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INTRODUCTION

References to the sexual biology of spiders are numerous in the literature. This is not surprising in view of the unique morphological modifications of the genitalia of these animals. There is virtually no information, however, pertaining to one of the most fundamental phases of the sexual biology of spiders, viz, the actual mechanics of copulation. This paper deals with the problem of copulatory mechanics and its implications.

The following objectives were formulated for this investigation:

1. To determine the structure and function of each part of both the male and female genitalia; particularly of those structures directly involved in copulation.
2. To study in detail the process of copulation with correlations to mechanical structures.
3. To determine, if possible, the correlations between structural mechanics and certain patterns of copulatory behavior.
4. To determine, if possible, the validity of the lock-and-key concept in a representative group of agelenid spiders found in North America.
5. To investigate the mechanical feasibility of copulation between representatives of closely related species of agelenids.

The work herein considered was confined primarily to the agelenid genus *Agelenopsis* Giebel, 1869. Spiders of additional genera in the Agelenidae and other families of Entelegynae were used to a limited extent for determining whether certain features exist exclusively in this genus.

The males of several unrelated groups of animals display the curious condition in which ambulatory or tactile appendages, widely separated from the genital aperture, are modified for the purpose of transferring sperms to the female. Similar modified appendages are to be found in representatives of the common squid (*Loligo,* Mollusca),

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of the insect order Odonata, and of the arachnid orders Ricinulida, Araneida, and probably the Solpugida. The decapod Crustacea, the Chelonethida, and some of the Acarina also utilize a method of sperm transference somewhat analogous to that of the spiders but are excluded here because they apparently lack the modified appendages for effecting this transfer.

The evolutionary factors involved in the origin of this separation of the sperm-transferring structures from the immediate vicinity of the genital apertures of the males, and the phylogenetic significance of this separation are still unknown. Several facts become evident when reviewing the groups in which this morphological phenomenon is manifest. Geologically speaking, all these animals originated in the Paleozoic. The cephalopods are known at least from early Silurian. The Araneida have been traced back to the Devonian, the Ricinulida and the Solpugida to the early Carboniferous, and the Odonata to the early Permian. A study of fossils of the aforementioned arachnids shows that all three orders were already well established and discrete at the time of the earliest known specimens of each. Furthermore, it is evident that this separation of the sperm-transferring organs from the primary genitalic structures is no recent caprice of nature. Fossil evidence indicates that this separation was completed in the spiders long before the Permian. Petrunkevitch (1925, p. 559) stated that "the study of coenozoic spiders, the tertiary spiders of North America and especially the amber species of the Baltic, has revealed the presence of external reproductive organs of as great complexity as in recent forms." The fact that this genitalic separation appears in only certain groups of animals while not appearing in closely related forms indicates that this phenomenon arose independently in each of the groups considered.

Behavior patterns play a paramount role in the life of spiders. As one of the objectives of this paper is an evalution of certain behaviorisms, it is desirable to review this subject briefly. A reflex is a motor response to stimulation (Wigglesworth, 1947, p. 99). Such reflexes typically serve some useful function under normal conditions (Wigglesworth, op. cit., p. 100). Responses which orient the animal relative to the source of stimulation are referred to as topotaxes. A specific topotaxis which "implies that the muscular tone on the two sides of the body is proportional to the intensity of stimulus received in bilaterally symmetrical sense organs" (Wigglesworth, op. cit., p. 162) is called a tropotaxis. The animal thus turns toward the side which is most strongly stimulated until the sense organs are equally stimulated, thereby orienting itself relative to the source of stimulation.

One of the functions of the sense organs of insects is to increase the nerve tone of the central nervous system. This results in a responsive state during which reflexes may occur in a definite sequence. It appears that each reflex is instrumental in initiating a subsequent reflex. This self-perpetuating sequence constitutes a chain reflex (Wigglesworth, op. cit., p. 101). Probably most of the activities of spiders similarly result from such chain reflexes. The behavior patterns herein considered are interpreted on this basis. The writings of Hanstroem (1941), Wigglesworth (1947), Scheer (1948), and Prosser (1950) indicate that the fundamental physiology of the nervous system appears to be essentially the same, qualitatively, throughout at least most of the Animal Kingdom. Hence it is necessary, in animals, to interpret and evaluate qualitatively the effect of sensory stimulation. Such evaluations must be interpreted in terms of the responses evolving from such stimulation. That the male becomes aware of the female indicates that the presence of the female impinges upon the nervous system of the male, and that he then responds in a characteristic manner.

The inability of animals to mate because of the physical incompatibility of their genital structures is called mechanical isolation. Dufour formulated the lock-and-key concept as a result of his study of the close correlations existing between the morphological configurations of the male and female genitalia of insects. This concept advanced the idea that the configuration of the female genitalia was such as to preclude the possibility of introducing any intromittent organ except that of a male belonging to the same species as the female. Araneologists had long been aware of the elaborate development of the male intromittent organs, and the complex configuration of the female copulatory structures. The lock-and-key concept was readily accepted by many araneologists. Other araneologists endorsed the concept in essence, if not in fact.

Subsequently, however, the lock-and-key concept was challenged and attacked repeatedly. Berland (1932) suggested that the isolating factor in the spiders is physiological rather than mechanical. Petrunkevitch (1942, p. 177) and Kaston (1948, p. 16) concurred with Berland on this point. Gertsch (1949, p. 98) pointed out that while interspecific copulation was precluded by "fundamental instinctive patterns probably based on chemical stimuli, it must be admitted that in spiders the differences between the genitalia of allied groups are usually sufficiently great to make pairing impossible—in effect a 'lock and key' presenting an impassable barrier to all but the most closely related species." Few, if any, araneologists still hold that morphological incompatibility of the genitalia constitutes the sole factor precluding mating between spiders of different species.

The term "intraspecific copulation" is used hereafter in reference to matings involving two spiders belonging to the same species. The somewhat ambiguous term "interspecific copulation" is used as a matter of convenience, to indicate matings involving two spiders belonging to two morphologically distinct groups of animals that are generally accepted as being distinct species.

ACKNOWLEDGMENTS

Correspondence and personal interviews with Dr. W. J. Gertsch contributed materially to this investigation from its inception to the reading of the final manuscript. Dr. R. V. Chamberlin generously placed all material in the Institute of Arachnology (University of Utah) as well as his personal library at my disposal. Dr. Chamberlin was a challenging teacher and an inspiring friend throughout the entire study. I owe a special debt of gratitude to my wife for her active assistance in all phases of this study. To these people and the many others who contributed directly and indirectly to my work, I acknowledge my indebtedness and proffer my thanks.

REVIEW OF LITERATURE

The literature pertaining to the sexual biology of spiders, and its ramifications, is voluminous. Specific literature relevant to each phase of this study is reviewed in the text.

Blackwall (1843) was one of the first to write specifically of the palpi of spiders. Later (1844, 1873) he wrote of both the structure and the function of these appendages. Westring (1861), Menge (1866), Emerton (1875, 1878, 1889), Bertkau (1875, 1876, 1878, 1884), and van Hasselt (1876, 1877, 1886, 1888, 1889) wrote extensively on this subject. In 1882, Karpinski reported on the structure of the copulatory apparatus of both male and female spiders, including the mechanics of copulation. His work was limited to specimens of *Dictyna benigna* Walckenaer. Wagner (1886) considered both the morphological features and the development of the copulatory organs of spiders, and later (1887) strongly advocated the use of the palpi as systematic criteria. Chamberlin (1904, 1908) pointed out the significance of employing the female genitalia as well as the male palpus as taxonomic criteria. Comstock (1910) brought all this information together, added the results of his own studies, and produced a comprehensive treatise on the palpi of male spiders which is still the basic reference on this subject.

Subsequent work was done on the structural and functional aspects of the palpus by Szombathy (1913, 1915), Gerhardt (1921a, 1921b), Gassman (1925), and Harm (1931, 1934). Osterloh's work (1922) included an analysis of the mechanics of copulation as well as a study of the morphology of the copulatory structures. He worked with specimens of *Linyphia triangularis* Clerck, *Lycosa amentata* Clerck, *Agelena similis* Keyserling, and *Meta segmentata* Clerck. Petrunkevitch (1925) pioneered the detailed study of the copulatory apparatus of agelenid spiders in America. Working specifically with *Agelenopsis naevia* (Walckenaer) and *Agelena labyrinthica* Walckenaer, he considered both male and female structures. Seyler (1941) extended Petrunkevitch's work by studying the copulatory structures, particularly those of the female, in three additional species of agelenopsids. Homann's work (1935) with hydraulic inflation of the palpus marked a major technical advance in the comprehension of the mechanism of palpal activation and thus of copulation. Blauvelt (1936) made a critical comparative study of the copulatory structures of spiders belonging to *Linyphia* and other related genera. She based her revision of these genera on this study. The revision of the genus *Cicurina* by Chamberlin and Ivie (1940) similarly was based, to a large extent, on a detailed comparative study of the genital structures. Gertsch (1949) added important information pertaining to the structure and, particularly, to the function of the palpus during copulation.

Literature pertaining specifically to the female copulatory structures is much more limited. No general study, comparable to that of the male palpi by Comstock, is known for the female structures. Van Hasselt (1892a, 1892b) studied the epigyna of female spiders in considerable detail. The work of Jaervi (1905, 1908, 1912, 1914) on the "Vaginalorgane" of the lycosids and sparassids was outstanding. Engelhardt's (1910) study involved eight families of spiders. The only agelenid included was *Agelena labyrinthica*. The investigations of Chamberlin and Ivie (1940), Blauvelt (1936), Petrunkevitch (1925), and Osterloh (1922) upon the epigyna have already been mentioned. In 1938, Kolosvary presented the first extensive study of variation found in the epigyna of females (*Argyope lobata* Pallas). Further studies of this nature are essential for a better understanding of female structures.

The study of courtship and mating has been popular with araneologists. Menge reported on the courtship of *A. labyrinthica* as early as 1843, but the first detailed studies of courtship and mating were made by Peckham and Peckham (1889, 1890). Their classical work with the Salticidae (formerly known as Attidae) continues to exert considerable influence on investigations of all phases of sexual biology. Montgomery reported on the mating habits of spiders (1903) and upon the secondary sexual characteristics (1910).

Outstanding work has been done on the sexual biology of spiders since 1910. In Germany, Gerhardt limited himself primarily to this field of investigation, and published numerous papers (1911-1938) pertaining to various phases of sexual biology. In England, Bristowe (1926, 1929, 1930) made many contributions to this subject, as did Locket (1923, 1926, 1927). In 1926 Bristowe and Locket considered the courtship of British Lycosidae. In France, Bonnet (1924, 1929, 1930a, 1930b, 1932, 1933a, 1933b, 1935, 1937, 1938) wrote extensively on all phases of sexual biology. In the United States, Kaston (1936) greatly extended courtship and copulation records during his study of the senses involved in courtship. Kaston (1948. pp. 31-34) included a concise summary of sexual biology in his "Spiders of Connecticut." Gertsch (1941) gave an excellent description of copulation in his revision of the Misumeninae. Gertsch (1949) and Savory (1928) devoted several sections in their books to this subject. Crane (1948-1950) added materially to our understanding of display in the courtship of the Salticidae.

Gerhardt's technical section on the sexual biology of spiders in Araneae (Gerhardt and Kaestner, 1937-1938, pp. 530-560) probably is the most comprehensive treatment available on this subject. With the active cooperation of many of his colleagues, Gerhardt integrated and systematized the preponderance of relevant information from the widely scattered literature.

A number of papers pertaining to the systematics of the Agelenidae were used extensively during this investigation. These included the series of generic revisions by Chamberlin and Ivie (1932, 1933, 1937, 1940, 1941, 1942), the papers of Exline (1935, 1936, 1938), and the generic reviews of Muma (1946, 1947).

One additional paper warrants special mention. Ellis (1944) established the fact that haemolymphatic pressure is a major factor in the extension of the legs. This mechanism appears to be equally functional in the male pedipalpus.

MATERIALS AND METHODS

While spiders of the genus *Agelenopsis* were used almost exclusively for the detailed portion of this study, the genital structures of representatives of the following agelenid genera were also cleared and examined during the investigation: *Agelena, Blabomma, Calilena, Calymmaria, Chorizomma, Cicurina, Coelotes* (Old World genus), *Coras, Cryphoeca, Cybaeina* (males only), *Cybaeota, Cybaeus, Hololena, Novalena, Ritalena* (males unknown), *Rualena, Tegenaria,* and *Wadotes.* As only type specimens of the following genera were available, the copulatory structures were studied without subjecting them to KOH treatment: *Chorizommoides* (males unknown), *Cybaeozyga, Ethobuella, Melpomene,* and *Tortolena.* The copulation of representatives of *Chiracanthium inclusum* Hentz (Clubionidae) and of *Misumena calycina* (Linnaeus) (Thomisidae) was subjected to detailed scrutiny both in the field and in the laboratory.

A total of 618 living specimens of *Agelenopsis aperta* (Gertsch), *A. oklahoma* (Gertsch), and *A. pennsylvanica* (C. Koch) were collected in Kansas and Utah for this investigation. Representatives of 13 additional species were used for detailed studies in vitro: *A. actuosa* (Gertsch and Ivie), *A. aleenae* Chamberlin and Ivie, *A. aperta guttata* Chamberlin and Ivie, *A. emertoni* (Chamberlin and Ivie), *A. kastoni* Chamberlin and Ivie, *A. longistylus* (Banks), *A. naevia* (Walckenaer), *A. oregonensis* Chamberlin and Ivie, *A. potteri* (Blackwall), *A. spatula* Chamberlin and Ivie, *A. utahana* (Chamberlin and Ivie), *A. texana* (Gertsch), and *A. barrowsi* (Gertsch). The last two species belong to the subgenus *Barronopsis* Chamberlin and Ivie. It should be noted, however, that the genital bulbs of the barronopsids differ so radically from those of the other agelenopsids that the term agelenopsid is used, in this paper only, in reference to the genus *Agelenopsis* exclusive of the subgenus *Barronopsis.* All known species of *Agelenopsis,* except *A.* (*Barronopsis*) *jeffersi* Muma (1945), have been included in this investigation. All specimens used are now at the Institute of Arachnology of the University of Utah.

The living spiders were collected directly into large shell vials. A separate vial was used for each specimen. Each vial was numbered to facilitate recording data pertaining to the specimen contained therein. As spiders are sensitive to low humidity, a few drops of water were added periodically to a thin layer of cotton on the bottom of each vial.

Transparent plastic gelatine molds with lids were used when studying the behavior of the spiders. A white cardboard disk was placed on the bottom of each of these mating cases. The disks not only increased the ease of observation but provided a suitable surface on which the spiders moved naturally and mated readily. Once copulation was initiated, the lid was removed and the spiders were studied in detail with the aid of a wide field binocular microscope. A magnification of 20 diameters was sufficient for most observations.

A wire recorder was used extensively during the studies of copulation. This permitted the recording of detailed, uninterrupted observations over long periods of time. By replaying each recording any necessary number of times, it was possible to obtain a most detailed account of each mating.

The pedipalpi of the male spiders were cleared and the genital bulbs were simultaneously expanded by boiling them in KOH. The pedipalpi were then washed in several changes of water, and transferred to glycerin for preservation and study. The copulatory structures of the females were treated in the same manner.

The mechanics of the palpus were hypothesized on the basis of observations of the palpus during copulation, and with the assistance of scale models. These hypotheses were then checked by a study of the palpus in vitro, and finally verified by additional observations of the palpus during copulation.

Hypotheses pertaining to the mechanical functions of the various parts of the genital bulb were further tested by means of artificial inflation of the bulb. This was accomplished by placing the palpus in a concentrated solution of KOH for several minutes, and then transferring it into distilled water. Osmotic pressure inflated the genital bulb. By alternately placing the palpus in distilled water and absolute alcohol the genital bulb was inflated and deflated at will. The mechanical results of this artificial inflation were checked against those of normal inflation. The two were found to agree well.

Little use was made of histological sectioning in this study. Where such sectioning was done, standard histological procedures for sclerotized material were followed.

Most of the figures were made with the aid of a camera lucida. The angles of articulation were measured by means of a grid ocular and a large-scale model of the grid superimposed on a protractor.

MORPHOLOGY AND FUNCTION OF REPRODUCTIVE ORGANS

Spiders are dioecious. Their gonads, and associated ducts leading to the external surface of the body, are relatively constant in basic organization throughout the order. This paper deals with the specialized copulatory apparatus of both sexes.

REPRODUCTIVE ORGANS OF THE MALE

The reproductive organs of the male consist of the internal testes and associated ducts, and the external pedipalpi. The pedipalpi are the first pair of leglike appendages of the prosoma (figs. 1, 2).

TESTES AND ASSOCIATED INTERNAL STRUCTURES

The testes of the spider are paired organs lying in the lower portion of the abdomen (fig. 50). They are elongated, and extend caudally from the epigastric furrow. These organs are simple and tubular. Each testis continues cephalically as a long, coiled vas deferens. These paired, tubular structures open into a common seminal vesicle, which in turn opens to the outside through the seminal aperture on the midline of the cephalic margin of the epigastric furrow.

PEDIPALPUS

Each pedipalpus consists of a coxa, trochanter, femur, patella, tibia, and tarsus. The segments distal to, and exclusive of, the coxa are referred to collectively as the palpus or palp. Systematists have long utilized the great variety of modifications of the palpi of male spiders in classification.

Coxa.—The coxa (*c*) is a large structure located between the chelicerae (*cl*) and the cephalic margin of the sternum (*sm*) (figs. 1, 3). The labrum (*lb*) separates the two coxae. Ventrally each coxa is produced into an endite (*en*), the distal margin of which is inclined sharply toward the chelicerae. In the agelenopsids the ectoventral margin of the endite bears a heavily pigmented carinate ridge (*cr*), and a scopula consisting of setae (not shown in figures). Laterally the coxa articulates with the small trochanter. The articulation of the coxa with the body is largely membranous; while the coxa-trochanteral articulation is entirely membranous.

The function of the coxa is twofold: (1) The endite endows it with a masticatory function; and (2) it serves as the basal segment of the pedipalpus.

Trochanter.—The trochanter is a small segment, subrectangular when viewed in profile, articulating with the lateral margin of the coxa (figs. 1, 3, *tr*). Within the agelenopsids, the trochanteral proportions range from 0.67 times as long as broad in *A. longistylus* to 0.91 times as long as broad in *A. oklahoma,* with the typical proportion being 0.82 times as long as broad as found in *A. potteri* and *A. utahana.* There is no marked variation in the trochanteral facies. The ectodistal margin is somewhat more heavily sclerotized and pigmented than the remainder of the segment. The ventral margin of the distal end is produced into a strong condyle. The trochantero-femoral articulation is dicondylar.

The trochanter is the basal segment of the palpus. Its importance in palpal movement is indicated by the size and number of muscles which insert on it, and the great degree of vertical and horizontal flexibility afforded by the membranous coxal articulation (figs. 9, 10).

Femur.—The femur is an elongated, parallel-sided structure (figs. 1, 2, *f*). Femoral proportions range from 4.1 times as long as broad in *A. pennsylvanica* and *A. actuosa* to 5.2 times as long as broad in *A. potteri.* The typical proportion is 4.5 times as long as broad as found in *A. kastoni* and *A. oklahoma.* The femoral facies are relatively constant. The proximal end of the femur is dicondylar.

The femoropatellar articulation is also dicondylar. The upper margins of both femur and patella are strongly sclerotized, and the fact that they impinge upon each other is the limiting factor in maximum extension. Maximum flexure likewise obtains when the sclerotized ventral portions of both segments impinge upon each other (figs. 9, 10).

A small chitinous plate is located ventrally in the membrane between the femur and patella. This plate was first described by Gaubert (1892) in the legs of spiders. Ellis (1944) showed that this plate normally lies in a horizontal position. A special muscle, the levator,

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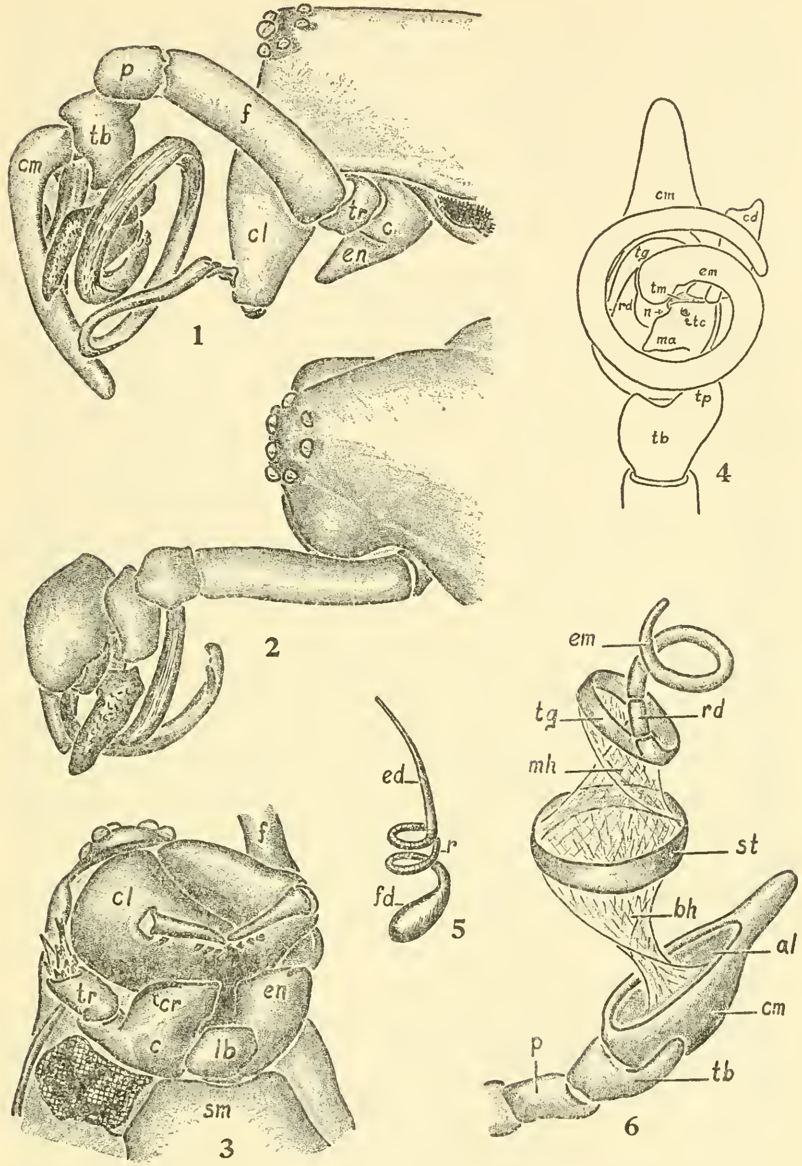
Explanation of lettering on figures

al	alveolus.
an	anelli.
at	atrium.
bc	bursa copulatrix.
bd	blind tube of diverticle.
bh	basal haematodocha.
bs	blind tube of spermathecum.
c	coxa.
cc	coupling cavity.
cd	conductor.
cl	chelicera.
cm	cymbium.
cr	carinate ridge of chelicera.
ct	connecting tube.
dv	diverticle.
ed	ejaculatory duct.
ef	epigastric furrow.
em	embolus.
en	endite of coxa.
f	femur.
fd	fundus.
ft	fertilization tube.
g	guide.
lb	labrum.
lp	lunate plate.
ma	median apophysis.
mh	middle haematodocha.
n	notch of median apophysis.
p	patella.
pm	posterior median sclerite.
pt	petiole.
r	reservoir.
rd	radix.
sm	sternum.
sp	spermathecum.
st	subtegulum.
tb	tibia.
tc	tubercle.
tg	tegulum.
tgr	tegular ridge.
tm	tethering membrane.
tp	tibial process.
tr	trochanter.
u	uterus.
v	vagina.



FIGS. 1-6

1, Pedipalpus, left, ectal aspect, *Agelenopsis aperta* (Gertsch). 2, Pedipalpus, left, dorsal aspect, *A. aperta.* 3, Mouth region, subventral aspect, *A. aperta.* 4, Genital bulb, left, unexpanded, frontal aspect, diagrammatic, genus *Agelenopsis.* 5, Receptaculum seminis, diagrammatic. 6, Genital bulb, left, expanded, subectal aspect, diagrammatic, genus *Agelenopsis.* (For explanation of lettering see p. 10.)

of the chitinous plate (Ellis, op. cit., p. 47) can draw the plate into a vertical position, and thus largely limit the increased haemolymphatic pressure, with its resultant extension, to the femur, trochanter, and coxa of the leg. The writer's observations and dissections indicate that a chitinous plate plays a similar role in the pedipalpi.

Being the longest single segment of the pedipalpus, the femur plays a major role in palpal movements and general orientation of the more distal genital bulb.

Patella.—The patella articulates proximally with the femur. It is subtriangular in outline when viewed ectally (figs. 1, 2, 6, *p*). Patellar proportions range from 1.5 times as long as broad in *A. pennsylvanica* to 2.0 times as long as broad in *A. aperta* and *A. kastoni,* with the typical proportion being 1.7 times as long as broad as found in *A. spatula* and *A. longistylus.* The patellar facies are relatively constant in the agelenopsids. Distally there is a small ectal process on the ventral apex of the patella. This is slightly more heavily sclerotized than the remainder of the patella. This process limits patellar-tibial flexure. The patellar-tibial articulation is monocondylar, and thus is not limited to a single plane of movement. This versatility of movement is important to the agelenopsids in the proper orientation of the genital bulb during copulation. Extension of the tibia appears to be limited by the impingement of the sclerotized dorsal portions of the patella and tibia and, more probably, by the extent of elasticity of the ventral intersegmental membrane. The morphological limits of maximum extension and flexure and of lateral articulation are shown in figures 9 and 10. Lateral articulation also appears to be limited by the segments themselves, and by the intersegmental membrane.

The patella is particularly important because of its monocondylar articulations with the tibia, and the lateral tibial movement which is thus permitted.

Tibia.—The tibia (*tb*) is roughly subtriangular in shape, with a pronounced ectal tibial process (*tp*) extending distally along the side of the cymbium (figs. 1, 2, 4, 6). Kaston (1948, p. 15) stated that this process was called the "carpoblem" by Hull. The tibial proportions range from 1.3 times as long as broad in *A. aperta* to 1.9 times as long as broad in *A. longistylus,* while the most frequent proportion is 1.5 times as long as broad as found in *A. actuosa.* The variability in the configuration of the tibial process in the agelenopsids is shown in figures 11-13. The tibiotarsal articulation is dicondylar. The ectal condyle, located approximately midway between the tibia proper and the distal end of the tibal process, is weakly developed. The mesal condyle is actually a condylar area. The limits of articulation are shown in figures 9 and 10. The writer has been unable to demonstrate the existence of a chitinous plate in the palpus comparable to that found by Ellis (1944) between the tibia and the metatarsus in the ambulatory legs of spiders. As will be shown later, however, the mechanical aspects of the genital bulb are such that extension of the distal palpal segments can be achieved without the chitinous plates.

The tibia serves as a base for the cymbium. The tibial process serves to limit the extent of cymbial flexure.

Tarsus.—The tarsus of the mature female spider retains the unmodified appearance of the tarsi of the ambulatory legs, even to the point of bearing a small, terminal claw. The tarsus of the mature male, however, is highly specialized into the copulatory organ consisting of (1) the cymbium and (2) the genital bulb.

1. Cymbium. Westring (1861) used the term "lamina" for this structure. Comstock (1910, p. 165), however, adopted Menge's (1866) term "cymbium," because of general usage. The body of the cymbium is oval when viewed from frontal aspect, with a short, heavy, distal extension (figs. 4, 6, 39, *cm*). Cymbial proportions range from 1.9 times as long as deep in *A. utahana* to 3.3 times as long as deep in *A. oklahoma,* with the typical proportion being 2.0 times as long as deep as found in *A. emertoni, A. potteri,* and *A. spatula.* The alveolus is the concavity in the frontal portion of the cymbium (figs. 6, 39, *al*). Comstock (op. cit., p. 163) adopted this term from Menge (1866). Usually the genital bulb lies almost wholly within the alveolus.

The ectoproximal margin of the cymbium has a weakly produced depression, which normally is somewhat more heavily pigmented and sclerotized than the surrounding area (figs. 11-12, 39). The tibial process rests in this depression when the palpus is locked.

The cymbium consists of a thin, sclerotized material and is abundantly covered with short and variously developed setae. Some of these setae are distinctly longer than others, and generally are much heavier. This vestiture has been omitted from all drawings to emphasize the morphological configurations.

The cymbium, with its alveolus, appears to serve a dual purpose: (1) It is the foundation for the genital bulb and the bulb's activity during copulation, and (2) it is a protection for the delicate membranes of the unexpanded genital bulb.

2. Genital bulb. The genital bulb includes all portions of the copulatory apparatus of the male arising from within the alveolus of the cymbium (fig. 6). The receptaculum seminis (fig. 5), consisting of

the fundus, reservoir, and the ejaculatory duct, is the only internal structure found in the genital bulb. Comstock (1910, p. 171) stated that there is no muscle tissue within the genital bulb. The writer's studies verify this in the agelenopsids. Osterloh (1922) presented evidence of the role of a hydraulic mechanism in the movements of the copulatory apparatus. Homann (1935) utilized hydraulic pressure to activate the genital bulb. Osmotic pressure was used for the same purpose in the study herein reported.

Wagner (1887, p. 64) introduced the term "receptaculum seminis." The fundus forms the proximal end of the receptaculum seminis (fig. 5, *fd*). This saclike structure is enclosed within the subtegulum in the agelenopsids. In some specimens (e.g., *A. oklahoma*) the fundus extends upward into the sclerotized lunate plate of the subtegulum. Distally the fundus opens into the reservoir, which can be seen distinctly through the walls of the tegulum following KOH treatment. Comstock (1910, p. 174) was unable to demonstrate taenidia in the intima of the fundus, and inferred that this structure serves as a compressible bulb when subjected to the increased haemolymphatic pressures found in the genital bulb during copulation. The total absence of muscles within the genital bulb strengthens this hypothesis. The fact that the distal end of the fundus bridges the articulation of the tegulum and the subtegulum in many of the agelenopsids, might indicate that some of the force needed for ejaculation may stem from this source.

The reservoir constitutes the middle portion of the receptaculum seminis (fig. 5, *r*). It is a heavily sclerotized, darkly pigmented tube which is in intimate contact with the wall of the tegulum. This tube is characterized by the presence of taenidia. The reservoir gradually narrows distally and merges with the ejaculatory duct near the base of the radix.

The ejaculatory duct (*ed*) is the terminal portion of the receptaculum seminis. It consists of a slender tube traversing the radix and the embolus. Because of its dark color, the ejaculatory duct is easy to trace, especially in expanded bulbs. Distally the duct opens at or near the embolic terminus.

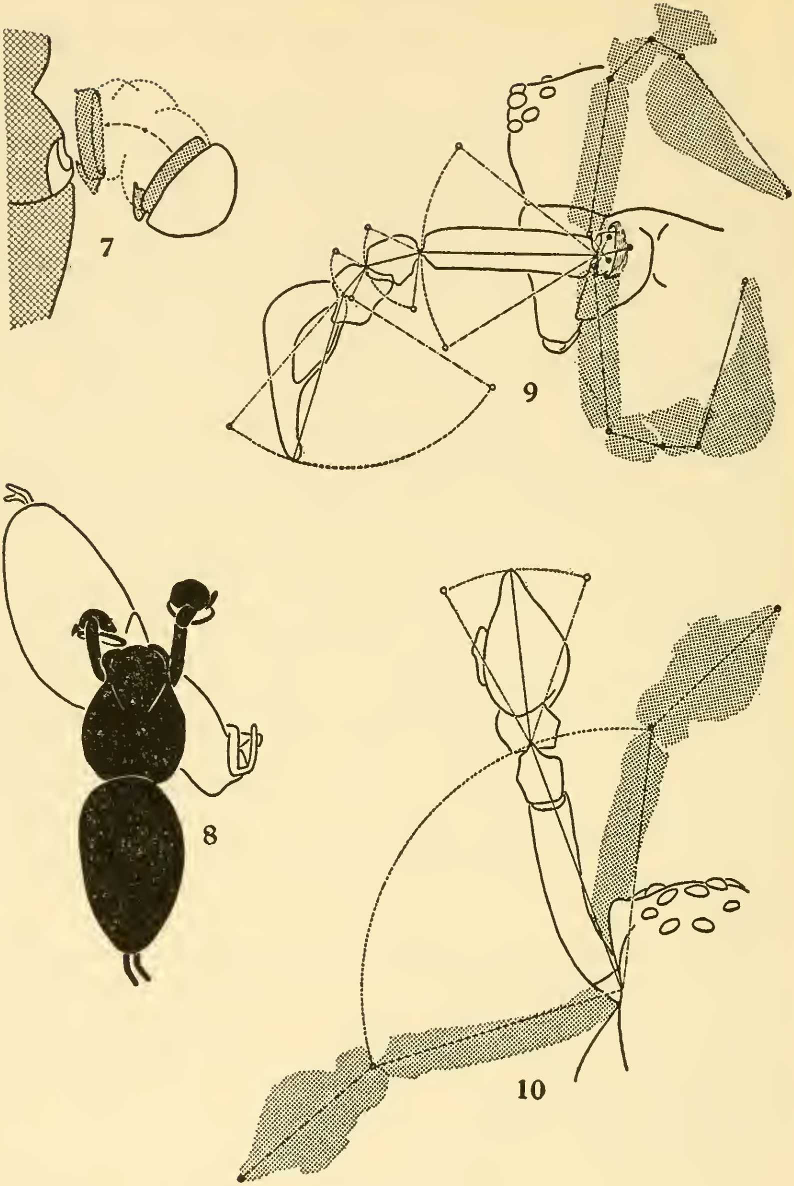
Seminal fluid passes through the ejaculatory duct and the reservoir, and is stored in the fundus. Sperm induction is considered later. Subsequently this fluid is driven out of the receptaculum seminis during ejaculation by the collapse of the fundus. This probably is due to increased haemolymphatic pressure within the genital bulb and, possibly, in part, to a folding of the fundus at the tegular-subtegular articulation.

The basal haematodocha, petiole, and subtegulum are referred to collectively as the basal division of the genital bulb. Wagner (1887, pp. 64, 65) first used the term "haematodocha" because this structure was distended with "blood" during copulation. Comstock (1910, p. 171) showed that Menge's term "spiral muscle" was inappropriate for the basal haematodocha because of the total absence of muscles from the genital bulb. The agelenopsid haematodocha is membranous, with its proximal end connected to the cymbium inside of the alveolus, and its distal end connected to the subtegulum (fig. 6, *bh*). The alveolar wall is incomplete ectally (fig. 39), permitting the haematodochal lumen to communicate with the cymbial lumen, and thus, ultimately, with the body cavity through the segments of the pedipalpus. Distally the basal haematodocha is attached to the subtegulum (fig. 6). When not expanded, this membranous tube is folded and twisted upon itself, typically to the extent of approximately 500° (fig. 38).

Haemolymphatic activation of the genital bulb is the only hypothesis that is supported by both morphological and experimental investigation. This activation includes distention, rotation, and extension of articulated segments. Homann (1935) found that the genital bulb could be inflated with water under 1.5 atmospheres of pressure. He stated that the action thus induced closely approximated normal inflation of the haematodocha during copulation. The writer found that artificially induced osmotic pressures elicited the same response. Normal and artificial inflations of the genital bulb were compared. Artificial inflation was found to duplicate the normal sequence with accuracy.

Contraction of body muscles, particularly of the abdominal muscles, probably is responsible for increasing the haemolymphatic pressures, although experimental evidence to support this hypothesis is lacking. Gertsch (1949, pp. 93-94) also held this view. The increased haemolymphatic pressure inflates the basal haematodocha, and subsequently the middle haematodocha.

Expanding, the basal haematodocha unfolds and uncoils from its normal resting position within the alveolus. In so doing, two distinct operations are performed: (1) The genital bulb is forced outward and ectad from the alveolus, permitting unrestricted movement and rotation of the distal portions of the bulb (fig. 7). (2) The subtegulum and the more distal parts of the genital bulb are rotated (figs. 44, 45). This specific rotation is an integral part of the mechanics of copulation.



Figs. 7-10

7, Mechanics of genital bulb displacement, right palpus, dorsal aspect, diagrammatic, genus *Agelenopsis.* 8, Copulatory stance, dorsal aspect, genus *Agelenopsis.* [Male black, female white.] 9, Limits of pedipalpal articulation, ectal aspect, semidiagrammatic, based on *Agelenopsis aperta* (Gertsch). Extreme total extension and flexion indicated by stippled structures. 10, Limits of pedipalpal articulation, dorsal aspect, semidiagrammatic, based on *A. aperta.* Extreme total extension and flexion indicated by stippled structures.

The term "petiole" was proposed by Chamberlin (1904, p. 174). The petiole is a straplike, sclerotized segment found within the alveolus, and closely associated with the proximal end of the basal haematodocha (figs. 27, 39, *pt*). It is located on the ectal side of the alveolus.

Comstock (1910, p. 166) indicated that the petiole is located in the articulating membrane connecting the genital bulb and the cymbium, and further stated (op. cit., p. 182) that in *A. naevia* it articulated with a condyle found at the proximal end of the lunate plate of the subtegulum. Using cleared, unexpanded genital bulbs from specimens of *A. naevia* and 10 other species of *Agelenopsis,* the writer found that the proximal part of the subtegulum lies in juxtaposition with the distal end of the petiole, but the evidence of articulation is inconclusive. In expanding these bulbs, the petiole appeared to serve as a lever in the ectal displacement of the basal haematodocha. Even in partially inflated bulbs the petiole was found to be widely separated from the subtegulum (fig. 27). During deflation the petiole appeared to exert a weak, though distinct, retracting influence on the remainder of the genital bulb, tending to draw it back toward the alveolus. Osterloh (1922) also attributed a retractor function to the petiole. The primary function of the petiole appears to be that of facilitating ectal displacement of the genital bulb during inflation, and probably that of actively assisting in retraction of the deflating genital bulb back into its normal position within the alveolus. This latter action, however, is also assisted by the natural elasticity of the membranes comprising the basal haematodocha.

Wagner (1887) used the legend "S. teg." to indicate the subtegulum in his figures, but failed to mention anything pertaining to the subtegulum in his paper. In fact, he stated (op. cit., p. 64) that the haematodocha ends in the tegulum. Comstock (1910, p. 171) corrected this statement, and named this structure the subtegulum. The subtegulum constitutes the distal portion of the basal division of the genital bulb (fig. 6, *st*). Typically, the subtegulum is ringlike in configuration. In the agelenopsids this ring configuration is not strongly developed. The mesal margin of the subtegulum forms the sclerotized lunate plate which terminates in a condyle. This condyle articulates with the proximal end of the tegulum, whereas the proximal end of the subtegulum is subcontiguous with the petiole in the unexpanded genital bulb. The remainder of the subtegular margin consists of a slightly sclerotized tubular structure. The anelli (*an*) are also a part of the subtegulum. The proximal end of the middle haematodocha has its origin on the subtegulum (fig. 6, *mh*).

The term "lunate plate" was introduced by Chamberlin (1904, p. 174). It applies to that portion of the subtegulum which is sclerotized (fig. 31, *lp*). The lunate plate frequently is the only visible portion of the subtegulum in the unexpanded bulbs (figs. 25, 33, 34, 37, 38). In some agelenopsids, the distal end of the fundus of the receptaculum seminis terminates within the lunate plate. In the agelenopsids, the lunate plate varies considerably in the extent of its sclerotization, but the articulation condyle remains the same in basic position and configuration.

While the lunate plate forms a heavily sclerotized section on one side of the subtegulum, the opposite side is made up of a series of parallel, incompletely ringlike sclerites which are called anelli. The anelli are distinctly sclerotized and pigmented in most, but not all, agelenopsids, e.g., *A. naevia* (fig. 38). Comstock (1910, p. 182) suggested that there may be characteristics of taxonomic value and importance in the anelli. Figures 27, 28, 31, and 35-38 indicate the range of variability found in agelenopsid anelli.

The several parts of the subtegulum have their own specific functions: (1) The semirigid tubular rim of the subtegulum serves as a region of attachment for the basal and middle haematodochae. (2) The subtegulum contains the fundus, and consequently plays a major role in ejaculation. (3) The lunate plate furnishes a sufficiently solid structure to be rotated as a discrete unit, and thus forms the base for rotation of all the more distal parts of the genital bulb. (4) The lunate plate further furnishes a condyle for articulation with the tegulum. (5) The anelli probably serve to strengthen the subtegulum. (6) The writer's earlier investigations indicated a major role for the anelli in retraction of the genital bulb. Subsequent studies of agelenopsids having weakly developed anelli indicate that while the hypothesis of this role of retraction is probably correct, its degree of function is highly variable in the different species, and in individuals of the same species.

The middle haematodocha, the tegulum, and the median apophysis of the tegulum make up the middle division of the genital bulb. In the agelenopsids, the middle haematodocha is the membranous bulb found between the subtegulum and the tegulum (fig. 6, *mh*). It resembles the basal haematodocha physically, and, like it, is somewhat twisted and folded upon itself. In the unexpanded bulb, the middle haematodocha is entirely hidden between the subtegulum and the tegulum. The proximal end of the middle haematodocha opens directly into the distal end of the basal haematodocha. The mechanism for inflation is the same in both.

As the middle haematodocha is inflated, the tegulum rotates on its articulation with the lunate plate (figs. 31, 36, 38). This rotation is in the same direction as that of the basal haematodocha. The rotation serves two functions: (1) The embolus is oriented parallel to the long axis of the bursa copulatrix of the female, permitting maximum total insertion of the embolus; and (2) it gives the embolus an additional rotation needed to insure maximum total insertion during copulation.

Wagner (1887, p. 64) applied the term "tegulum" to all the heavily sclerotized portions of the genital bulb. Comstock (1910, pp. 171-172) indicated the desirability for having distinctive names for each sclerite, and restricted this term to "the sclerite that forms the wall of the middle division." Petrunkevitch (1925, pp. 569-571) referred to the "thread" of *A. naevia,* and to "two sclerites" which are "limited to the ventral portion of the thread." This is obviously in reference to the tegulum. Blauvelt's description (1936, p. 82) of the tegulum of *Linyphia,* particularly of the basic tegular configuration, agrees well with that found in the agelenopsids. The tegulum is a ringlike sclerotized structure in which the distal end slightly overlaps the proximal end when seen in frontal aspect (figs. 6, 31, *tg*). The distal portion of the tegulum is expanded into a wide tegular plate which incompletely covers the frontal face of the tegulum. This plate is the "bezel" of Crosby and Bishop. The median apophysis arises from this plate. The outer margin of the tegulum forms a narrow, heavy tegular ridge (fig. 31, *tgr*). This ridge is most strongly developed at the proximal end of the tegulum, but is entirely wanting from the distal half. The tegulum is basically U-shaped in cross section, with the closed portion being peripherally located. The distal portion of the fundus and all of the reservoir of the receptaculum seminis are enclosed within the tegulum. Distally, the tegulum articulates synarthrodially with the radix. The nature of this articulation largely eliminates movement between the two structures.

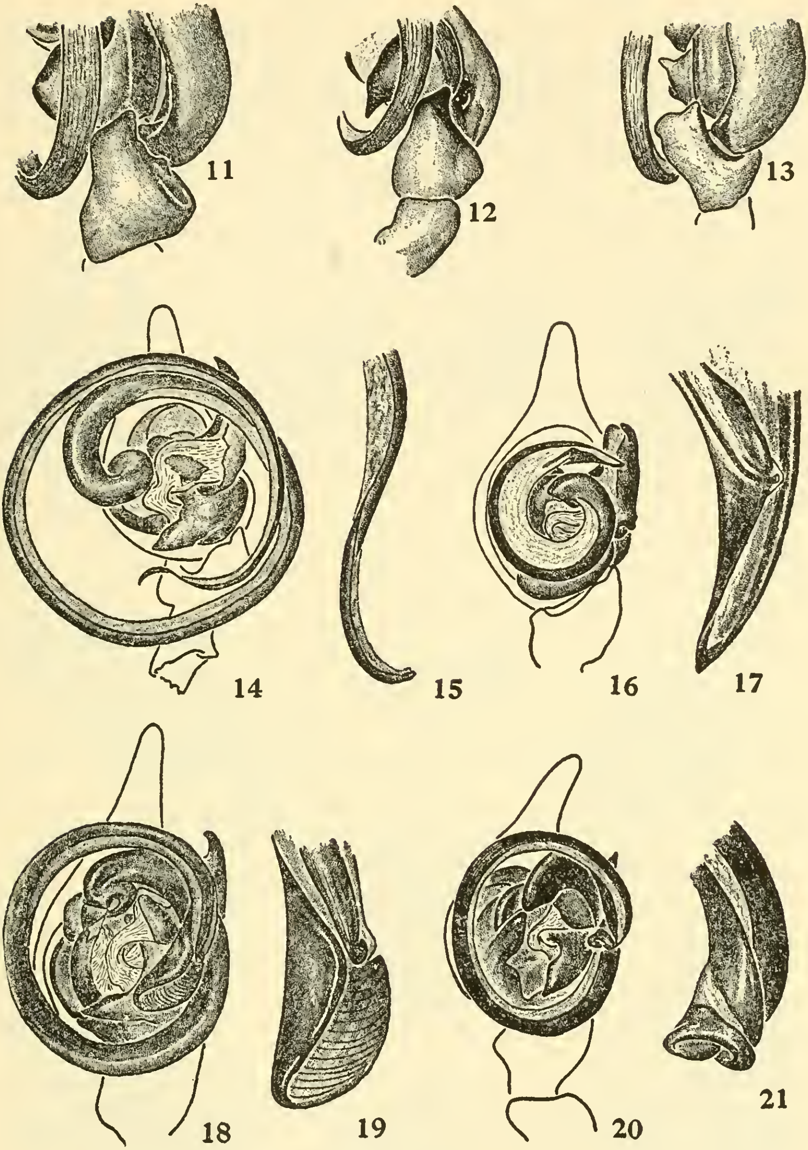
The function of the tegulum in final orientation of the embolus, after it is already in the bursa copulatrix of the female, and the additional rotation which it imparts to the embolus during copulation has already been mentioned in connection with the middle haematodocha. It further serves to protect the portion of the receptaculum seminis which it contains and serves as a solid base for supporting and activating the embolus.

The median apophysis is an appendage arising from the distal margin of the tegulum. Chyzer and Kulczynski (1891, 1894, 1897) used the terms "lamella characteristica" and "apophysis mediana" for this structure. F. O. Pickard-Cambridge (1897) used the terms "clavis" and "unca" respectively, while Chamberlin (1904) used the term "scopus." Comstock (1910, p. 172) urged the continued use of the term "median apophysis" on the basis of priority and general usage. Petrunkevitch (1925, pp. 569, 570) referred to this structure as the "ventral apophysis" and stated that it "marks the end of the haematodocha." The median apophysis of the agelenopsids is a plate-like structure arising from the tegular plate (fig. 4, *ma*). It is usually heavily sclerotized. The ectal margin and the proximal end of this apophysis are fused with the tegulum and tegular plate respectively, making it an integral part of the tegulum. The mesal margin of the median apophysis is free, and in most species is strongly and distinctively developed (figs. 14, 18, 20, 22-25). Near its ectodistal margin, the median apophysis is strongly sclerotized, and forms the outer rim of a groove found between the apophysis and the tegulum (figs. 36, 38, 41, 42). There is a distinct notch in the mesal margin (fig. 4, *n*). The portion of the tegulum lying behind (when viewing the genital bulb in frontal aspect) the median apophysis is weakly sclerotized, or may even be membranous.

Near the proximal end of the median apophysis is found a small, mammae-like tubercle (fig. 4, *tc*). This may be homologous to the distal haematodocha described by Comstock (1910, p. 177) in the aranea-type genital bulb. This tubercle was figured but not otherwise considered by Chamberlin and Ivie (1941, pp. 620-622).

There is still some question as to the complete role of the median apophysis in copulation. Some functions, however, are obvious. Because of its size, position, and sclerotic nature, it increases both the strength and rigidity of the tegulum, and aids in protecting the receptaculum seminis. The role of the apophysis in the process of locking the genital bulb during maximum insertion is considered later, as is the role of the mesal notch of the apophysis.

Comstock (1910, p. 169) adopted the term "conductor" in preference to Menge's (1866) term "spermaphorum" because the former term was already in general usage, and because the latter term, suggested by a misconception of function, was inappropriate. Petrunkevitch (1925, pp. 569-570) figured and briefly described the conductor. Seyler (1941) utilized the conductor and the embolus extensively in his study of the agelenopsids. The conductor of the agelenopsids is a heavily sclerotized segment (fig. 4, *cd*). It occupies a prominent position ectal to the main portion of the genital bulb. This segment is subrectangular in outline, with the ectodistal margin produced into a



FIGS. 11-21

11, Tibial apophysis, left, ectal aspect, *Agelenopsis naevia* (Walckenaer). 12, Tibial apophysis, left, ectal aspect, *Agelenopsis actuosa* (Gertsch and Ivie). 13, Tibial apophysis, left, subectal aspect, *Agelenopsis oklahoma* (Gertsch). 14, Genital bulb, left, frontal aspect, *A. oklahoma*. 15, Embolic terminus, left, frontal aspect, *A. oklahoma*. 16, Genital bulb, left, frontal aspect, *Agelenopsis pennsylvanica* (C. Koch). 17, Embolic terminus, left, frontal aspect, *A. pennsylvanica*. 18, Genital bulb, left, frontal aspect, *Agelenopsis spatula* Chamberlin and Ivie. 19, Embolic terminus, left, frontal aspect, *A. spatula*. 20, Genital bulb, left, subfrontal aspect, *Agelenopsis actuosa* (Gertsch and Ivie). 21, Embolic terminus, left, frontal aspect, *A. actuosa*.

toothlike process. In cross section, the conductor is somewhat U-shaped, with the open portion visible in frontal aspect. The range of variability in the configuration of the agelenopsid conductor is shown in figures 22-25. An elongated process is found near the proximal end of the conductor. This process and a somewhat smaller process from the proximal end of the conductor are directed mesally toward the base of the embolus (fig. 40). The outline of the concavity formed by the mesal margin of the conductor and the large mesal process are shown in figures 22-25. This concavity plays an important role in the locking mechanism which is considered later.

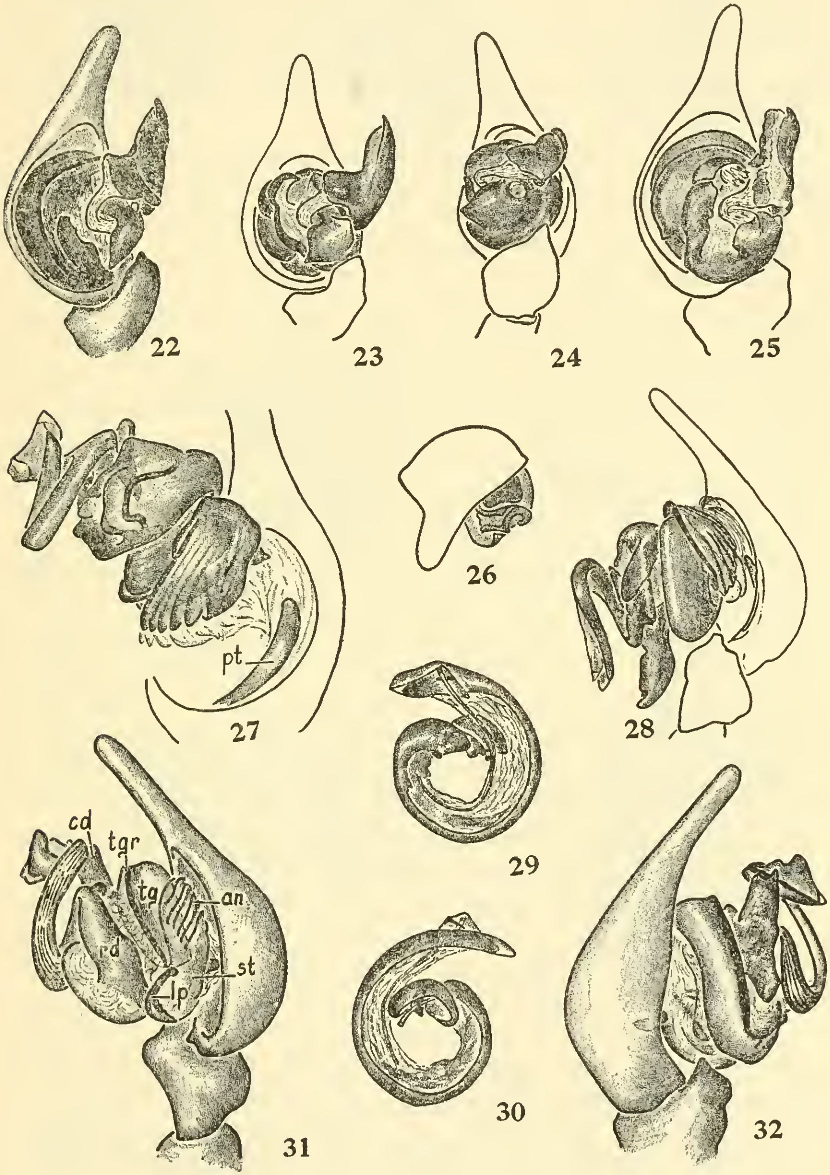
The proximal end of the conductor is connected to the genital bulb by means of a cordlike tethering membrane. This membrane has its origin in the membranous region of the tegulum immediately behind (when viewed in frontal aspect) the median apophysis (fig. 4, *tm*). The tethering membrane was figured by Seyler (1941, p. 69) and by Chamberlin and Ivie (1941, pp. 620-622). Blauvelt (1936, p. 83), however, appears to have been the first to mention it. She described this structure as a "membrane from the lamellar arm of the radix" which connects with the lateral process in the genus *Linyphia.*

Comstock (1910, p. 172) stated that "in every case the embolus in the unexpanded bulb occupies such a position that its tip is protected by the conductor." This is probably in reference to *Linyphia.* Petrunkevitch (1925, p. 570) stated that the function of the conductor (in males of *A. naevia*) "remains uncertain." Gerhardt (Gerhardt and Kaestner, 1937-1938, p. 533) divided conductors into three basic types on the basis of their fundamental configurations, and supported the theory of protection or support as their function. While this protective function undoubtedly is correct for many groups of spiders, the conductor of the agelenopsids has a radically different and more vital function in the process of copulation.

FIGS. 22-32

22, Genital bulb with embolus removed, left, subfrontal aspect, *Agelenopsis actuosa* (Gertsch and Ivie). 23, Genital bulb with embolus removed, left, subfrontal aspect, *Agelenopsis longistylus* (Banks). 24, Genital bulb with embolus removed, left, frontal aspect, *Agelenopsis utahana* (Chamberlin and Ivie). 25, Genital bulb with embolus removed, left, frontal aspect, *Agelenopsis pennsylvanica* (C. Koch). 26, Genital bulb, left, as seen from apex of cymbium, *A. utahana,* showing configuration of conductor. 27, Genital bulb, left, expanded and displaced mesad, subfrontal aspect, *A. pennsylvanica.* 28, Genital bulb, left, partially expanded, subectal aspect, *A. pennsylvanica.* 29, Embolus, right, disarticulated, frontal aspect, *A. pennsylvanica.* 30, Embolus, right, disarticulated, reverse side of fig. 29, *A. pennsylvanica.* 31, Genital bulb, right, slightly expanded, mesal aspect, *A. pennsylvanica.* 32, Genital bulb, right, slightly expanded, ectal aspect, *A. pennsylvanica.* (For explanation of lettering see p. 10.)

The most important function of the conductor is that of coupling during copulation. The protective function, if it persists at all in the agelenopsids, is negligible. As the haematodocha expands during the initiation of copulation, the genital bulb is forced out of the alveolus.



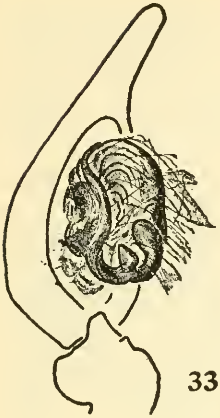
FIGS. 22-32.—See opposite page for legend.

The initial engagement of the embolic terminus in the female's atrium places the conductor directly above the coupling cavity in the caudal margin of the epigynum. It is shown later that the coupling of the conductor with this cavity is one of the most crucial events in agelenopsid copulation. Continued rotation of the genital bulb apparently results in a locking of the entire male palpus to the epigynum because of the tethering membrane, and of the mechanical configurations of the conductor, the embolic base, the tegulum, and the median apophysis.

The radix and the embolus make up the embolic subdivision of the genital bulb. Comstock (1910, p. 173) introduced the terms "radix" and "stipes" respectively for the proximal and distal segments connecting the embolus to the tegulum. He noted (op. cit., p. 181), however, that in the pisaurid type of palpus "the radix and stipes are not developed as distinct segments." In her study of *Pityohyphantes,* Blauvelt (1936, p. 87) found that the palpus of *P. phrygiana,* when treated with caustic potash, appeared to have these two discrete segments, but that "examination of an untreated specimen, and the comparative study of *Linyphia* palpi make certain that these two pieces are parts of a single sclerite." She used the term radix for this single structure. Osterloh (1922) found only a single structure, and called it the "Stuetzapparat." Neither Petrunkevitch (1925) nor Seyler (1941) mentioned the radix in their studies of agelenopsids. The agelenopsid radix is the segment that appears to be a distal prolongation of the tegulum (figs. 4, 6, *rd*). It is the heavily sclerotized portion into which the distal end of the fundus of the receptaculum seminis disappears (fig. 27). While the radix is synarthrodially articulated with the tegulum, on the bases of sclerotization, pigmentation, and function it appears to be a distinct segment (figs. 25, 31, 38). Distally the radix articulates diarthrodially with the embolus (figs. 36, 38, 41). Like the tegulum, the radix is roughly U-shaped in cross section, with the closed portion being peripherally located.

The radix apparently serves as a passive link between the tegulum and the embolus, imparting the thrust and rotation of the tegulum to the embolus. While the evidence in the agelenopsids is indirect, it appears that the base of the embolus folds up under the radix as a result of the diagonal radix-embolic articulation. This would place the outer, convex portion of the embolic base in the notch in the mesal margin of the median apophysis (figs. 42, 46, 48).

Menge (1866) first used the term "embolus." Simon (1892) later used the term "style," but the former term is now used universally.



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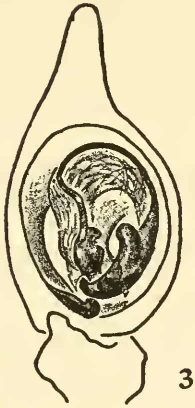

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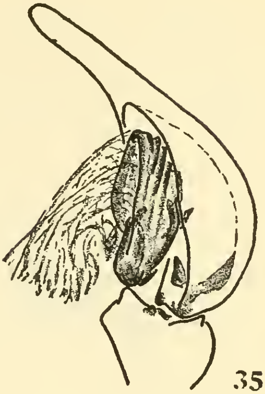

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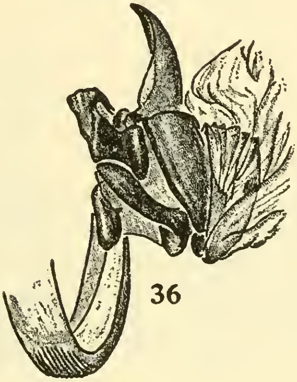

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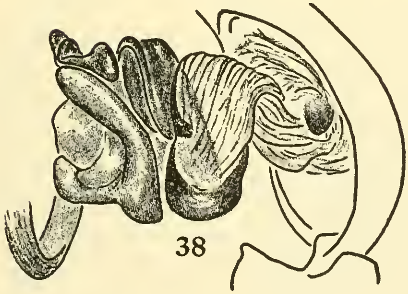

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Figs. 33-39

33, Subtegulum, right, subectal aspect, *Agelenopsis pennsylvanica* (C. Koch). 34, Subtegulum, right, subfrontal aspect, *A. pennsylvanica.* 35, Subtegulum, right, mesal aspect, *A. pennsylvanica.* 36, Genital bulb, right, expanded, mesal aspect, *Agelenopsis aperta* (Gertsch). 37, Subtegulum, left, frontal aspect, *A. aperta.* 38, Genital bulb, right, expanded, mesal aspect, *Agelenopsis naevia* (Walckenaer). 39, Cymbium, right, frontal aspect, *A. pennsylvanica.*

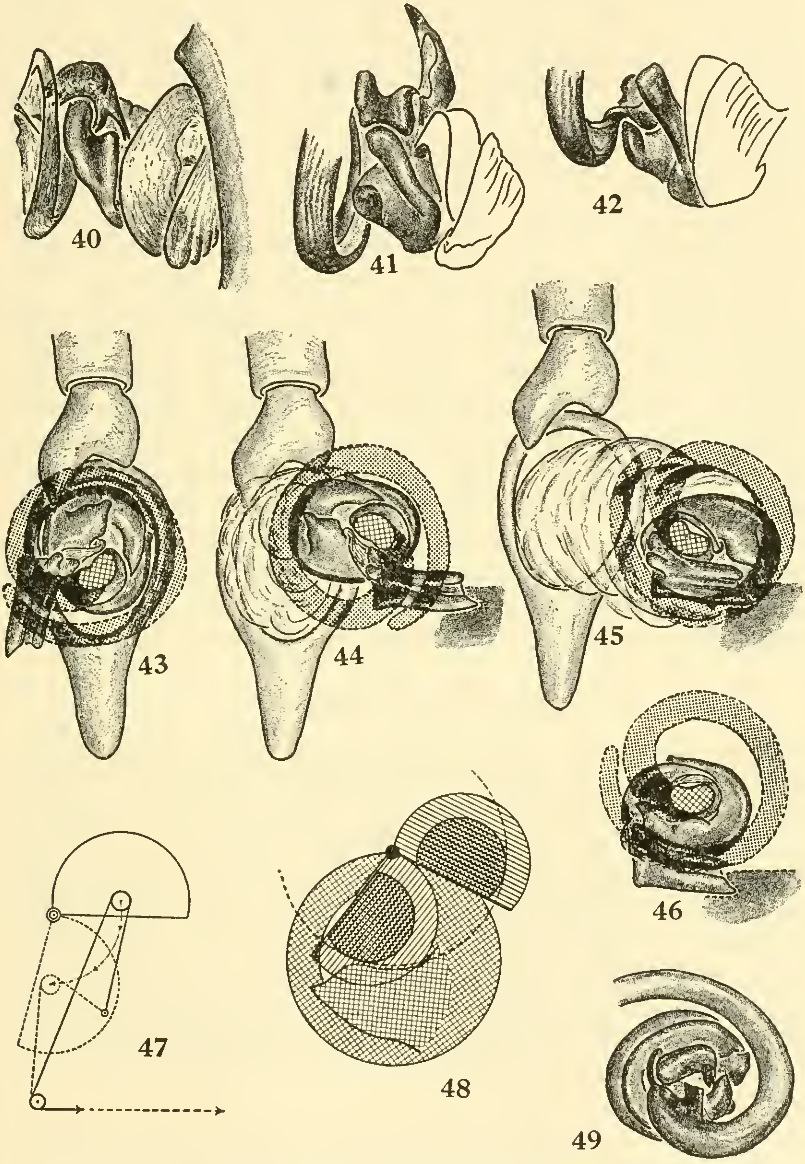
Numerous authors have given special consideration to the embolus as a taxonomic feature. Chamberlin and Ivie (1941) and Seyler (1941) placed particular emphasis on the embolus of the agelenopsids in this respect. Comstock (1910, p. 183) was responsible for the embolic nomenclature now in use. Barrows (1925) and later Harm (1931, 1934) advanced evidence that the embolus is homologous to the tarsal claw of the immature male palpus and of the female palpus. Gerhardt (Gerhardt and Kaestner, 1937-1938, pp. 534-535) was of the opinion that these structures needed a more exhaustive investigation in order to determine whether they are actually homologous. The agelenopsid embolus is a heavily sclerotized, coiled structure (figs. 4, 6, *em*). It varies markedly in males of the genus *Agelenopsis*. In specimens of *A. pennsylvanica*, the embolus forms a spiral of approximately 470° (figs. 16, 29, 30); in *A. oklahoma* it approaches 720° (fig. 14); while in most agelenopsids the spiral is approximately 540° (figs. 18, 20).

The proximal portion is heavy in construction and more or less hemispherical in configuration (figs. 29, 30). The truncus of the embolus is the body of this structure, extending distad from the base. It also is U-shaped in cross section, with the closed portion being peripheral. The truncus shows distinct, longitudinal fluting on its flattened, peripheral margin (figs. 31, 32). The pars pendula is the membranous portion of the embolus which is attached to the concave side of the truncus. In expanded genital bulbs this membrane becomes prominent. The ejaculatory duct can be traced through cleared emboli, particularly toward the less heavily pigmented distal end.

FIGS. 40-49

40, Genital bulb, right, partially expanded, subdorsal aspect, *Agelenopsis pennsylvanica* (C. Koch). 41, Genital bulb, right, expanded, mesal aspect, *Agelenopsis spatula* Chamberlin and Ivie, showing normal position. 42, Genital bulb, right, expanded, mesal aspect, *Agelenopsis spatula* Chamberlin and Ivie, showing embolus in extreme rotated position. 43, Genital bulb, right, frontal aspect, semidiagrammatic, genus *Agelenopsis*, showing normal position of bulb before inflation. Embolus stippled, hemispherical groove of embolic base cross-hatched. 44, Genital bulb, right, frontal aspect, semidiagrammatic, genus *Agelenopsis*, after three-quarters turn, showing conductor engaged. [*Note:* Displacement is here shown to be mesad to simplify illustration; actual displacement of genital bulb is ectad. Cf. fig. 7.] 45, Genital bulb, right, frontal aspect, semidiagrammatic, genus *Agelenopsis*, after one and one-quarter turns, showing rotation of tegulum onto anchored conductor. 46, Genital bulb, right, frontal aspect, semidiagrammatic, genus *Agelenopsis*, after one and three-quarters turns of tegulum, showing genital bulb relationships during locked condition. [*Note:* Additional one-half turn of embolus only resulting from articulation of embolus.] 47, Mechanics of articulation of embolus due to strain produced on embolic base by tethering membrane, schematic, genus *Agelenopsis*. 48, Mechanics of articulation of groove on embolic base with median apophysis, schematic, genus *Agelenopsis*. 49, Genital bulb, right, subfrontal aspect, *A. spatula*, showing embolic base in fully articulated position during locked condition.

Distally, the truncus of the embolus loses its U-configuration, becoming flattened and tapering into a relatively thin structure. The extreme tip of the terminus is unpigmented in most agelenopsids. A subtriangular segment is found on the dorsoconvex side of the embolic



Figs. 40-49.—See opposite page for legend.

terminus. This is most evident in the embolic terminus of *A. pennsylvanica* (figs. 17, 30). The sclerotized portion of this triangular structure is called the apical sclerite of the embolus. The opening of the ejaculatory duct is contiguous to this sclerite (figs. 29, 30).

The primary function of the embolus is to carry the ejaculatory duct deep into the genital tract of the female for deposition of the seminal fluid. The complex functions of the heavy embolic base are discussed later. Structurally the truncus is light. While it is rigid enough to be forced into the bursa copulatrix, it also is sufficiently flexible to negotiate the necessary turns in order to reach the distal end of the bursa without breaking. Breakage of the distal portion of the embolus, however, is not unknown. Dahl (1902) reported finding embolic fragments in the bursa. Gerhardt (Gerhardt and Kaestner, 1937-1938, p. 537) credited Bertkau, Jaervi, Wiehle, and himself with having described such fragments in the atria of representatives of the genera *Delena, Clastes,* and *Nephila.* Dr. R. V. Chamberlin has told the writer of finding such fragments in many families of spiders. The writer has found several such instances in females belonging to *A. oklahoma,* and one in a female of *A. kastoni.* The apical sclerite precludes, in a large measure, the possibility of collapse of the ejaculatory duct aperture during maximum total insertion and ejaculation. Petrunkevitch (1925, p. 570) stated that the embolus "is very flexible, and when the haematodocha is turgescent the spiral is wider than in the quiescent state." The writer has not been able to verify this statement conclusively, but it appears to be correct.

ACTIVATION OF PEDIPALPUS

Petrunkevitch (1909) and Brown (1939) studied the musculature of the legs of spiders. Brown worked specifically with representatives of *A. naevia.* Petrunkevitch showed that the extensor muscles are entirely wanting in the femoropatellar and the tibiometatarsal joints. Ellis (1944) subsequently demonstrated the hydraulic extensor mechanism for these extensorless joints. Osterloh presented evidence of a hydraulic mechanism for the copulatory structures as early as 1922, while Homann (1935) ably demonstrated the role of hydraulic activation of the genital bulb. That haemolymphatic pressure is involved in the activation of the palpus is further substantiated by the simultaneous erection of the setae with each paroxysmatic inflation of the haematodochae.

Dissections of the legs of agelenopsids by the writer revealed no essential deviation from the findings of Ellis. Dissections of the agelenopsid pedipalpi agreed with Barrows's (1925) findings. The chitinous plate at the distal end of the femur, which Ellis indirectly showed to be responsible for extension of the leg proximal to the patella, is readily demonstrable in the femur of the agelenopsid pedipalpus. The chitinous plate of the interarticular membrane of the tibia-metatarsus is found in the ambulatory legs of the agelenopsids also, but apparently is wanting between the pedipalpal tibia and the cymbium. Homann (1935) showed that approximately 1.5 atmospheres of pressure are necessary to inflate the genital bulb, making a special mechanism to confine normally increased haemolymphatic pressures proximad of the cymbium unnecessary. The writer's observations of living male agelenopsids revealed that the portion of the pedipalpus distal to the femur is extended rarely except during copulation. The vast preponderance of pedipalpal activity is restricted to the trochanter and the femur.

Flexure of the pedipalpus, on the contrary, apparently is entirely under muscular control. With these two different mechanisms available, it appears that a combination of both is involved in directing the specific movements of the pedipalpus, particularly in the case of the monocondylar articulations. Differential or selective contraction of muscles which are normally involved in flexure, but having points of insertion at opposite sides of the distal segment, thus would combine with the extensor movements in producing directed movements, both of an extensor and flexure nature. Hence, with all the muscles in a given segment in a state of normal or uniform tonus, the extensor movements would be in a vertical plane. Increasing the degree of contraction in any one group of muscles would produce a variation in the plane of articulation.

The same haemolymphatic pressure which extends the proximal segments of the pedipalpus is responsible for inflation of the haematodochae and thus, for the activation of the genital bulb. Reduction in the haemolymphatic pressure within the haematodochae results in their collapse. The natural elasticity of the membranous portions is apparently the most important single factor in recovery. The petiole probably plays a considerable role in the retraction of the collapsing genital bulb. The less heavily sclerotized segments, e.g., the subtegulum and its anelli, appear to assist in this reduction and retraction of the genital bulb, but the exact degree of their importance is still unknown.

PEDIPALPAL VARIATION

The most marked variations found in the pedipalpi of the agelenopsids are those pertaining specifically to the genital bulb. Variations found in the segments proximal to the tibia are confined almost exclusively to proportional differences. The facies of these segments, when compared with those of other agelenid genera, are remarkably constant. Furthermore, the intersegmental angles were found to be essentially the same in all species here considered.

The tibial process shows some variation in superficial configuration. The position of this process, its length, and the manner in which it fits into the depression in the ectoproximal margin of the cymbium, indicate that it is a constant feature within the genus. The cymbium and the alveolus are subject to proportional differences, but along with such morphological features as the incomplete alveolar wall and the depression for the tibial process, are relatively constant.

The haematodochae display no apparent variation. The subtegulum varies in degree of sclerotization, but not in fundamental configuration. The anelli vary markedly among some species of agelenopsids, particularly with regard to the general facies and the degree of sclerotization. No instances were found, however, in which the anelli could not be demonstrated. The general facies of the lunate plate deviates considerably among the various species of agelenopsids, but the strongly sclerotized condyle of this structure is found in every specimen. In some species, but not all, the distal end of the fundus appears to terminate within the lunate plate. The receptaculum is relatively constant throughout the genus *Agelenopsis*.

The tegulum proper is constant in facies throughout the agelenopsids with only superficial differences being demonstrable. The median apophysis also is constant in fundamental configuration, although its facies is highly variable. The median apophysis of males belonging to *A. pennsylvanica* is the nearest approach to deviation from the basic mechanical design (fig. 25), but it still conforms closely enough to be capable of fulfilling its role in the locking of the genital bulb. The size of the mammae-like tubercle on the median apophysis is highly variable (figs. 22-25), and subject to considerable individual variation within any given species. In some agelenopsid species (e.g., *A. utahana*) this tubercle is reduced to a membranous area having a heavily sclerotized margin (fig. 24). The ectoproximal margin of the conductor in these instances is sufficiently small in size, and occupies a position such that it may easily be introduced into this membranous area. While the function performed by the tubercle, when it is present, apparently is essential, the tubercle itself is not. For example, the peg-and-socket relationship between the conductor and the median apophysis of specimens of *A. utahana* fulfills the essential function of the tubercle without the tubercle, as such, being present. Hence, the tubercle is not universally found in all species of agelenopsids, but when lacking an analogous mechanism is always demonstrable.

The facies of the conductor varies markedly in the different species. The ectodistal process is always present, and is closely correlated with the configuration of the coupling cavity of the female in all agelenopsids. The mesal curvature of the conductor, its mesal processes and their articulation with the embolic base, and the tethering membrane also are constant throughout the males of this genus.

The radix displays proportional and configurational deviations which are only of a superficial nature. The diagonal articulation between the radix and the embolic base is found in all male agelenopsids.

The embolic base is relatively divergent in superficial configuration; however, the fundamental mechanical design is invariable. The truncus varies in length, in the circumference of its spiral, and in its diameter in the various species. There is little individual variation in these respects within any given species. The embolic terminus varies drastically in the different species (figs. 15, 17, 19, 21), with the apical sclerite apparently being entirely wanting in males of such species as *A. oklahoma.* The marked variability of the embolus in the different species is paralleled by a correlated variability of the bursa copulatrix of the corresponding females. The variability of the embolus, particularly in the light of the close correlation between the bursa and the embolus, is limited to configurational superficialities and not to mechanical fundamentals.

Excluding the subgenus *Barronopsis,* the agelenopsid pedipalpi are remarkably homogeneous in fundamental mechanical design and basic configuration.

Considerable diversity is found in the palpal configurations of representatives of the various genera of Agelenidae. In the following summary the genus *Agelenopsis* is used as the basis for comparison. Unless otherwise stated, the genera are essentially in agreement with the agelenopsids. Males are as yet unknown in the genera *Chorizommoides* and *Ritalena.*

The tribal apophyses are reduced in males of *Blabomma, Chorizomma, Ethobuella, Melpomene,* and *Wadotes.* In contrast, the apophyses are strongly developed in *Hololena, Novalena,* and *Rualena.* In representatives of some species of the genus *Cicurina,* the tibial apophysis is nearly as long as the cymbium. The ectoproximal portion of the tibia bears accessory processes in many genera of agelenids, but these processes are most elaborate in *Coras. Cybaeota* and *Cybae-*

ina are unique in that the tibial processes of the males are found behind the cymbium rather than in front of it. Thus, in these two genera, the extension, rather than the flexure, of the cymbium is limited. A similar condition exists in males of *Zelotes duplex* Chamberlin (Gnaphosidae). The tribal apophysis in *Tegenaria domestica* (Clerck) [=*T. derhami* (Scopoli)], is in such a position that the cymbium cannot impinge against it.

The cymbial apex tends to be somewhat shortened in some genera, e.g., *Calilena* and *Cicurina,* while it is markedly elongated in *Calymmaria* and *Tortolena. Coras* and *Wadotes* have a flat, platelike elaboration of the ectoproximal margin of the cymbium. In *Hololena* the ectoproximal margin of the cymbium presents a square configuration when viewed from the frontal aspect. The proximomesal margin of the cymbium in *Wadotes* is greatly enlarged, and bears a deep excavation. The size and position of this excavation, along with the marked reduction of the tibial apophysis, suggests that it might serve in the locking mechanism of the palpus during copulation. If such a function actually does exist, however, the copulatory position and the copulatory sequence would, in all probability, be markedly different from those of the agelenopsids because of the radically different mechanical configurations involved.

In males of *Agelena labyrinthica* a sclerotic, triangular partition is found originating on the mesal side of the cymbial margin. The apex of this partition is directed toward the middle of the alveolus. Nothing comparable to this was demonstrable in any of the other genera of Agelenidae. The petiole is well developed in all genera except *Calymmaria, Cybaeina,* and *Cybaeus.* In *Cicurina brevis* Emerton, the petiole is reduced to a tiny, buttonlike sclerite approximately one-half the way distad along the ectal margin of the alveolus. In males of *Chorizomma,* the petiole is filamentous but darkly pigmented. In *Cryphoeca peckhami* Simon, this same filamentous configuration of the petiole is found except that it terminates distally in a definitive, sclerotic bulb. The petiole is well developed in such divergent spiders as are represented by males of *Spirembolus vallicolens* Chamberlin (Micryphantidae), *Pardosa xerampelina* (Keyserling) (Lycosidae), and *Clubiona abboti* L. Koch (Clubionidae).

The haematodochae of the agelenids vary only slightly in relative size, and little, if any, in configuration. The subtegulum is found in all agelenids. The anelli and the lunate plate are definitive structures showing varying degrees of sclerotization and pigmentation. In the genus *Wadotes,* however, the subtegulum is virtually wanting as a sclerotized structure. It consists of a delicate sclerotic ring, and a vestigeal lunate plate. The anelli are entirely obliterated. In most agelenid genera, the fundus of the receptaculum seminis is clearly discernible within the subtegular lumen after the palpi have been cleared. The subtegula found in males of *Spirembolus* and *Clubiona* are very similar to those of the agelenopsids. Specimens of *Pardosa,* while having a strongly developed lunate plate, have neither a definitive subtegulum nor the slightest traces of anelli. The tegulum of *Clubiona abboti* suggests that of the agelenopsids in its morphological configuration.

The basic mechanical configuration of the tegulum is relatively constant in the agelenids. The tegula found in representatives of *Wadotes* are superficially aberrant, but appear to retain the fundamental configuration of the other agelenids. *Hololena* agrees closely with the agelenopsids in tegular configuration. The tegulum is only weakly developed in *Calymmaria* and *Cybaeus.* In *Chorizomma* and *Cryphoeca* the tegulum has extensive membranous areas.

The heavy agelenopsid-type embolus is found in *Tegenaria,* but it is short. In *Agelena* the embolus is slightly arched and is much shorter than even that of *Tegenaria.* The embolic configuration of the agelenopsids is retained in *Calilena, Calymmaria, Ethobuella,* and *Novalena.* In these four genera, however, the emboli are short, describing less than a sixth of a turn. The emboli of *Tortolena* are bizarrely twisted into an S-configuration. Males of *Melpomene singula* (Gertsch and Ivie) have the heavy, agelenopsid-type embolus coiled around so as to produce a conelike configuration, which is strikingly suggestive of the emboli found in males of the subgenus *Barronopsis.* The emboli of *Melpomene bicavata* (P. Cambridge), on the contrary, are unquestionably of the filamentous type. Other agelenid genera having the filamentous type of embolus include *Blabomma, Chorizomma, Cicurina, Coras, Cybaeina,* and *Cybaeus.* The transitional forms of emboli found in the Agelenidae typically have a heavy proximal portion, but taper down to a long filamentous terminus. Genera displaying this transitional form of embolus include *Cybaeota, Cybaeozyga, Hololena, Rualena,* and *Wadotes.*

Because of the addition or loss of certain tegular apophyses, and the elaborate modifications of the distal portions of the genital bulb in the various genera of agelenids, there is no general agreement as to the nomenclature of these structures. The addition of a terminal apophysis, in such genera as *Wadotes,* further complicates the process of ascertaining homologies.

Structures similar to the agelenopsid conductor (including the membranous attachment to the tegulum) are present in representatives of the following genera: *Calilena, Calymmaria, Coras, Cryphoeca, Cybaeina, Cybaeus, Novalena, Rualena, Tegenaria,* and *Wadotes.* The conductorlike structures of *Agelena, Blabomma,* and *Cybaeota* appear to be fused to the tegulum.

Deviations from the basic configurations of the component parts of the agelenid genital bulb appear to be limited almost exclusively to those distal portions which come into actual physical contact with the copulatory structures of the female. Apparently these distal modifications are correlated with parallel modifications found in the copulatory structures of the females. Furthermore, there appears to be a close similarity between the proximal portions of the genital bulb of the agelenids and other families of spiders, such as the Clubionidae, Lycosidae, and Micryphantidae.

REPRODUCTIVE ORGANS OF THE FEMALE

The reproductive organs of the female spider are organized into two separate systems, connected only by a pair of delicate fertilization tubes (fig. 51). The ovaries and their associated structures constitute one system; the other consists of the copulatory system proper. The copulatory system is here considered to include all structures, both external and internal, which are involved in copulation and insemination. This system is the equivalent of Jaervi's "Vaginalorgane" (1905) and his "Vaginalsystem" (1908, 1912, 1914). The ovaries and their associated structures are not involved in the actual process of copulation in the agelenopsids.

OVARIES AND ASSOCIATED STRUCTURES

The ovaries and their respective oviducts are simple, paired structures situated in the ventral portion of the abdomen (fig. 51). They

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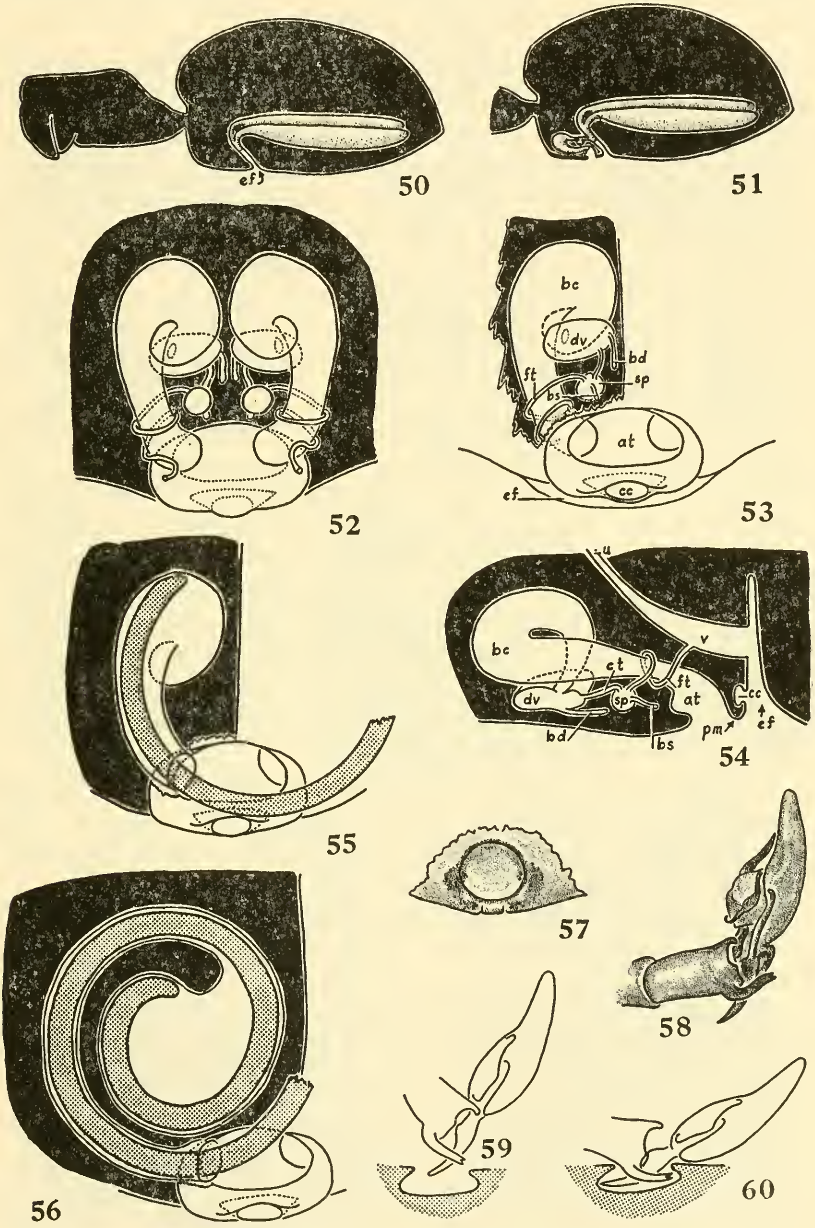
Figs. 50-60

50, Longitudinal section of male, diagrammatic, genus *Agelenopsis,* showing internal genital structures. 51, Longitudinal section of abdomen of female, diagrammatic, genus *Agelenopsis,* showing internal genital structures, including copulatory structures. 52, Copulatory structures of female, dorsal aspect, diagrammatic, genus *Agelenopsis.* 53, Epigynum and copulatory structures of female, ventral aspect, diagrammatic, genus *Agelenopsis.* 54, Epigynum and copulatory structures of female, ectal aspect, diagrammatic, genus *Agelenopsis.* 55, Maximum initial insertion of embolus into bursa, ventral aspect, diagrammatic. Embolus stippled. 56, Maximum total insertion of embolus into bursa, ventral aspect, diagrammatic, genus *Agelenopsis.* Embolus stippled. 57, Epigynum, ventral aspect, *Chiracanthium inclusum* Hentz (Clubionidae). 58, Palpus, left, ectal aspect, *C. inclusum.* 59, Coupling initiated, diagrammatic, *C. inclusum.* Female structure stippled. 60, Coupling completed, diagrammatic, *C. inclusum.* Female structure stippled. (For explanation of lettering see p. 10.)

extend caudad from the general region of the epigynum. Cephalad, the oviducts unite to form a common uterus (*u*), which opens into the vagina (fig. 54, *v*). The vagina opens mesally through the vulva which is located near the cephaloventral margin of the epigastric furrow (*ef*).



FIGS. 50-60.—See opposite page for legend.

Fertilization tubes (*ft*) transport the seminal fluid from the spermatheca to the vagina where fertilization occurs. This basic organizational pattern is common to all female spiders.

COPULATORY SYSTEM

An urgent need exists for a comprehensive study of the copulatory system of female spiders, with at least an effort at standardization of terminology. Comstock's work (1910) on the palpi of male spiders did much to unify and clarify nomenclature pertaining to those structures. As Blauvelt (1936, p. 92) stated "the early authors mention the organ but do not describe it with sufficient accuracy to clarify their terminology." Menge especially was given to the use of several names for each part, and was rather indiscriminate in his application of them. Blauvelt (loc. cit.) justifiably attributed much of the confusion in nomenclature to the unquestioning adoption of the terminology of Menge by subsequent workers.

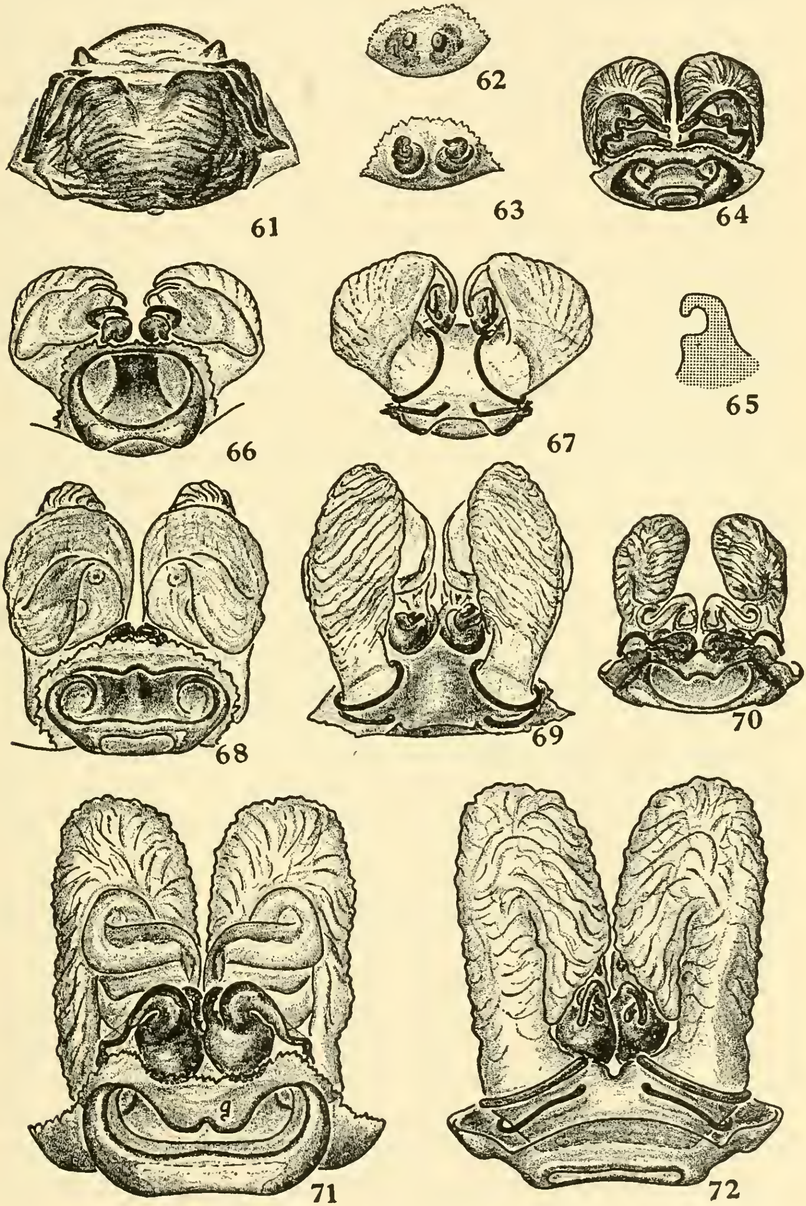
Walckenaer (1837) introduced the term "epigyne" for the external portion of the copulatory apparatus. This term, however, has since become rather generally accepted as embracing both the internal and external portions of the copulatory apparatus of the female. Petrunkevitch (1925, p. 564) objected to this usage, being of the opinion that the term should be restricted (in *A. naevia*) to a specific portion (viz, structure *g*, fig. 71) of the external surface of the copulatory structure. On the basis of priority and general convenience of usage it appears preferable to retain Walckenaer's interpretation and to apply the term to the entire external portion of the female copulatory structure only. The term is thus used in this paper.

Epigynum.—The epigyna of spiders have been described and figured by so many araneologists that a detailed review of this literature would be prohibitive here. As previously indicated, Walckenaer introduced the term. Menge variously referred to this structure as the "sarum," "claustrum," and the "schloss," while Dahl used the term "vulvafeld."

FIGS. 61-72

61, Epigynum, ventral aspect, *Coras medicinalis* (Hentz) (Agelenidae). 62, Epigynum, ventral aspect, *Cryphoeca peckhami* Simon (Agelenidae). 63, Copulatory structures, dorsal aspect, *Cryphoeca peckhami* Simon. 64, Epigynum and copulatory structure, ventral aspect, *Agelenopsis utahana* (Chamberlin and Ivie). 65, Coupling cavity, cross section, schematic, *A. utahana.* 66, Epigynum and copulatory structure, ventral aspect, *Agelenopsis pennsylvanica* (C. Koch). 67, Copulatory structure, dorsal aspect, *A. pennsylvanica.* 68, Epigynum and copulatory structure, ventral aspect, *Agelenopsis oklahoma* (Gertsch). 69, Copulatory structure, dorsal aspect, *A. oklahoma.* 70, Epigynum and copulatory structure, ventral aspect, *Agelenopsis longistylus* (Banks). 71, Epigynum and copulatory structure, ventral aspect, *Agelenopsis naevia* (Walckenaer). 72, Copulatory structure, dorsal aspect, *A. naevia.*

Petrunkevitch (1925) and Seyler (1941) followed Dahl by using the term "vulva" for this external plate. McCook (1894, p. 126) introduced the term "atriolum" for this structure. Several authors, including Comstock (1948, p. 132) and Blauvelt (1936, p. 92) adopted this



Figs. 61-72.—See opposite page for legend.

term. Jaervi (1905, 1908) used the terms "epigynum" and "receptacula" respectively to distinguish between the single external and the paired internal portions of the copulatory apparatus.

Gerhardt (1937-1938, p. 535) stated "Die Simonsche Unterscheidung zwischen haplogynen und entelegynen Spinnen is berechtigt, und sogar in weiterem Umfange, als ihr ihr Urheber zugestanden hat." In the Haplogynae, the females lack a definitive epigynum, while the male palpi consist of a simple bulb with a terminal embolus and lack a distensible bulb. The males of this group typically employ simultaneous insertion of both emboli during copulation. Included in the Haplogynae are such families as the Dysderidae, Oonopidae, Segestriidae, Leptonetidae, and Scytodidae. In the Entelegynae, the females possess a definitive epigynum, while the males have a distinctly formed conductor and a distensible haematodocha intercalated between the tarsus and the embolus. The males typically copulate by applying the palpi singly. The Entelegynae include such families as the Agelenidae, Gnaphosidae, Linyphiidae, and Lycosidae.

The agelenopsid epigynum is a strongly sclerotized plate found immediately cephalad of the epigastric furrow on the venter of the female (fig. 53). The atrium is a large, single cavity in the epigynum (figs. 53, 54, *at*). The atrium is typically ellipsoid in the agelenopsids. Atrial proportions range from 1.7 times as broad as long in *A. longistylus* (fig. 70) to 4.7 times as broad as long in *A. oklahoma* (fig. 68), with the most frequent proportion being 2.4 times as broad as long as found in *A. kastoni, A. spatula,* and *A. utahana* (fig. 64). The proportions are based on typical specimens. The writer found, however, that in a series of more than two hundred females of *A. pennsylvanica* taken within a period of less than one month from a single locality, the atrial proportions ranged from 1.8 times as broad as long to 3.9 times as broad as long, with the most frequent proportion being 2.0 times as broad as long.

The atrial wall is heavily sclerotized. A pair of large, round apertures are located ectally in the cephalic portion of the atrium. These apertures are the entries into the internal bursae copulatrices.

In some females (e.g., those of *A. naevia*) the cephalad margin of the atrial rim is projected, ledgelike, back over a portion of the atrial cavity (fig. 71, *g*). It was to this structure that Petrunkevitch limited the term "epigynum" in *A. naevia.* It appears, however, that this structure corresponds to the guide (Chamberlin, 1904, p. 174) of the lycosid epigynum and is so considered in this paper.

The posterior median sclerite (Chamberlin and Ivie, 1941, p. 587) constitutes the caudal margin of the epigynum (fig. 54, *pm*). The vulva opens into the epigastric furrow immediately dorsal to the posterior median sclerite. The coupling cavity, located on the caudal margin of this sclerite, is discussed later.

The epigynum serves a triple function: (1) It serves to protect the delicate, internal portions of the copulatory system; (2) it bears the coupling cavity; (3) the atrium constitutes a cavity in which the embolic terminus is initially engaged prior to final orientation of the palpus for copulation.

Coupling cavity.—The writer proposes the term "coupling cavity" for the transverse cavity found in the caudal margin of the posterior median sclerite (figs. 53, 54, *cc*). Ectally this cavity terminates in a pair of conical depressions lying deep within the sclerite (fig. 53). The coupling cavities range from 0.3 to 0.4 times as long as the atrial breadth in *A. utahana* and *A. oregonensis,* respectively, to 1.6 times as long as the atrial breadth in *A. longistylus,* with the most frequent proportion being 0.8 times as long as the atrial breadth being found in such forms as *A. kastoni, A. actuosa, A. emertoni, A. spatula,* and *A. oklahoma.* In the literature this cavity is shown in all drawings of the epigyna of agelenopsids. Petrunkevitch (1925, p. 563) stated that the function of this structure "remains unknown" and suggested that it might "have something to do with the process of egg laying." Petrunkevitch (op. cit., p. 564) credited Jaervi with having described "similar pouches in *Torania occidentalis*—a spider belonging to the family Sparassidae, under the name of 'Lobaltaschen.' " No function was indicated for the "Lobaltaschen" by Jaervi. Savory (1928, p. 226) figured similar excavations in the posterior median sclerite in *Sparassus* (=*Micrommata*) *virescens* (Clerck), and discussed Bristowe's description of the correlations between these concavities and the tibial apophysis of the male. Bristowe found that copulation could not transpire until the tibial apophysis was properly engaged in these cavities, coupling the palpus and the epigynum together. The same vital correlation, existing between the conductor and these concavities in the agelenopsids, justifies using the term "coupling cavities" for these morphological structures.

Seyler (1941, p. 56) stated that in the epigynum of *A. utahana* the "concavities at the lateral extremities are not prominent and are sometimes lacking." Seyler's material consisted of 25 females taken in Ohio. The writer examined 112 females of this species, including the allotype and 5 female paratypes, as well as 42 males including the holotype and 5 male paratypes taken from 10 States and three provinces of Canada. Two of the female paratypes showed reduced ectal concavities of the coupling cavity. Six other females showed extreme reduction of these lateral depressions amounting to virtual obliteration (fig. 64). The configuration of the coupling cavity (figs. 64, 65), and particularly the correlated configuration of the ectal process of the male conductor (figs. 24, 26) are such, however, that the coupling function is mechanically feasible even though the ectal depressions are reduced or even wanting. This same type of reduction of the ectal depressions of the coupling cavity is found in *A. oregonensis.* The ectal process of the conductor of the male in this species is very similar in configuration to that of *A. utahana.*

The agelenopsid coupling cavity serves as a repository for the ectal process of the male conductor during copulation (figs. 44-46). Hence, the cavity provides a means of anchoring the conductor and thus is involved in activating the locking mechanism which is essential for copulation.

Bursa copulatrix.— Siebold (1848) stated "Die Scheide oeffnet sich mit einer Querspalte nach aussen, nachdem sie Einfuehrungsgaenge von zwei nebeneinander liegenden Receptacula seminis aufgenommen hat" (quoted from Engelhardt, 1910, p. 34). Wagner (1887), however, used the term "receptaculum seminis" in reference to the internal portion of the male genital bulb. This latter usage has become so generally accepted that it appears advisable to retain Wagner's term and interpretation for the male structure. Engelhardt (1910, p. 51) used the expression "beckenfoermige Vertiefung" for the bursae of *Agelena labyrinthica.* Petrunkevitch (1925, p. 565) stated that as he had always found the sperm in the spermathecum and not in the bursa, he believed that the bursa "is a true bursa copulatrix and not a receptacle." Petrunkevitch, therefore, used the term "copulatory pouch," as did Seyler (1941). Blauvelt (1936) used the term "bursa copulatrix" as did Chamberlin and Ivie (1940, 1941). The bursae copulatrices are paired membranous structures extending cephalad from their atrial origin (figs. 52-54, *bc*). The walls are nearly transparent, and are typically traversed by distinctive plications (figs. 64, 67, 69, 70, 72). Distally, the bursae communicate with the diverticles. There is considerable variation in the general configuration of the internal portion of the copulatory apparatus (figs. 66-72). The bursae are relatively constant within each species.

The plications of the bursae are somewhat variable in their degree of development. Their orientation, however, remains relatively constant in each agelenopsid species. While the bursal plications are obscure in many specimens of *A. pennsylvanica,* the writer found vague traces of these plications in the majority of specimens of this species examined (figs. 66, 67). The plications of the bursae of *A. naevia* (figs. 71, 72) are strongly developed as indicated by Petrunkevitch (1925) and Seyler (1941) except for a small percentage of specimens. In this group the plications are only weakly developed. The typical orientation of the plications was found to be the same in any given species irrespective of the degree of development.

Petrunkevitch (1942, p. 177) stated:

> The embolus and the conductor, if the latter is present, do not in any way correspond with the structure of the seminal receptacles and their ducts. Where a resemblance is present it is only superficial. For example, in *Agalena* [= *Agelenopsis*] *naevia* the embolus and the fertilization duct are both spirally wound, but the embolus is too thick to be introduced into the duct and is held during copulation in the atrium.

The bursae of the agelenopsids were subjected to detailed study by the writer through use of both in vivo and in vitro methods. Their function is that of receiving and accommodating virtually the entire length of the embolus during copulation. The fundamental spiral configuration of the ectal margin of the bursae conforms closely to that of the emboli (fig. 55).

The plications apparently endow the bursae with the ability to stretch, permitting the bursae to accommodate the emboli. Petrunkevitch (1925, p. 567) also stated, "Nor can the pouch be stretched by an increase of internal pressure, since the wall is quite rigid." The writer, using freshly excised copulatory structures from newly killed specimens of *A. aperta, A. oklahoma,* and *A. pennsylvanica,* found that the bursae stretched readily upon manual introduction of the emboli. The stretching of the bursae caused virtual obliteration of the plications. Removal of the emboli permitted the bursae and their plications to resume their original configuration. Further investigations of a similar nature with preserved copulatory structures of the remaining species of agelenopsids gave identical results, although the elasticity of the preserved bursae was considerably reduced.

Diverticle.—The diverticle (Petrunkevitch, 1925, p. 567) is a pouchlike structure composed of the same light-colored, membranous material as are the bursae (figs. 52-54, *dv*). The diverticle, however, has heavier walls and a smoother surface than does the bursa (figs. 66, 68, 71). The proximal opening into the diverticle is located at the distal end of the reverted portion of the bursa. Distally, the diverticle terminates in a small blind tube on the dorsal surface of the internal copulatory structures between the bursae (figs. 52-54, *bd*). Each diverticle is connected to its own spermathecum by means of a single connecting tube. The connecting tube's point of origin on the diverticle is variable, both in individuals and in the various species. Examples of the variability found in the agelenopsid diverticle are shown in figures 64, 66, 68, 70, and 71.

The function of the diverticle is probably twofold: (1) Reception of the seminal fluid from the embolic terminus, and (2) possibly that of an accessory reservoir for temporary storage of seminal fluid in cases of rapidly repeated copulations. The blind terminus of the diverticle is universally present in the agelenopsids, but it is highly variable. Its function is unknown.

Connecting tube.—The spermathecum communicates with the diverticle by means of the connecting tube (figs. 52-54, *ct*). This tube is so variable both interspecifically and intraspecifically that its configuration is difficult to generalize. Seyler (1941, p. 57) indicated that in some of his specimens this tube "is so short that the receptacle appears to be connected directly with the copulatory sac." Typically, however, the tube is long and narrow. It is composed of the same heavily sclerotized and pigmented material found in the spermathecum. In some species the proximal end of the connecting tube arises "from the medial edge of the copulatory sacs along with, and as a part of the diverticle" (Seyler, 1941, pp. 57-58). At the other extreme the tube is found arising from the ectal margin of the diverticle and connecting with the spermathecum after passing under the ventral surface of the bursa.

The sole function of the connecting tube is that of carrying seminal fluid from the diverticle to the spermathecum.

Spermathecum.—Englehardt (1910) used the terms "receptaculum seminis I" and "primaerer Samenbehaelter" interchangeably for the structure which Petrunkevitch (1925, pp. 565-566) called the "seminal receptacle." The latter term is used rather extensively, although the term "spermathecum" is not infrequently found in literature. The use of the term seminal receptacle for a female structure is somewhat objectionable in view of the general acceptance of the term receptaculum seminis for the internal structure of the male palpus. The writer, therefore, has adopted the term spermathecum (Chamberlin and Ivie, 1940, 1941) for this structure. The paired spermatheca of the agelenopsids are located just cephalad of the atrium, and ventral to the bursae (figs. 52-54, *sp*). These structures are heavily sclerotized and pigmented. Because of their proximity to the ventral surface of the body and their dark color, the spermatheca are prominent landmarks in cleared specimens. They often are discernible even through uncleared epigyna. While the two spermatheca frequently are fused, their lumina are always discrete. The spermatheca are connected to the diverticle by means of the connecting tubes, and they are also the point of origin for the fertilization duct.

Extending from each spermathecum is a short "blind tube" (figs. 52-54, *bs*). This tube apparently is homologous to Engelhardt's (1910) "receptaculum seminis II" and "sekundaerer Samenbehaelter." Engelhardt's (op. cit.) "receptaculum seminis III" or "tertiarer Samenbehaelter" in *Agelena labyrinthica* is wanting in the agelenopsids.

The semen is stored in the spermathecum. Engelhardt (1910) indicated that both the receptacula seminis II and III have a glandular function, or serve as ducts for glands. Petrunkevitch (1925, pp. 567-568) found that the blind tube of the spermathecum in *A. naevia* was capped by a gland, each cell of which opened separately into the blind duct through a series of pores.

Fertilization tube.—The term "fertilization tube" is used almost universally in the literature. This tube originates on the ectal margin of the spermathecum (figs. 52-54, *ft*). Passing under the ventral surface of the bursa, the fertilization tube describes one and one-half turns around the neck of the bursa before it terminates in the vagina on the dorsal surface of the atrium (figs. 67, 69, 72). The tube is darkly pigmented and heavily sclerotized. Its lumen is small but distinct and extends throughout the entire length of the tube. The size and configuration of the tube is relatively constant in the agelenopsids.

The function of the fertilization tube is limited to conveying the seminal fluid from the spermathecum to the vagina. The eggs apparently are fertilized as they pass through the vagina during oviposition.

COPULATORY SYSTEM VARIATION

The copulatory system of the agelenopsid female is given to considerable variation, both interspecifically and intraspecifically. Typical configurations and some extremes of configurational deviation within the genus *Agelenopsis* are shown in figures 61-72.

The epigyna are relatively constant in basic configuration. Atrial variations have already been considered. The guide is present in females of *A. longistylus, A. naevia, A. oregonensis,* and *A. utahana.* The coupling cavity is strongly developed in all agelenopsids, although the ectal concavities may be considerably reduced in specimens of

A. oregonensis and *A. utahana.* In species showing a reduction of these ectal concavities, the conductors of the males show a correlated modification.

The bursae copulatrices are relatively long in the agelenopsids (e.g., *A. naevia,* figs. 71, 72), except in *A. pennsylvanica* (figs. 66, 67). In the latter species, the bursae tend to be markedly shorter than in the other agelenopsids. The bursae of *A. utahana* (fig. 64) are intermediate in length between those of *A. pennsylvanica* and those of the remaining species which resemble *A. naevia.* All bursae are distinctly plicated, except in *A. pennsylvanica.* In this latter species the plications are demonstrable, but are weakly developed. The bursae are widely separated in *A. kastoni, A. longistylus* (fig. 70), and *A. spatula,* while in the remainder of the genus the bursae are contiguous mesally, or nearly so.

The diverticles are so variable interspecifically that generalizations are virtually impossible. All diverticles agree, however, in having the coils oriented in a direction opposite to that of the bursa to which they are attached. *A. utahana* (fig. 64) is distinctive in having diverticles which are rather heavily sclerotized and pigmented.

The connecting tubes are too variable intraspecifically to permit generalizations. The connecting tubes in *A. kastoni,* however, are rather distinctive. They are unusually thick, and are both heavily sclerotized and pigmented.

The spermatheca are heavily sclerotized and pigmented in all agelenopsids. *A. utahana* (fig. 64) is distinctive in having the spermatheca widely separated. They lie near the ectal margins of the bursae instead of between them, as is typical of the agelenopsids. The spermatheca of *A. actuosa, A. oklahoma* (figs. 68, 69), and *A. pennsylvanica* are sufficiently dorsal that they are effectively hidden by the bursae and the diverticles. On the contrary, the receptacles of *A. emertoni, A. kastoni, A. longistylus* (fig. 70), *A. naevia* (figs. 71, 72), and *A. potteri* lie so near the ventral surface of the body that they may be seen through the body wall. In the remaining species, the spermatheca are somewhat more dorsal than in this latter group, but less so than in the former. In this intermediate group the spermatheca are seen through the body wall only rarely.

The fertilization tubes describe 1½ turns around the bases of the bursae before terminating on the dorsal surface of the atrium in all agelenopsids. In *A. kastoni,* these tubes are thick, heavily sclerotized, and deeply pigmented. The fertilization tubes of *A. longistylus* are relatively large as compared with those of the other agelenopsids. The tubes of *A. spatula* are typical in size, but are considerably more heavily pigmented than are the tubes of other agelenopsid species.

The fundamentally basic features of the agelenopsid copulatory system are the presence of the coupling cavity; the mesally curved, plicated bursa; the oppositional curvature of the diverticle; the connecting tube leading to the spermathecum; the spermathecum itself; and the coiling of the fertilization tube around the base of the bursa. While all these vary superficially, both interspecifically and intraspecifically, the fundamental configuration of each appears to vary only within certain mechanical limits.

Before summarizing the copulatory structures of the agelenid females, it should be noted that the writer has not had an opportunity to study the internal structures of representatives of the genera *Chorizommoides, Cybaeozyga, Ethobuella, Melpomene,* and *Tortolena.* The fundamental morphological configurations of the copulatory structures of the females are radically divergent in the various agelenid genera (cf. figs. 61, 66). Most of the genera have a common atrium opening into the paired, internal copulatory structures. In the genera *Blabomma, Chorizomma, Cryphoeca* (fig. 62), *Tegenaria,* and *Tortolena,* however, two discrete openings replace the typical atrium. In *Chorizommoides, Cybaeina,* and *Cybaeus,* specimens of some species have a typical epigynal atrium, while other species of the same genus have two separate copulatory apertures.

A specialized bursa copulatrix, such as is found in the agelenopsids, is uncommon in the Agelenidae. Definitive, well-developed bursae are found in females belonging to *Agelena, Ritalena,* and *Wadotes.* These are directed caudally, in contrast to the cephalic orientation of the agelenopsid bursae, and are less elaborate in structure. The bursae found in *Cicurina* are directed cephalically, but apparently serve to guide the emboli of the males toward the spermatheca rather than to accommodate the emboli in the same sense as the bursae of the agelenopsids do. The bursae found in *Coras* are somewhat reminiscent of the agelenopsid bursae, but they are highly complex. The simple copulatory system of *Cryphoeca* is shown in figure 63. Only the agelenopsids possess plicated membranous bursae and membranous diverticles.

The coupling cavity, which is so distinctive in the agelenopsids, is duplicated in miniature in the posterior median sclerite of the genus *Blabomma.* In *Calilena,* a pair of small cavities can be demonstrated in the posterior median sclerite. It is possible that the caudal ridge, which is a part of the posterior median sclerite in the genus *Rualena,* also could serve a coupling function. Various lesser ridges, concavities, and definitive processes on the posterior median sclerites of representatives of *Novalena, Tegenaria,* and *Wadotes* might also have a coupling function. These are so weakly developed in most instances, however, that such a function appears problematic. In *Blabomma, Calilena,* and *Rualena* the mechanical configurations are such that relatively secure coupling probably could be achieved.

Well-developed atrial guides are distinctive features in *Calilena, Ethobuella,* and *Wadotes.* The role of the guide, and other accessory processes found on the epigyna of many of the agelenid genera, in securing the palpus to the epigynum during copulation can only be hypothesized until such time as detailed studies, both in vivo and in vitro, can be made. In view of the importance of coupling in the agelenopsids and in the genus *Agelena,* as reported by Osterloh (1922), it appears possible that a comparable mechanism might well exist in other genera in this family.

All genera of the family Agelenidae examined agreed in having the spermatheca well developed, heavily sclerotized, and darkly pigmented. Fertilization tubes were demonstrable in all mature females, and all communicated with the vagina. The fertilization tubes were heavily sclerotized and pigmented in all specimens examined.

INTRASPECIFIC COPULATION

Much has been written in regard to the courtship and mating of spiders. Unfortunately, much of this information is based on superficial observations. Most of it is limited to only certain phases of these two processes. Gerhardt (Gerhardt and Kaestner, 1937-1938, pp. 537-557) contributed materially to this field of investigation by bringing together the widely scattered literature, and then summarizing and systematizing the data. Several noteworthy sections on courtship and mating are found in Gertsch's recent book (1949).

The investigation relative to intraspecific copulation herein presented was based on detailed observations of 85 matings (see Appendix, A) involving specimens of *Agelenopsis aperta, A. oklahoma,* and *A. pennsylvanica.* Typically there is considerable difference in the mating behavior patterns in different species within a genus. This has been demonstrated by the Peckhams (1889, 1890) in the Salticidae; by Montgomery (1903) in some Agelenidae; by Bristowe (1926) in the Thomisidae and Sparassidae; by Kaston (1936) in the Lycosidae, Pisauridae, Salticidae, and Thomisidae; and most recently by Crane (1948-1950) in the Salticidae. Therefore, a special effort was made to find such differences in the agelenopsids. The fundamental sexual behavior patterns were found to be so similar that a single discussion of the mechanics of copulation will suffice for all three species here considered.

As this paper is devoted specifically to an analysis of the mechanical dynamics of copulation a detailed consideration of the preceding courtship is not included. It is anticipated, however, that an analysis of the considerable data pertaining to courtship which accrued from this investigation will be published as a separate paper at a later date.

The sexual biology of spiders may be divided into five distinct, behavioristic stages, viz, precourtship, courtship, precopulation, copulation, and postcopulation.

PRECOURTSHIP

The precourtship stage consists of sperm induction by the male, and has no counterpart in the female. Sperm induction is the process whereby the male spider transfers the seminal fluid from his genital aperture to the receptaculum seminis in his palpus. The genital bulb apparently cannot be activated prior to sperm induction. Petrunkevitch (1911, p. 372) stated "my observations leave no more room for doubt that a male with empty palpi does not court and avoids contact with the female."

The charging of the palpus was first reported by Menge (1843) in *Agelena labyrinthica.* Gerhardt (Gerhardt and Kaestner, 1937-1938, p. 537) stated that sperm induction subsequently was reported in over 80 species of spiders, principally by Bertkau, Montgomery, Bristowe, and himself. Gerhardt (op. cit., p. 539) classified sperm induction as being either direct or indirect, i.e., the embolic terminus is introduced directly into the seminal drop, or else it is introduced into the seminal drop indirectly after first being forced up through the meshes of the semen web. The agelenids utilize the indirect method.

As each male spider attains sexual maturity, he spins a special semen web of simple construction. Standing over it, he rubs his abdominal venter against the web. This behaviorism appears to be correlated with the concentration of heavy setae near the genital orifice. The male's action presumably produces a tactile stimulation which causes extrusion of the seminal fluid droplets. These droplets coalesce to form a single drop of seminal fluid which remains on the web.

The agelenopsid male reaches back under and up through the web with his palpi, touching the embolic terminus to the drop of seminal fluid. The small size of the receptaculum seminis lumen produces a strong capillary action which draws the fluid into the ejaculatory duct. The palpus is raised from time to time, permitting the fluid to flow down through the reservoir into the fundus. Kaston (1948, p. 32) stated that "it is possible that sperm induction is effected by a lowering of the pressure around the sperm duct, causing the semen to be sucked in."

The writer witnessed only three such induction operations by the agelenopsids, and only one of these in its entirety. The limited data thus obtained were in agreement with Gerhardt's (Gerhardt and Kaestner, 1937-1938, pp. 539-540) account of this process. Two points could be added, however: (1) There was no indication of haematodochal swelling during induction, and (2) the male agelenopsids appeared to be hypersensitive to disturbances of any kind during induction. This is particularly unusual in view of the males' relative insensitivity to handling and observation during copulation. Petrunkevitch (1911, p. 371), on the contrary, found that the male of *Dugesiella hentzi* was not easily disturbed during sperm induction. Once the receptaculum seminis is charged, and the subsequent period of quiescence is passed, the male becomes sexually active. In nature he leaves his web and wanders about until he finds a sexually mature and receptive female.

Except for the rudimentary semen webs, male agelenopsids do not spin webs after undergoing terminal ecdysis. Only rarely do male spiders retain the ability to spin extensive webs during their terminal stadium. Like most male spiders, however, the male agelenopsids continue to produce drag lines. Isolated virginal females show no apparent change in behavior patterns as a result of reaching sexual maturity, except for the oviposition of unfertilized eggs. Both virginal and mated females make cocoons, deposit their eggs, and guard their egg masses in the same manner.

The writer found one male agelenopsid engaged in sperm induction even though this spider had been completely isolated from all other spiders for the entire duration of his penultimate and terminal stadia. Hence it appears likely that this process is stimulated from within the spider himself. Kaston (1948, p. 32) suggested that "the stimulus for sperm induction is presumably the sensation of fullness in the testes and of emptiness in the palpal organs." Whatever the stimulus is, it manifests itself whenever the receptaculum seminis is empty. Furthermore, this initial stimulus seems to be instrumental in initiating the chain-reflex sequence that apparently constitutes the sexual biology of spiders.

COURTSHIP

The courtship stage is that phase of the spider's mating behavior sequence during which the sexual instincts of the female are sufficiently aroused to permit the male to approach the female safely, and to establish physical contact. The colorful antics of the Salticidae during their courtship dances were described in great detail by the Peckhams (1889, 1890). Kaston (1936) vividly described the courtship of many of the Lycosidae, Pisauridae, Salticidae, and Thomisidae. In the agelenopsids, however, the courtship stage is prosaic, and in most instances brief. Petrunkevitch (1911) and Kaston (1936) presented considerable evidence indicating that the courtship of each species of spider is of such a nature as to exploit the sense or senses most highly developed in that species. This is also borne out by Crane's analysis of display (1949) in the salticids. On the basis of this evidence the agelenopsid courtship should be, and apparently is, restricted primarily to tactile stimulation.

Savory (1928, p. 208) reported placing a male "house spider" (probably *Tegenaria domestica*) on the web of a mature female. The male, using both palpi, initiated a unique strumming on the web. The female remained passive amid the resultant vibrations as the male approached. Gertsch (1949, p. 89) reported that the male of *A. pennsylvanica* "moves on the web of the female and signals to her by tapping the silk with his legs and palpi. His advance is usually slow and measured until he is able to touch her with his legs, whereupon he actively seizes her." This agrees with the writer's field observations of *A. aperta, A. oklahoma,* and *A. pennsylvanica.*

Later, the behavior of the male was observed in a mating case with a binocular microscope, using strong, condensed light. It was not possible to demonstrate conclusively that the palpi are tapped against the substratum. The palpi moved rhythmically, but they appeared never to quite touch the substratum. It is probable that vibrations from any movements of the body were transmitted to the female through the cardboard substratum at the bottom of the mating case.

Upon being placed in the mating case, both the male and female normally are inactive for a few minutes. Then follows a period of variable duration during which they move about the case slowly. It is during this period that either one or both of the spiders shows the first evidence of being aware of the presence of a second animal by instantly elevating the palpi. Typically this response is elicited when the activated spider sees its partner or, more rarely, when physical contact is accidentally established prior to seeing its partner.

When sexually mature agelenopsids are placed together the male ultimately recognizes the female. Only sexually mature females belonging to the same species as the male elicit this response in the agelenopsids here considered. Both animals remain quiet for a variable period of time. A slight palpitation of the abdomens and legs of both animals, and a rhythmic movement of the male palpi are the only discernible movements.

In a few instances the female suddenly moved toward the male and struck at him with legs I. This occurred when the female recognized the male, but before the male showed any evidence of being aware of the female. In each instance, the male initially attempted to escape, but later assumed the typical male role, while the female became passive. Never was any attempt made to injure the male.

Slowly, and with progressively stronger palpitations, the male moves straight toward the female. At times he raises his entire body briefly, and then lowers it to the normal position. Occasionally the female moves. The male then immediately reorients himself so as to compensate for this movement. The tarsi of legs I are frequently elevated very slightly and directed toward the female momentarily before they are lowered to the substratum. During the period of elevation, the tarsi palpitate strongly and synchronically with the less apparent palpitation of the body.

The male's approach to the female spider appears to be a positive tropotaxis. Finally, the male attains a position sufficiently close to the female to be able to grasp her with a single rapid lunge. Establishment of continuous physical contact terminates the courtship stage in the agelenopsids, and initiates the precopulation stage.

The physiological processes involved in both the precourtship and the courtship stages of the agelenopsids are obscure. Kaston (1936, p. 152) concluded that the sense of sight, or the sense of touch, or a combination of both are involved in the courtship of the vagabond spiders which he investigated. While no special study of this phase of mating was included in the investigation herein reported it appears that both sight and touch are involved in the courtship of the agelenopsids. The sense of touch, however, appears to be the more important of the two.

PRECOPULATION

The precopulation stage is initiated with the establishment of continuous contact between the male and the female, and includes all subsequent activities preceding engagement of the embolic terminus in the atrium. This stage is made up of a series of distinct behavior sequences on the part of the male. These behaviorisms are referred to here as the contact, reversal, positioning, and the cleaning phases. During the precopulation stage, and the two subsequent stages, the female is passive. This passive condition is the manifestation of the catalepsis phenomenon, which is discussed later.

Contact phase.—Contact is usually established quickly and vigorously. The male suddenly darts or lunges at the female, grasping her with legs I and embracing both her legs and carapace. The female immediately lapses into catalepsis. Generally the male approaches the female from the side and somewhat from the rear. Approaches from all quarters were observed, however, including a few instances in which the male approached the female directly from the front. Occasionally the female makes an effort to escape. She almost invariably succeeds initially, but runs only a few steps before stopping. In this event, the male shifts his position and pauses for a period of time ranging from a few seconds to several minutes. Then he resumes his efforts to establish contact with the female. The male usually needs to make only a single lunge to reach the female again. If the female, however, has moved a considerable distance, the male resumes his characteristic courtship approach until he is sufficiently close to make his contacting move. In several instances this procedure was repeated as many as eight times before continuous contact was finally established. In no instances did the male fail to establish contact after he had once initiated these efforts.

Having succeeded in grasping the female with legs I, the male starts to mount the female. In so doing he is able to further embrace her with his legs II, and to a limited extent with legs III. In no instance are legs IV used in this initial embrace. The male normally mounts the female from the rear; although when the male approaches the female from the front, he usually mounts her from that direction.

As the male embraces the female, he extends his chelicerae almost horizontally in front of himself, and opens them widely. He then quickly grasps the proximal ends of the female's patellae of legs II (rarely, legs III), holding them firmly between the fangs and the distal end of the falces, or the body of the chelicera. The male then completes the mounting of the female. This is accomplished by minor shifts of the male's legs, but with no relaxation of his hold on the female's patellae. A quiescent period, lasting for several minutes, follows. During this period the carapace and abdomen of the male are directly above those of the female. Cardiac and respiratory pulsations can be seen in both animals. The male shifts his body and legs slightly from time to time.

Catalepsis of female.—Reference to feigning death, sham death, immobilization reflexes, and to the cataleptic trance are found relatively frequently in literature pertaining to the biology of spiders. This unique reaction to sudden disturbance is found almost universally throughout the Araneida. Robertson (1904) studied this mechanism by making neural transections and applying various types of stimuli in representatives of *Epeira producta* (L. Koch), *Amaurobius candidus* (?) (L. Koch), and *Celaenia excavata* (L. Koch). He found that in active species of spiders, as represented by *E. producta* and *A. candidus,* either the two anterior or the two posterior thoracic ganglia, even when severed from the remainder of the central nervous system, were capable of activating the cataleptic response. In "sluggish species," as represented by *C. excavata,* this mechanism appeared to stem from the thoracic ganglia, but could not be induced without the assistance of the "head ganglia."

Catalepsis is a state of muscular tetany involving the entire body of the spider, but particularly the appendages. Catalepsis serves a particularly significant function during copulation. At the instant the male agelenopsid establishes continuous contact with the female, she manifests the cataleptic condition. The body drops to the substratum as if the haemolymphatic pressure in the legs had suddenly decreased. The legs are drawn up high above the carapace until the patellae of legs II, III, and IV are subcontiguous. Legs I are drawn close together throughout their entire length, and are extended forward and down so that the tarsi are curled up under the mouth parts. The metatarsi and the tarsi of legs II and III are extended and initially remain affixed to the substratum. The legs lie close to the sides of the body, but the distal portions are extended sufficiently far ectad to maintain the position of the body. Legs IV are directed caudad, and slightly ectad, giving the body additional stability.

The female is capable of making sudden, independent efforts to escape, especially during the early phases of the precopulation stage. In no instance, however, did the female make an attempt to escape after the positioning phase, except when the spiders were disturbed rather violently. In most instances, the female's efforts to escape are successfully resisted by the male. In two instances in which the female succeeded in escaping, she made a rapid circuit of the mating case, and then, without hesitation, crawled back into her original position beneath the male. The male remained entirely passive during her brief escape. In both instances, the copulatory sequence was resumed as though there had been no interruption.

In view of the complexity of both the genitalia and the mechanics of copulation, the cataleptic state of the female agelenopsid assumes major importance. Even relatively slight movements of the female during certain phases of copulation could effectively preclude the possibility of mating.

Reversal phase.—The reversal phase follows the period of inactivity which terminates the establishment of contact between the male and female agelenopsid. During this phase, which is usually of brief duration, the male moves his body around so as to face in the opposite direction. He momentarily loosens but does not release the grasp of his chelicerae on the female's patellae in order to accomplish this. The reversal phase terminates when the male has successfully accomplished this change of position, and has once again lapsed into inactivity. Upon completion of reversal, the male's carapace is directly above that of the female with the long axes of their bodies parallel, but facing in opposite directions. After reversing his position, the male once again firmly embraces the female. He continues to maintain his hold on the patellae of the female. From the reversed position, the male is better able to position the female and then to move himself into the copulatory stance.

Positioning phase.—Occasionally the male first attempts to roll the female on her side before reversing his position. Almost invariably he meets with considerable resistance on the part of the female. Usually, however, the male makes no effort to move the female into the copulatory position until after he has reversed his position. The positioning phase includes the successful rolling of the female into a position suitable for copulation, with the subsequent assumption of the copulatory stance by the male. This suitable position of the female is one in which the vertical axis of her body is inclined approximately 70° either dextrally or sinistrally.

Making use of his hold on the patellae of the female almost exclusively, the male lifts the female slightly as he tries to turn her over on her side. From one to nine attempts are needed to position the female. Once the female is positioned, the male releases the hold of his chelicerae on the patellae of the female. Bristowe (1929, p. 350) reported on the use of the chelicerae in positioning the female in the genus *Agelena.* The slight movements of the female during these attempts are difficult to evaluate or interpret. They may be movements of actual resistance, or they may be manifestations of the male's activity. If this resistance is active on the part of the female it would appear to consist of such subtle actions as moving her legs slightly farther ectad to increase her stability, or grasping the substratum more tenaciously.

The first evidence of movements of the spines on the male's appendages appears after the male has succeeded in positioning the female. The distinct though not pronounced movements of the spines correspond with the cardiac pulsations. There is no evidence of any swelling of the haematodochae at any time prior to the actual copulatory stage.

After positioning the female, and prior to moving into the copulatory stance himself, the male initiates the cleaning of the palpi. This behaviorism is considered later. As the tempo of the cleaning process reaches its climax, the male moves his body in the direction of the female's dorsum until he has placed himself at approximately a 45° angle to the long axis of the female's body. Thus he faces ventrocaudad relative to the female (fig. 8). This is the copulatory stance of the male. The male immediately resumes the cleaning of his palpi. There is no quiescent period following the positioning phase. This phase terminates with both spiders in the copulatory position.

Gerhardt (Gerhardt and Kaestner, 1937-1938, pp. 546-549) recognized five basic copulatory stances in the Araneida, but he also noted (op. cit., p. 545) "dass sich immer mehr gezeight hat, dass man nicht zu streng schematisieren darf, und dass es Uebergaenge gibt, die von der einen Begattungsstellung auf zweifellos verschiedenen Wegen erreicht werden konnte." Gerhardt's (op. cit., p. 547) agelenid- or lycosid-type copulatory stance is typical of most agelenids, including the genus *Agelenopsis*. Other families utilizing this couplatory position include the Lycosidae, Salticidae, Pisauridae, and the Clubionidae. It should be noted that the agelenid-type copulatory position necessitates rolling the female over on her opposite side each time before the alternating palpus can be applied. Emerton (1878, p. 36) gave a brief description of the copulatory stance of *A. naevia* which agrees essentially with the writer's observations of other agelenopsids.

Cleaning the palpi.—The process of cleaning the palpi during mating is so distinctive that special consideration is warranted. Savory (1928, p. 226) credited Blackwall (1873) for first reporting pauses in the mating process during which the palpi were drawn between the chelicerae. Savory (loc. cit.) further stated that Locket later investigated this phenomenon more closely and found that it was actually the embolus that was involved.

In the agelenopsids, the process of cleaning the palpi is initiated previous to the assumption of the copulatory stance by the male. The palpi are placed well back and between the chelicerae, and then are rapidly withdrawn. A fluid from the oral region is spread over the palpi during this process. The palpi are drawn between the chelicerae in a random fashion prior to the male's assumption of the copulatory position. Gradually the male limits the cleaning process to the genital bulbs, and finally to the embolic termini only. Once having assumed his copulatory stance, however, he becomes rigidly selective as to which palpus is cleaned. If the female rests on her right side, the left atrial opening is uppermost, and the male commences to clean the left palpus. While the right palpus is also cleaned sporadically, the cleaning process is concentrated on the left. The male then uses the left palpus for copulation. Reversal of the female's position results in the right palpus being cleaned instead. No deviation from this behavior pattern was observed in the agelenopsids.

As the cleaning process continues, the pulsations of the spines become stronger. At this time the first evidence of their actual erection is evidenced. The spinnerets also appear to pulsate more strongly. The female remains in her cataleptic state. Her only movements consist of vague, rapid pulsations of the tips of her tarsi and spinnerets.

Suddenly the male ceases his cleaning activities and immediately attempts to engage the embolus in the atrium of the female's epigynum. This action terminates the precopulation stage and initiates the copulation stage. The position of the female determines which palpus is used for copulation, and it is this circumstantially selected palpus which is initially cleaned after the male assumes his copulatory stance. This same palpus is cleaned almost to the exclusion of the nonutilized palpus, and it is the last palpus cleaned prior to actual copulation.

The number of times that each palpus is drawn between the chelicerae after the male assumes his copulatory position ranges from two to more than fifty. The variability in any given male is great.

The writer's studies support Savory's suggestion (1928, p. 226) that the cleaning process serves to lubricate the genital bulb and its component parts. Genital bulbs which have not been subjected to the cleaning process are dry; those that have are well moistened. This is true particularly of the membranous portions of the bulbs. The cleaning process precedes every instance of haematodochal inflation in the agelenopsids.

COPULATION

The copulation stage includes all phases of sexual activity involved during the period of actual physical contact between the palpal structures of the male and the copulatory structures of the female. The mechanical aspects of this stage have been largely neglected except by a few men such as Osterloh (1922). The copulation stage consists of a series of distinct processes: engaging the embolus, inflation of the haematodochae, coupling of the conductor, locking of the palpus, maximum distention, ejaculation, reduction of the haematodochae, breaking of the locking mechanism, uncoupling of the conductor, retraction of the embolus, and the embolic terminus release. Each mating consists of a series of separate insertions or copulations. The number of insertions per mating is highly variable (Appendix, B).

Engaging embolus.—In the agelenopsids, the process of engaging the embolus is initiated without pause after completion of the embolic cleaning of the preceding stage. It should be noted again that the position of the female determines which palpus is used for copulation.

The process of engaging the embolus was found to be one of the most critical points in the mechanics of copulation in the agelenopsids. The male initiates a series of slapping movements which move the genital bulb in an arc across the face of the epigynum. The entire palpus is involved in this process. The swings are started a short distance caudad of the epigastric furrow, and move back and forth over the atrium. The number of attempts needed to engage the embolus, the frequency rates, and the duration of this process are given in Appendix, B. Ultimately, by means of slight changes in the position of the palpus, in the degree of distention of the haematodochae, and even of the position of his body, the male succeeds in engaging the tip of the embolus in the female's atrium. The necessity for the catalepsis of the female is most obvious during this process. Once the tip of the embolus is engaged, the random nature of the copulatory act ceases; the remainder of the copulation follows an almost invariable sequence with machinelike precision.

Inflation of haematodochae.—As the male draws his palpus from between the chelicerae and lowers it into position to initiate the swinging movements just described, the basal haematodocha is activated suddenly and begins to swell rapidly. This inflation lacks the spasmodic pulsations that are so distinctive of the activated haematodochae during later phases of copulation. There is no evidence of even the slightest haematodochal swelling prior to this time. While the middle haematodocha inflates slightly, pronounced distention does not occur until later.

The initial inflation of the basal haematodocha forces the genital bulb out of the alveolus and ectad, probably with the assistance of the petiole (fig. 7). This ectal displacement is accompanied by sufficient rotation to place the embolic terminus in a position suitable for engagement in the atrium, during the swinging movements. Once the embolic terminus is engaged in the atrium, continued swelling of the basal haematodocha provides the rotation necessary for consummation of copulation. As previously stated, the haematodochae are inflated by increased haemolymphatic pressures.

Insertion of embolus.—The continuing inflation of the basal haematodocha causes the tegulum to rotate. As the tegulum rotates, the embolic terminus, which is already within the atrium is forced ectad and cephalad (fig. 55). The configurations of both the atrium and the embolus are obviously responsible for directing the embolic terminus through the aperture into the bursa. Further entry beyond the point of maximum initial insertion (fig. 55) is accomplished only by short, abrupt advances of the embolus resulting from strong, spasmodic pulsations of the basal and middle haematodochae. The middle haematodocha starts to inflate strongly during the insertion process.

The following interpretation of this insertion process is based on observations and detailed studies of both specimens and models: The embolic terminus is rotated into the bursa smoothly and rapidly until it reaches the cephalic end of the bursa. This constitutes the point of maximum initial insertion. Any subsequent advance of the embolus can be accomplished only by exerting sufficient force to cause the plicated walls of the bursa to stretch, and to cause the embolus itself to bend sufficiently to conform to the configuration of the stretching bursa (fig. 56). In this way, maximum total insertion can be achieved with the embolic terminus coming to rest at the distal end of the recurved bursa. The opening of the ejaculatory duct thus is in close proximity to the opening between the bursa and the diverticle (figs. 52, 53, 55, 56).

Coupling of conductor.—The conductor rotates as an integral part of the tegulum during the initial portion of insertion (figs. 43, 44). However, as the conductor strikes the posterior median sclerite during this process, the genital bulb stops rotating briefly. The conductor is, thereby, properly oriented to be engaged in the coupling cavity. The ectodistal process of the conductor is introduced into the coupling cavity by a slight depression of the palpus. By means of a second slight palpal movement this process is then forced into the ectal depression of the coupling cavity (fig. 44). The conductor is always engaged in the ectal depression opposite to the bursa being utilized, e.g., if the right embolus of the male is introduced into the right bursa of the female, the ectal process of the conductor is engaged in the left depression of the coupling cavity.

The conductor is always engaged prior to completion of maximum initial insertion of the embolus. The coupling of the conductor is the second critical point in the mechanics of copulation in the agelenopsids. Unless coupling is satisfactorily accomplished, the embolus is partially retracted (by a slight deflation of the basal haematodocha) with complete disengagement of the conductor. Subsequent attempts at coupling follow immediately and continue until this is achieved (Appendix, B). In no instance was the embolus found to attain maximum initial insertion unless the conductor was first securely coupled. The existence of a comparable coupling mechanism was reported for *Dictyna benigna* by Karpinski (1882, pp. 714-715) and for *Agelena similis* Keyserling and *Lycosa amentata* Clerck by Osterloh (1922, pp. 412, 414). Both of these authors maintained that maximum distention of the haematodocha was dependent on successful coupling. The obvious function of the conductor is that of securing the genital bulb to the epigynum, and thereby forming a solid base to facilitate driving the embolus farther into the bursa in spite of the considerable resistance met with there.

Locking of palpus.—Once the conductor is securely coupled, maximum initial insertion is quickly accomplished. As maximum total insertion is being attained, however, several other actions are manifest. The conductor remains fixed in the coupling cavity, and the entire genital bulb is drawn down into intimate contact with it as the tegulum continues its pulsating rotation. The entire palpus shows marked evidences of becoming progressively more tense. The middle haematodocha can be seen quite clearly through the greatly swollen, transparent basal haematodocha, particularly at the zeniths of the paroxysms. The middle haematodocha is strongly inflated, forcing the tegulum to rotate out of and away from the subtegulum except for their common articulation. The spines on all the appendages of the male are erected to a nearly vertical position with each pulsation of the haematodochae, and then drop back slowly to a nearly horizontal position. The spinnerets and the abdomen show marked pulsations corresponding with those of the haematodochae.

Suddenly, the segments of the entire palpus appear to lock into a rigid position with the cymbium drawn tightly against the tibial apophysis. Simultaneously, the entire genital bulb jerks sharply, as though some solid restraint had been removed suddenly, and then remains immobile. The embolus, however, moves forward sharply, although for only a short distance. Maximum total insertion has been attained. The female remains completely passive throughout the entire process.

The transparent nature of the haematodochae during maximum distention permits observations of the relative positions and the functions of many of the components of the genital bulb. Unfortunately, however, the heavily pigmented tegulum conceals much of the radix and the embolic base, while the median apophysis and the tethering membrane are hidden entirely. For this reason, only indirect evidence is available to substantiate some of the following hypotheses pertaining to the mechanical aspects of the locking mechanism.

The following interpretation of the locking process is based on hypotheses formulated from observations of agelenopsids during copulation, and with the aid of models and manual manipulation of the genital bulbs from both preserved and newly killed males: Maximum total insertion is accomplished by means of higher haemolymphatic pressure than is needed to attain maximum initial insertion. This is substantiated by the more nearly vertical erection of the appendicular spines during the paroxysms than is evidenced prior to this point in copulation. Observations reveal that as the genital bulb continues its spasmodic rotation and the conductor remains fixed in the coupling cavity, the tethering membrane is brought under tension and presumably begins to stretch (fig. 45). This can be demonstrated by manipulation of genital bulbs taken from newly killed males. The elasticity of the tethering membrane from preserved genital bulbs is considerably reduced by the preservative. As the tethering membrane becomes taut, the tegulum literally rolls down along the membrane toward the anchored conductor. The paired proximomesal processes of the conductor articulate with the hemispherical groove and ridges on the embolic base (figs. 36, 38, 40, 41). The genital bulb thus is drawn into the large, mesal curvature of the conductor. This also can be observed.

The tegular ridge slides down along the caudal surface of the conductor, while the embolic base and radix similarly are drawn down into the atrium in front of the cephalic surface of the conductor. As the genital bulb continues to rotate, the tethering membrane continues to stretch and appears to be drawn through the groove at the embolic base. The decreasing rate of insertion, as the locking process continues, is very apparent during this phase of copulation in the agelenopsids. Three factors appear to be responsible for this decreasing rate: (1) Increased resistance within the bursa, (2) additional resistance resulting from the intimate physical contact between the tegulum and the conductor, and (3) increasing resistance from the tethering membrane as it is progressively stretched.

When rotation has virtually ceased, a particularly strong haematodochal paroxysm is observed. The tegulum rotates sharply, driving the embolus forward, and simultaneously completing the locking process. During the ejaculation period which follows the entire genital bulb is completely immobile. If the tethering membrane has reached its limit of elasticity immediately prior to the aforementioned paroxysm, the resulting action may be hypothesized as follows: The tethering membrane, no longer capable of further stretching, is very tightly drawn into the groove at the base of the embolus. The rotation of the tegulum, resulting from the particularly strong haematodochal inflation, thus produces sufficient tension on the embolic base to cause the already-strained embolic-radix articulation to buckle (fig. 47). Manipulation of the embolus reveals that this flexure can be induced only by the application of considerable force. This articulation permits the base of the embolus to fold up under the radix (figs. 42, 46, 48, 49). As the embolic base folds under the radix, the median apophysis fits into the groove of the embolic base (figs. 46, 48). The purpose of this mechanical configuration obviously is that of increasing the strength and rigidity of the union between the embolus and the remainder of the genital bulb during this critical period. The morphological configurations of the structures involved in this mechanism make such a hypothesis mechanically feasible, while the actions which are manifest during the attainment of maximum total insertion further substantiate it.

Maximum distention of haematodochae.—Maximum distention of the haematodochae is achieved only after the locking of the palpus is completed. During this period, the haematodochae pulsate quite constantly during any single insertion. The pulsation rates and the duration of maximum distention vary markedly even in the several insertions making up a single mating (see Appendix, B).

Maximum distention is actually a dynamic state in which complete inflation of the haematodochae is maintained only momentarily, followed by a slow, slight deflation. The pulsating erections of the spines of the male are synchronous with the haematodochal palpitations, and are markedly manifest during this period. As the haematodochae reach the zenith of each spasmodic swelling, they become transparent, losing the textured appearance which makes them semitranslucent at all other times. The transparency of the haematodochae is somewhat counteracted by the slight turbidity of the haemolymph, which can be seen swirling inside of them.

Ejaculation.—In all probability, ejaculation occurs during the maximum distention of the haematodochae. Apparently the seminal fluid is forced from the receptaculum seminis, upon collapse of the fundus, by the greatly increased haemolymphatic pressure which produces the maximum distention. As suggested previously by the writer, the articulation of the tegulum on the subtegulum may play a minor role in collapsing the fundus. In the agelenopsids, the seminal fluid is presumably ejaculated within the distal end of the bursa in the immediate vicinity of the aperture between the bursa and the diverticle. The duration of ejaculation is probably as variable as is that of maximum distention. Considerable work yet remains to be done relative to the receptaculum seminis, and particularly to the detailed mechanics of ejaculation.

Reduction of haematodochae.—Following ejaculation, the haematodochae begin to deflate. This process introduces a reversal of all the mechanical functions which led to maximum distention and maximum total insertion. Deflation is slow until after the locking mechanism is released, while subsequent deflation is accomplished rapidly. The reduction of the haematodochae is a progressively accelerated process. There is no appreciable retraction of the embolus until after the palpus has been unlocked. During the latter part of deflation there is little or no indication of the paroxysms which are so characteristic of the maximum distention phase.

Breaking of locking mechanism.—Once maximum distention is reduced, the effects of the locking mechanism of the palpus are terminated. This can be predicted accurately by observing the entire palpus. The spasmodic contractions of the haematodochae are paralleled by slight, synchronous movements of the entire palpus. As the haematodochae begin to deflate, the throbbing of the palpus becomes progressively stronger. As the palpitations gain in intensity, the palpal segments flex rather slowly at first, and then more rapidly. Suddenly, the palpus flexes sharply indicating clearly that the locking mechanism has been broken. This is accompanied by a simultaneous breaking of the conductor coupling (Appendix, B). Once the effect of the locking mechanism is eliminated, the speed with which the haematodochae are reduced is greatly accelerated. The palpitations of the entire palpus, which are so evident in the haematodochae during the period of maximum distention, are reduced in intensity in direct proportion to the degree of deflation.

Uncoupling of conductor.—As the haematodochae begin to deflate, the embolus retracts slightly. This initial retraction is apparently due to a slight counterrotation of the tegulum, which somewhat relieves the strain on the tethering membrane. This in turn permits the restoration of the normal radix-embolic configuration. The elasticity of the tethering membrane could conceivably be a major factor in producing the initial counterrotation of the tegulum.

Continued counterrotation of the tegulum further retracts the embolus, and further reduces the tension on the tethering membrane. As this tension on the tethering membrane is completely eliminated, the tegulum rotates away from the conductor, while the conductor itself is disengaged from the coupling cavity. Finally, only the embolic terminus remains in contact with the copulatory structure of the female.

Retraction of embolus.—The retraction of the embolus occurs simultaneously with the uncoupling of the conductor (see preceding section). The final phase of retraction is accomplished rapidly when compared with the relatively slow initial stages of withdrawal. If, however, the agelenopsids are disturbed during couplation, retraction of the embolus is virtually instantaneous. It appears likely that the embolic termini are subjected to greater danger of breakage during such hasty retractions than in normal withdrawals. The embolic fragments occasionally found in the bursae of females probably indicate an interrupted copulation. Data pertaining to the retraction of the embolus are given in Appendix, B.

Embolic terminus release.—Almost invariably, the embolus is smoothly retracted until only the terminus remains within the atrium. The entire palpus is then subjected to a series of jerking movements reminiscent of the swinging movements used to engage the embolic terminus in the atrium at the onset of copulation. The number of disengaging movements necessary to free the embolic terminus is highly variable (Appendix, B). This characteristic behaviorism is manifest except in instances of disturbed copulation. When the animals separate suddenly, the additional force thus obtaining forcibly pulls the terminus from the atrium. As the genital bulb swings free from the epigynum, the first of the series of insertions which make up a single mating is completed.

POSTCOPULATION

The postcopulation stage includes all those activities which take place following the release of the embolic terminus. Ultimately the male has two alternatives during the postcopulation stage: he may either repeat insertion (Appendix, B), or he may terminate the mating process and leave the female. During the postcopulation stage, the female generally remains in a state of catalepsis until the male leaves her. In some instances, however, the female may make feeble attempts to right herself. Usually the male has little or no difficulty in suppressing these efforts.

Immediately upon release of the embolic terminus the male resumes the process of cleaning his palpi. This is a continuation of the cleaning process which immediately precedes insertion. Even when disturbed, the male runs only a few steps before he stops to clean his emboli.

In instances where reentry is made almost immediately following release of the embolic terminus, the process of cleaning the terminus is reduced to little more than a formality, i.e., the termini are drawn between the chelicerae only once or twice. Not a single instance of release of the terminus was observed, however, which was not immediately followed by the cleaning process.

The mechanics of each subsequent insertion were found to be the same as that described for the initial insertion. The period of time that elapses between insertions is highly variable (see Appendix, B). Typically, however, subsequent insertions are initiated within a few seconds. Following the terminal insertion, the male cleans his palpi and then walks away from the cataleptic female unhurriedly. Almost immediately thereafter, the female rights herself. She then frequently commences to groom herself by drawing her legs between her chelicerae and then brushing her body with them.

Savory (1928, p. 225) stated that the "total number of insertions during one mating varies from one to over a hundred." Osterloh (1922, pp. 401-402) reported six consecutive matings between a pair of spiders belonging to *Agelena similis,* in which the right palpus was used twice, and the left, four times. In other spiders he found the number of insertions per mating to range from 45 to 272, with an average of 131.5 insertions per mating. In the agelenopsids herein considered the number of insertions per mating ranged from 3 to 18 (Appendix, B). These figures do not present a completely accurate account, however, because the mating spiders were usually separated after approximately six insertions had been observed and recorded.

One and two unsuccessful attempts were observed respectively in *A. oklahoma* and *A. aperta,* in which males endeavored to turn the females on their opposite side to permit copulation with the other palpus. Of the five similar attempts witnessed in *A. pennsylvanica,* three were successful.

Several facts were revealed during laboratory observations of 7 matings involving spiders of *Chiracanthium inclusum* (Clubionidae) and 11 involving *Misumena calycina* (Thomisidae). In both of these species the cleaning behaviorism is as manifest as it is in the agelenopsids. Courtship, likewise, is virtually nonexistent in both species. Moreover, in both, the inflation of the haematodochae and the rotation of the tegulum agree closely with that of the agelenopsids.

The males of *C. inclusum* apply the right palpus to the right portion of the copulatory apparatus, as do the agelenopsids. The coupling of the genital bulb to the epigynum is accomplished by means of a pair of processes located on the base of the cymbium and at the distal end of the tibia respectively (fig. 58). The mechanism of this locking process is shown in figures 59 and 60.

Upon being placed in the mating case, the tiny male of *Misumena calycina* immediately runs over the body of the female and assumes his copulatory position on the venter of her abdomen. He applies his chelicerae to the epigynum, and while he manipulates his fangs in the atrium, an oral fluid is extruded and drawn back into his mouth. The function of this behaviorism is unknown. Following this, the mating is consummated. Gerhardt (Gerhardt and Kaestner, 1937-1938, p. 546) stated "Im Falle von *Segestria* beisst sich das Maennchen mit seinen Cheliceren an der Bauchhaut des Weibchens fest," and further indicated a similar behaviorism had been reported in the Dysderidae, Sicariidae, and Pholcidae by Bertkau and himself.

The mechanical configuration of the male's palpus (*M. calycina*) necessitates a shift in his position each time he alternates his palpi. The right palpus is applied to the right portion of the copulatory apparatus and vice versa. No evidence of a special locking mechanism is apparent in *M. calycina.*

INTERSPECIFIC COPULATION

The purpose of this portion of the investigation was to determine, if possible, the validity of the lock-and-key concept in the agelenopsids. The 23 attempts (Appendix, A) to effect copulation between spiders belonging to discrete morphological groups which are generally accepted as being valid species were entirely negative. Instances of cross copulation between members of different species of spiders are reported, however, in the literature. Gerhardt (Gerhardt and Kaestner, 1937-1938) reported the occurrence of copulation between spiders belonging to two different species of the genus *Eresus*. Bonnet (1933b) reported two cases between males of *Dolomedes fimbriatus* and females of *D. plantarius*. Bonnet found it necessary to anesthetize the females before these matings could be consummated. Locket (1939) briefly reported still another instance of interspecific copulation in spiders. None of the females produced viable eggs following these copulations.

Initially it appeared possible that *A. pennsylvanica* and *A. oklahoma* would provide ideal material for studies relative to interspecific copulation because: (1) These two species attain sexual maturity during the same period; (2) although *A. oklahoma* typically is slightly smaller than *A. pennsylvanica,* sufficiently large numbers of spiders were available to permit selection of individuals of comparable size; (3) the general coloration and morphological configurations of these two species is remarkably similar; (4) preceding studies of intraspecific matings showed the copulatory behavior patterns to be virtually identical in each of the species considered; and (5) using both preserved and freshly killed material no major mechanical incompatibilities were apparent which should have prevented such cross matings. In spite of these encouraging indications, interspecific copulation between members of *A. oklahoma* and *A. pennsylvanica* did not occur. Attempted cross matings involving spiders of *A. aperta* with those of the aforementioned species were also unsuccessful (Appendix, A).

Mature males were placed in the same mating case with immature males of the same and different species; and with both immature and mature females of the same and different species. The reactions of the males to the presence of mature females of their own species have already been described. In any other combination the spiders displayed the following reaction sequence: The male became aware of the presence of another spider, but there was little, if any, evidence of the initiation of courtship. Both spiders typically displayed a mutual indifference toward each other. In a few instances one attacked the other. Unless the writer intervened, these attacks always culminated in the death and consumption of one of the spiders. Kaston found (1936) that certain males of the families Salticidae, Lycosidae, Pisauridae, and Thomisidae could be stimulated to initiate courtship by the presence of females of other species, and even by other males. The writer has been unable to demonstrate satisfactorily a comparable response in male agelenopsids. Additional investigation of this specific problem is indicated, however, by the data already obtained.

All spiders used in the attempted cross matings were permitted to copulate with spiders of their own species both before and after the attempts at interspecific mating. This was done to insure selection of individuals that were capable of sexual stimulation. In many instances one or both of the spiders failed to copulate with members of their own species after attempts at cross mating. These instances have not been included in Appendix A, as their significance is questionable.

DISCUSSION AND CONCLUSIONS

While few araneologists have attempted to unravel the complexities presented by the mechanical aspects of copulation in the spiders, the literature is quite voluminous relative to the superficial aspects of mating. Nevertheless, virtually nothing has been reported with reference to correlating the behavioristic manifestations with the morphological and physiological characteristics of the copulatory structures. In the investigation herein reported the characteristics of the copulatory structures were found to be responsible for many of the behavioristic manifestations of the agelenopsids. On the basis of the correlations found to exist, this investigation was expanded as much as time and material permitted in order to determine the morphological possibility of the existence of similar correlations in other genera of Agelenidae and in other families of Entelegynae.

STRUCTURE AND FUNCTION OF GENITILIA

In spite of the fact that the structure of the palpus of the agelenopsids appears to be very complex and to vary markedly in representatives of the various species of this genus, the fundamental structural design is relatively simple and remarkably constant throughout the genus.

The fundamental configuration of the proximal segments of the palpus is constant in all agelenopsids. Similarly, the functions, including such things as the angles of articulation and the extensor mechanism, appear to be similar. The same basic similarities are found in the other genera of Agelenidae.

The tibial apophysis serves in the locking mechanism of the agelenopsid palpus. The position of this apophysis varies sufficiently in members of *Cybaeota* and *Cybaeina* as to possibly necessitate slight modifications of the behavior pattern of locking. The lack of the tibial apophysis in *Wadotes* appears to be compensated for by the strongly produced depression in the proximomesal margin of the cymbium. A special problem is posed by the fact that the cymbium cannot impinge upon the tibial apophysis in the specimens of *Tegenaria domestica* available for this study. Studies in vivo of representatives of the four genera just mentioned would be necessary to determine the extent of the behavioristic changes which probably would be necessitated by the morphological variations. In such genera as *Erigone* (Micryphantidae), *Epeira* (Epeiridae), *Dolomedes* (Pisauridae), *Gnaphosa* (Gnaphosidae), *Clubiona* (Clubionidae), *Oxyptila* (Thomisidae), and *Habronattus* (Salticidae) the frequent occurrence of a tibial apophysis, which is similar to that of the agelenopsids, indicates that this apophysis is commonly present, and probably serves a similar function in all these genera.

Morphologically, the proximal portion of the genital bulb is relatively invariable not only in the Agelenidae, but also in a considerable number of other families of the Entelegynae. Structurally, the basal haematodochae of representatives of *Chiracanthium* and *Clubiona* (Clubionidae), *Gnaphosa* (Gnaphosidae), *Pardosa* (Lycosidae), *Spirembolus* (Micryphantidae), and *Misumena* (Thomisidae) are similar. Moreover, the agelenopsid rotating type of haematodochal expansion is demonstrable, by means of artificial inflation, in each of the aforementioned genera. In some instances, however, the magnitude of this rotation appears to be somewhat less than that of the agelenopsids. Thus, the morphology of the basal haematodocha is strikingly uniform in all representatives of the Entelegynae examined during this investigation. A comparable similarity can be observed in the function of the basal haematodocha during copulation in the Agelenidae, Clubionidae, and Thomisidae. These observations indicate that the fundamental mechanical aspects of the activities of the genital bulb are similar, if not identical, in these three families. Furthermore, it appears probable that the fundamental mechanics of the genital bulb, as previously described in the agelenopsids, may apply to most of the Entelegynae as well.

The petiole varies considerably in its degree of development in the various genera of Agelenidae. It is strongly developed in the Clubionidae, Lycosidae, and Micryphantidae. Owing to the extreme reduction of this structure in some genera of Agelenidae, it appears that the function of the petiole may be advantageous but not necessarily vital to the activity of the genital bulb. When the petiole is present, however, its apparent function in facilitating the ectal displacement of the inflating genital bulb is clearly indicated.

Only superficial variations are found in the subtegulum of the agelenopsids. The lunate plate is well developed in every specimen of Entelegynae examined. The fundus also is demonstrable in virtually every expanded subtegulum. The anelli, although variable in their degree of development and in morphological configuration, are found in all Agelenidae except in the genus *Wadotes*. The anelli are also found in the Clubionidae and the Micryphantidae, but are wanting in the genus *Pardosa* (Lycosidae). Thus the subtegulum should probably be considered as a vital structure in the genital bulb of the Agelenidae, and possibly in most, if not in all, of the Entelegynae. The lunate plate, likewise, appears to be a vital structure. Strongly developed anelli, on the contrary, are not universally found in either the Agelenidae or in the Entelegynae. Probably the most important function of the anelli is that of strengthening the subtegulum. What effects the absence of the anelli would have on the action of the genital bulb are not known.

The middle haematodocha is found in all Entelegynae examined, although its degree of development varies somewhat in the different families. The facies of the tegulum are extremely variable. Fundamentally, however, the tegulum is essentially the same throughout the Agelenidae, and in the other Entelegynae considered. The frontal plate of the tegulum is rather variable even within the homogeneous agelenopsids. That the tegulum constitutes a solid base for the embolus and accessory structures is amply attested by this investigation.

The conductor performs an essential function in the locking mechanism in the agelenopsids. Conductorlike structures of comparable basic configuration are found in functionally suitable positions on the tegula of representatives of other genera of Agelenidae. However, only studies in vivo can conclusively determine whether or not they also have a coupling function. In view of the dual locking and coupling function performed by the tibial apophysis of males of the species *Sparassus virescens* observed by Bristowe, and the same function performed by the tibial and cymbial apophyses of males of *Chiracanthium inclusum* as herein reported, it appears that the locking mechanism may also occur in other Entelegynae. Gertsch (1949, p. 97) was of the opinion that some of the apophyses of the genital structures were used to "fix the palpus in just the right position to make pairing possible," but he further considered that many of these structures have undergone excessively elaborate modifications beyond those needed to fulfill their original function. The tibial apophyses found in *Hololena* and *Novalena* appear to be such excessively elaborate developments, although they probably are still functional.

In the agelenopsids, the locking mechanism serves not only in orienting the embolus, but in providing a sufficiently solid base to permit forcing the embolus into the bursa. In view of the considerable resistance incidental to maximum total insertion, this anchoring effect of the locking mechanism assumes major importance. The locking mechanism is so vital in the copulation of the agelenopsids, and apparently in the clubionid genus *Chiracanthium,* that further investigations relative to the locking mechanism in other Entelegynae are indicated.

The morphological configuration of the long, heavy embolus of the agelenopsids is closely correlated with the large, cavernous bursa of the female. In the *Cicurina,* the long, filamentous embolus appears to be closely correlated with the slender, convoluted tubes extending from the atrium to the spermatheca. The emboli of the agelenids are highly variable in length and in diameter. Fundamentally, the agelenid embolus has a circular configuration when viewed from the frontal aspect. This circular configuration is not limited to the Agelenidae, however. It occurs in such widely divergent genera as *Clubiona* (Clubionidae), *Dictyna* (Dictynidae), *Argiope* (Epeiridae), *Gnaphosa* (Gnaphosidae), *Linyphia* (Linyphiidae), *Walckenaera* (Micryphantidae), *Habronattus* (Salticidae), *Asagena* and *Theridion* (Theridiidae), and *Oxyptila, Tmarus,* and *Xysticus* (Thomisidae). The aforementioned examples display a strikingly diagrammatic conformity to the basic circular configuration of the embolus. The preponderance of other genera of the Entelegynae similarly have emboli which generally agree with this configuration. The circular embolus virtually necessitates a rotating movement of the genital bulb in order to accomplish insertion. This in turn indicates that the fundamental mechanical functions of the genital bulb are essentially the same in at least most members of the Entelegynae.

In the agelenopsids such features as the radix, the tethering membrane, and the median apophysis are important in the mechanics of copulation. The radix loses its identity in other genera of agelenids by being incorporated into the tegulum or the tegular plate. The functions of the tethering membrane and the median apophysis in the other genera of agelenids have not yet been determined. In fact, the existence of a tethering membrane has not been demonstrated in many of the agelenid genera.

The copulatory apparatus of the agelenid females can be classified conveniently as belonging to two fundamental morphological types: (1) Those having saccular bursae, and (2) those having filamentous bursae. The bursae of some *Cicurina* are more or less transitional between the two basic configurations. As previously indicated, a very close correlation exists between the size of the embolus of the male, particularly in reference to its diameter, and the degree of bursal development in the female. Thus, while it would be mechanically possible to introduce a filamentous embolus of the *Cicurina* into the saccular bursa of an agelenopsid, a reciprocal mating would be impossible. This incompatibility stems from the small diameter and the convoluted configuration of the bursa of the *Cicurina*. Cephalically directed, saccular bursae with definitive plications appear to exist exclusively in the agelenopsids.

The fundamental configurations of the epigyna are relatively constant in any given genus in the Agelenidae. The specific functions of the various accessory processes on the epigyna in this family can be determined only through studies in vivo. It appears likely, however, that at least some of these processes serve a function similar to that of the coupling cavity in the agelenopsids. The coupling cavity is an essential morphological feature in agelenopsid copulation. Morphological configurations of the posterior median sclerite, which would be mechanically suitable for coupling, are found in the agelenid genera *Blabomma, Calilena,* and *Rualena.* If the coupling mechanism does exist in other agelenids, the morphological structures involved in the process are still obscure. The occurrence of definitive coupling cavities in the females of *Sparassus virescens,* however, suggests that the coupling mechanism may occur more generally in the Entelegynae than has been suspected heretofore.

Because of the great variability of the female copulatory structures in the agelenids and other Entelegynae, generalizations are difficult to formulate. In the Entelegynae all females have atrial apertures leading through a bursa into a heavily sclerotized and darkly pigmented spermathecum.

In all probability, the various configurations of the agelenid bursae have necessitated marked modifications in the morphological configurations of the various parts of the genital bulb and their relative positions on the bulb of the male. These modifications in turn probably have necessitated additional modifications in the details of the coupling and the locking mechanisms, as well as in the process of insertion.

COPULATION AND MECHANICAL STRUCTURES

A close correlation exists between the process of copulation and the mechanical configuration of the copulatory structures in the agelenopsids. The proximal segments of the palpus permit the positioning of the genital bulb for copulation. The limits of articulation of these proximal segments play a major role in the locking mechanism. The tibial apophysis is an integral factor in the locking mechanism. The mechanical configurations of the proximal segments of the palpi of other agelenids indicate the probability of a similar mechanism in them also.

The mechanical configurations of the genital bulb of the agelenopsids are admirably adapted for their functions with relatively little indication of orthogenetic tendencies. The size, position, and the twisted configuration of the basal haematodocha permit ectal displacement of the genital bulb to a position directly over the epigynal atrium, while subsequent inflation provides sufficient rotation to drive the embolus to maximum total insertion within the bursa. Virtually the same morphological configuration of the basal haematodocha is found in every specimen of Entelegynae herein considered. While the petiole appears to assist in the ectal displacement of the genital bulb in the agelenopsids studied in vivo, its marked reduction in other agelenids raises some question as to its actual value in this process. The petiole is found, however, in a considerable number of other Entelegynae.

The lunate plate of the subtegulum is found in all male Entelegynae previously considered. Its articulation with the tegulum appears to be an integral part of the fundamental mechanical operation of the agelenid bulb, and probably is equally as important in the majority of other Entelegynae. The absence of anelli from the subtegula in *Wadotes* could be interpreted as being indicative of the relative unimportance of these structures in the mechanics of copulation. If the anelli are not vital, the strong development of these structures in the agelenids and certain other families of Entelegynae could conceivably be the result of orthogenesis.

The universal occurrence of the tegulum, with virtually no change in its fundamental morphological configuration throughout the Entelegynae, indicates that this structure probably is of major importance in the process of copulation in these spiders. It further suggests that the fundamental mechanics of copulation may be the same throughout the Entelegynae.

The intimate correlation existing between the conductor and the coupling cavity in the agelenopsids was discussed earlier. The importance of this physical correlation in the agelenopsids leads one to suspect that comparable mechanisms probably exist in other agelenids, and possibly in many other families of Entelegynae.

As previously indicated, a close physical correlation exists between the embolus and the bursa throughout the agelenids. The large, flattened embolus of the agelenopsids, with its ability to bend sufficiently to negotiate the turns necessary to attain maximum total insertion, conforms closely to the physical configuration of the agelenopsid bursa. Presumably similar correlations exist in other Entelegynae.

The function of the median apophysis of the agelenopsids has been discussed. The roles of the elaborate median apophyses found in other agelenids and in other Entelegynae are unknown. They may serve in the coupling and locking mechanisms; or they may be structures, with or without function, which have undergone marked orthogenesis.

STRUCTURAL MECHANICS AND COPULATORY BEHAVIOR

Most of the copulatory behavior patterns are essentially only manifestations of the mechanical aspects of copulation. Thus, the correlations existing between the copulatory structures and the mechanical details of the process of copulation are reflected in the more easily observed sexual behavior patterns.

The morphological configurations of the bursa and the embolus necessitate the assumption of the typical agelenid copulatory stance if copulation is to be accomplished by the agelenopsids. It can be demonstrated, by means of models, that coupling can be accomplished from other positions by the agelenopsids. However, the structural and functional limitations of the genital bulb preclude the possibility of bringing the locking mechanism into effective use except when the male is in the typical copulatory position. Hence it is impossible, except when the spiders are in the "normal" copulatory position, to force the embolus beyond the point of initial insertion. It is doubtful whether ejaculation could occur under these conditions. Even if ejaculation could occur, the seminal fluid would be deposited in the proximal portion of the bursa, and would tend to flow back down toward the atrium because of the inclined orientation of the bursa. Under these conditions, the entry of sufficient seminal fluid into the spermathecum to insure subsequent fertilization of any sizable number of eggs would be highly improbable.

The grasping of the patellae of the female by the male upon establishment of initial contact, the reversal of the male, the positioning of the female by the male, and finally the assumption of his own copulatory stance are all behavior patterns forced upon the male agelenopsid by the mechanical configurations of the copulatory structures. The possibility of successful copulation is largely precluded if the male deviates radically in his performance of any of these activities. The results of this investigation suggest that a similarly close correlation probably is demonstrable between the mechanics of copulation and many of the copulatory behavior patterns in other Entelegynae.

The habit of cleaning the palpi has been described in several different families of spiders. This study indicates a lubricative function for this process. The resistances encountered during the insertion of the embolus and in the process of locking warrants such a function in the agelenopsids. However, further study is indicated as necessary relative to the cleaning process, its function, and its significance.

It is becoming increasingly more evident that many of the behaviorisms seen during the copulation of spiders stem from limitations imposed on the spider by morphological configurations and the dynamics of copulatory mechanics rather than from "instinct patterns" originating within the animal's nervous system.

VALIDITY OF LOCK-AND-KEY CONCEPT

Extreme size difference will preclude both intra- and interspecific matings. It appears, however, that in agelenopsids of approximately comparable size all emboli can be introduced to the maximum total insertion position in any bursa, with one possible exception. The emboli of males of *A. pennsylvanica* are so short that maximum total insertion can be accomplished in representatives of other species only when the females are unusually small. Conversely, the bursa of females of *A. pennsylvanica* can accommodate the long emboli of males of *A. oklahoma*. Practically, however, it is questionable if a living female would submit to the treatment that such accommodation would necessitate. In the agelenopsids, neither the morphological configuration of the embolus nor that of the bursa appear to present incompatibilities which would conclusively preclude interspecific mating.

The coupling cavities found in females of *A. oregonensis* and *A. utahana* are unique in this genus because of the frequent reduction of the ectal depressions. The ectodistal process of the conductors of the males in these two species, however, are modified into a hook which fits in behind the strongly recurved margin of the coupling cavity. Thus coupling can be achieved in these two species. All other agelenopsids force the straight, fingerlike ectodistal process of the conductor into the coupling cavity depressions in order to accomplish coupling. Mechanically, it is possible for the straight conductor to be coupled to the epigynum of females of *A. oregonensis* and *A. utahana* whose ectal depressions are not too strongly reduced. Whether the males of these two species could secure a sufficiently firm attachment in the coupling cavities of other agelenopsid females in order to copulate can be determined only by further studies in vivo. The remaining features of the agelenopsid genital structures are sufficiently alike in morphological configuration that they may be eliminated as possible mechanical incompatibilities.

Thus it is possible that mechanical incompatibilities might prevent a male of *A. pennsylvanica* from successfully mating with a female of some other agelenopsid species. Mechanical incompatibilities might make interspecific mating difficult, though not necessarily impossible, between specimens of either *A. oregonensis* or *A. utahana* and the other agelenopsids. Except for extreme size differences and the aforementioned instances, there appear to be no mechanical incompatibilities which would prevent interspecific copulation within the agelenopsids. The lock-and-key concept is not applicable in the majority of agelenopsids. Additional studies, particularly studies in vivo, would be necessary in order to definitely establish whether or not the morphological features in the specimens of the species just mentioned actually do constitute mechanical incompatibilities.

While a close morphological correlation exists between the emboli of the males and the copulatory structures of the females in the other agelenids as well, the degree of this correlation does not appear to be sufficient to constitute a morphological incompatibility which could generally prevent cross mating. It appears likely that mechanical incompatibility, if it exists at all, will be found to be the exception rather than the rule within other genera of Agelenidae as it apparently is within the genus *Agelenopsis*. Gertsch (1949, p. 98) suggested that the possibility of copulation between specimens of different but closely allied groups of spiders would probably be impossible in most instances. Certainly copulation between males of the subgenus *Barronopsis* and females of any of the other species of *Agelenopsis* gives every indication of being mechanically impossible. The radically different configurations of the genital structures would preclude this possibility. Such matings, i.e., between representatives of different genera or subgenera, however, are of little importance from the evolutionary point of view. On the contrary, a functional isolating mechanism resulting from mechanical incompatibilities between specimens of two closely related species could be of major importance in the process of speciation. The preponderance of evidence indicates that the isolating mechanism in the agelenopsids is not mechanical incompatibility of the copulatory structures, but is rather of a psychological or physiological nature.

INTERSPECIFIC COPULATION

No instances of interspecific matings were obtained during the investigation herein reported, although the specimens used were known to be sexually excitable. In each instance the male became aware of the female, but apparently failed to recognize her as a potential mate. The response of the male toward a mature female of a different species was found to be essentially the same as that toward other males and immature females of his own and other species.

Kaston (1936, pp.143-144) stated:

> In those species in which the male does not court upon merely seeing the female, it may mean that either he has too low an acuity of vision and hence cannot recognize her, or that this recognition is insufficient stimulus to incite courtship. There may be a threshold value which constitutes a link in the chain of instinctive reactions. If this threshold is not attained courtship does not ensue. But if the visual stimulus is combined with another, such as touch, there will be a summation, the effect of which will bring about the response in question.

Kaston's explanation of the failure of the male vagabond spider to initiate courtship appears to explain the actions of the male agelenopsids equally as well. The fact that the males display their typical initial reactions upon seeing a female, or any other spider for that matter, indicates that they have been stimulated optically. Apparently some additional form of stimulation is needed to activate the courtship instinct in these males. As this additional stimulation is not forthcoming from the female of any species except his own, the male remains sexually passive. Thus the primary active isolating mechanism which prevents interspecific copulation in the agelenopsids appears to be either physiological or psychological in nature.

SUMMARY

1. The palpi of males in the genus *Agelenopsis* conform closely to a single, basic, mechanical configuration, with the exception of the subgenus *Barronopsis*. Furthermore, a fundamental pattern of the genital bulb exists throughout the other genera of the Agelenidae, and in representatives of 11 other families of Entelegynae.

2. The copulatory structures of females in the genus *Agelenopsis* conform closely to a single, basic, mechanical configuration. The copulatory structures in representatives of this genus are distinct from those of all other genera of Agelenidae in having plicated, saccular bursae which are directed anteriorly. The copulatory structures vary

radically in morphological configuration throughout the Agelenidae and other Entelegynae.

3. The previously unreported specific functions of the following copulatory structures are presented: the lunate plate, the middle haematodocha, the conductor, the tethering membrane, the median apophysis, the tibial apophysis, the coupling cavity, and the bursal plications.

4. The previously unreported probable functions of the following copulatory structures are discussed: the petiole, the anelli, and the diverticle.

5. During copulation the embolus of the male agelenopsid is introduced into the female's bursa copulatrix. The plications of the bursa permit it to stretch sufficiently to accommodate the embolus.

6. A close mechanical correlation exists between the genital bulb of the male and the copulatory apparatus of the female in many genera of Agelenidae. The detailed mechanical aspects of copulation are intimately correlated with the morphological configurations of the copulatory structures in the genus *Agelenopsis,* and apparently throughout the other genera of Agelenidae. The general conformity of the genital bulb to a fundamental mechanical configuration which is found in a considerable number of Entelegynae suggests that the detailed mechanics of copulation may be more or less uniform throughout the Entelegynae.

7. The mechanical configurations of the copulatory structures of the males and females in the genus *Agelenopsis* necessitate certain mating behavior patterns, or at least limit the range of variability found in these patterns. The mating process is virtually identical in all agelenopsid species observed.

8. The existence of a specific coupling and locking mechanism in the genus *Agelenopsis* is described. Coupling and locking are essential in the process of copulation in this genus. The significance of the mechanisms is discussed, as is the probability of their occurrence and their possible necessity in other Agelenidae and other Entelegynae.

9. The cataleptic state of the female is an essential feature in copulation in the genus *Agelenopsis.*

10. No examples of interspecific copulation were obtained during this investigation. The lock-and-key concept is poorly supported, if at all, by the morphological study of the genus *Agelenopsis.* There appears to be little if any mechanical preclusion of cross mating within this genus. The primary isolating mechanism preventing interspecific copulation appears to be either physiological, psychological, or a combination of both.

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APPENDIX

A. ATTEMPTED MATINGS

Family AGELENIDAE, genus *Agelenopsis*

	Males		
Females	*A. aperta*	*A. oklahoma*	*A. pennsylvanica*
A. aperta	21 (21)[1]	1 (0)	1 (0)
A. oklahoma	1 (0)	27 (27)	8 (0)
A. pennsylvanica	1 (0)	11 (0)	37 (37)

Family CLUBIONIDAE, genus *Chiracanthium*

	Males
Females	*C. inclusum*
C. inclusum	7 (7)

Family THOMISIDAE, genus *Misumena*

	Males
Females	*M. calycina*
M. calycina	11 (11)

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[1] Figures represent matings attempted (matings achieved).

B. COPULATION DATA

Family AGELENIDAE

	A. aperta	*A. oklahoma*	*A. pennsylvanica*
Copulations observed	21	27	37
Insertions observed	112	179	256
Insertions: Number per copulation.[1]	4– 16 (5)[2]	5– 18 (7)	3– 18 (7)
Engaging embolus: Duration (seconds)	1– 13 (4)	1– 11 (5)	1– 8 (3)
Engaging embolus: Attempts, including terminal	2– 16 (7)	1– 19 (9)	1– 11 (5)
Engagement of embolus to engagement of conductor (seconds)	4– 61 (13)	2– 41 (12)	2– 49 (8)
Engagement of embolus to maximum distention (seconds)	7– 73 (21)	5– 87 (16)	4– 68 (11)
Maximum distention: Duration (seconds)	3–193 (21)	2–142 (18)	3–171 (31)
Maximum distention: Zenith paroxysms (frequency/minute)	3– 43 (17)	6– 47 (13)	11– 62 (24)
Withdrawal:[3] Duration (seconds)	4– 39 (18)	2– 26 (16)	3– 34 (8)
Withdrawal: Paroxysms (frequency/minute)	7–120 (24)	16– 98 (22)	16–144 (32)
Initiation of withdrawal to conductor release (seconds)	2– 34 (11)	1– 23 (8)	2– 32 (7)
Terminus release: Attempts, including terminal	1– 31 (9)	1– 28+ (9)	1– 18 (4)
Terminus release: Duration (seconds)	1– 36 (8)	1– 23+ (9)	1– 18 (4)
Terminus release: Attempts (frequency/minute)	20–160+ (54)	34–140 (60)	22– 96 (60)
Duration of period between insertions (seconds)	4–192+ (15)	3–215+ (11)	3–138+ (9)

[1] See comment, last three lines, page 63.

[2] Figures represent minimum-maximum (mean).

[3] When disturbed, withdrawal of embolus is virtually instantaneous.