. Wm. C. Brown Co., Dubuque, Iowa, USA. 289 pp.

Lucas, F., J. T. B. Shaw and S. G. Smith 1955. V- The chemical constitution of some silk fibroins and its bearing on their physical properties, J. Tex. Inst., 46: T440-T452.

Lucas, F., J. T. B. Shaw and S. G. Smith 1958. The silk fibroins. Pp. 107-242, *In* Vol. 13, Advances in protein chemistry, (C. B. Anfinsen, Jr., Ed.). Academic Press Inc. New York, 525 pp.

Lucas, F., J. T. B. Shaw and S. G. Smith 1960a. Comparative studies of fibroins. I The amino acid composition of various fibroins and its significance in relation to their crystal structure and taxonomy. J. Mol. Biol., 2: 339-349.

Lucas, F., J. T. B. Shaw and S. G. Smith 1960b. The composition of arthropod silk fibroins. XI Int. Kongr. f. Entom., Wien 1960. Verh. BIII, 208-214, Verlag. Inst. Ent. Univ., Pavia.

Lucas, F. 1964. Spiders and their silks. Discovery, 25:2-26.

Peakall, D. B. 1964. Composition, function and glandular origin of the silk fibroins of the spider *Araneus diadematus* Cl., J. Exp. Zool., 156: 345-352.

SAS Staff 1979. SAS user's guide, 1979 ed., SAS Institute Inc., P.O. Box 10066, Raleight, North Carolina 27605, 494 pp.

Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics, 2nd ed. McGraw-Hill Book Co., New York. 633 pp.

Wainwright, S. A. 1976. Principles of the strength of materials: phenomenological description. Pp. 6-44, 353-354. *In* Mechanical design in organisms. (S. A. Wainwright, W. D. Biggs, J. D. Currey, and J. M. Gosline, eds.) John Wiley & Sons, New York, 423 pp.

Warwicker, J. O. 1954. The crystal structure of silk fibroin. Acta. Crystallogr., 7: 565-573.

Warwicker, J. O. 1956. The crystal structure of silk fibroins. Faraday Soc. Trans., 52: 554-557.

Warwicker, J. O. 1960. Comparative studies of fibroins. II The crystal structure of various fibroins. J. Mol. Biol., 2: 350-362.

Witt, P. N. 1971. Instructions for working with web-building spiders in the laboratory. Bioscience, 21: 23-25.

Work, R. W. 1974. Man-made textile fibers. Pp. 301-343. *In* Riegel's handbook of industrial chemistry, 7th ed. (J. A. Kent, ed.) Van Nostrand Reinhold, New York, 802 pp.

Work, R. W. 1976. The force-elongation behavior of web fibers and silks forcibly obtained from orb-web-spinning spiders. Text. Res. J., 46: 485-492.

Work, R. W. 1977a. Mechanisms of major ampullate silk fiber formation by orb-web-spinning spiders. Trans. Amer. Micros. Soc., 96: 170-189.

Work, R. W. 1977b. Dimensions, birefringences, and force-elongation behavior of major and minor ampulate silk fibers from orb-web-spinning spiders–The effects of wetting on these properties. Text. Res. J., 47: 650-662.

Work, R. W. 1978. Mechanism for the deceleration and support of spiders on draglines. Trans. Amer. Micros. Soc., 97: 180-191.

Work, R. W. 1981. Web components associated with the major ampullate silk fibers of orb-web-building spiders. Trans. Amer. Micros. Soc., 100(1):1-20.

Zemlin, J. C. 1968. A study of the mechanical behavior of spider silks. Technical report 69-29-CM, AD 684333, U. S. Army Natick Laboratories, Natick, Massachusetts 01760, USA.

Manuscript received May 1980, revised August 1980.