SPERMATOPHORES OF SOME NORTH AMERICAN SCORPIONS (ARACHNIDA, SCORPIONES)

Oscar F. Francke

Departments of Biological Sciences and Entomology, The Museum
Texas Tech University, Lubbock, Texas 79409

ABSTRACT

Two basic types of scorpion spermatophores are differentiated: flagelliform and lamelliform. The pre-insemination and post-insemination flagelliform spermatophore of *Centruroides sculpturatus* Ewing (Buthidae); and lamelliform spermatophores of *Didymocentrus comondae* (Stahnke) (Diplocentridae), *Vaejovis confusus* Stahnke and *Hadrurus arizonensis* Ewing (Vaejovidae); and the post-insemination lamelliform spermatophore of *Supersitionia donensis* Stahnke (Chactidae) are described and illustrated.

Comparisons with other arachnid spermatophores reveal no similarities with the flagelliform type, while the lamelliform type of scorpions is apparently homologous to the spermatophores of atemnid pseudoscorpions.

The family Buthidae is characterized by flagelliform spermatophores, by males having a complex type of reproductive system, and females having an "eight-celled" reticular ovariuterus. The families Bothriuridae, Chactidae, Diplocentridae, Scorpionidae and Vaejovidae are characterized by lamelliform spermatophores, by males having a simple type of reproductive system, and females having a "six-celled" reticular ovariuterus. The spermatophore of the family Chaerilidae is unknown, males have an intermediate type of reproductive system and females have a "six-celled" type of reticular ovariuterus. It is postulated that the Chaerilidae are more closely related to scorpions with lamelliform spermatophores than they are to buthids, and their spermatophores are probably of a lamelliform "type".

INTRODUCTION

Sperm transfer in scorpions is indirect, using a partially sclerotized spermatophore. This fact was originally reported, almost simultaneously, by four authors in 1955-1956. Since then, spermatophores representing 16 genera and five recent families have been described (Table 1).

The spermatophores are formed in the paraxial organs of the male reproductive system, the right paraxial organ producing the right half of the spermatophore (= hemispermatophore), and the left paraxial organ the left hemispermatophore. The hemispermatophores are mirror images of each other, and are always produced one pair at a time. During mating activities a sexually mature male locates a receptive female, grasps her pedipalps (and occasionally her chelicera), and proceeds to drag her along in his search for a suitable substrate onto which the spermatophore will be glued. This search may last for

several hours, and the behavior that the soon-to-mate pair goes through in this process has been described as a form of courtship (for a recent review see Garnier and Stockmann 1972). When the male finds a suitable substrate the hemispermatophores slide out of their respective paraxial organs, move past the genital atrium (where the hemispermatophores are glued together), and the spermatophore is attached to the substrate. The spermatophore contains the sperm mass in a concealed vesicle so that sperm are not exposed to a dessicating atmosphere. The male then pulls the female over the spermatophore, guiding her so that her genital opening reaches a position directly above the spermatophore. A brief struggle ensues and the female's rocking motion helps to engage the spermatophore with her genital operculi. Continued rocking by the female triggers spermatophore opening, and the sperm mass is transferred into her genital opening. The opening of the spermatophore often affects its overall appearance; consequently, spermatophores can be described in both the pre-insemination and post-insemination conditions.

The objectives of this contribution are to describe the pre-insemination and post-insemination spermatophores of *Centruroides sculpturatus* Ewing (Buthidae), *Didymocentrus comondae* Stahnke (Diplocentridae), *Vaejovis confusus* Stahnke and *Hadrurus arizonensis* Ewing (Vaejovidae); and the post-insemination spermatophore of *Superstitionia donensis* Stahnke (Chactidae).

MATERIALS AND METHODS

Scorpion spermatophores are not easy to obtain, especially if both the pre-insemination and post-insemination conditions are needed. A mating pair (with interlocked pedipalps) has to find a suitable substrate before the male will deposit the spermatophore. Very few people have observed scorpions mating in nature, and all published accounts of mating behavior are based on laboratory observations. Adult specimens have to be collected at the proper time and brought into the laboratory before the matings can be staged, and the spermatophores recovered. Consequently, most published spermatophore descriptions accompany and support information concerned primarily with studies on the mating behavior of scorpions, the descriptions are often quite brief, and the terminology used by different authors is variable. In addition, the difficulty of obtaining spermatophores accounts for the paucity of spermatophore descriptions both in species numbers and in the number of spermatophores examined per species.

The post-insemination spermatophore of *Superstitionia donensis* described below was recovered from a laboratory-staged mating, and the description of the spermatophore of *Didymocentrus comondae* is based on five spermatophores found in the field during studies of its mating behavior. The remainder of the spermatophores described in this contribution were recovered using a different, unorthodox approach that was discovered accidentally. A small number of adult *Centruroides sculpturatus* were collected at night with the aid of an ultraviolet light, and placed temporarily in a plastic bag containing a crumpled piece of newspaper (to provide hiding places) while the search for more specimens continued. The specimens were left overnight in the bag, and the following morning, when they were separated, examination of the crumpled newspaper revealed two attached spermatophores. This procedure was then repeated, yielding 10 additional spermatophores of *C. sculpturatus*, seven of *Vaejovis confusus*, and nine of *Hadrurus arizonensis*. Although this simple technique for obtaining spermatophores has not yet

been tried on other species, it should prove successful in a number of taxa. In the absence of a suitable substrate male scorpions will attach the spermatophore to newspaper, but the females are occasionally unable to retrieve the sperm (as indicated by the presence of pre-insemination spermatophores on the newspaper available to the three species reported herein).

TERMINOLOGY

The known spermatophores belong to two types based on the appearance of the free, distal end. The two types are briefly characterized below in order to introduce the terminology used in the descriptions which follow (italics indicate either new terminology, or the preferred term from those that have been used previously).

Flagelliform spermatophores.—The spermatophores of buthid scorpions are flagellate, and consist of three basic parts: (a) the base, foot, or *pedicel*; (b) the basal portion, stem, or *trunk*; and (c) the *flagellum* (Fig. 1). The pedicel attaches to the substrate and is the first part to emerge from the male during deposition. The *pedal flexure* connects pedicel and trunk. The trunk is rod-like, about five to ten times longer than its diameter, and contains the sperm vesicle. Distally the trunk (a) bears the sperm *tube*, which is ornamented with hooks, tubercles, lobes, or apophyses of importance during sperm transfer, and bears the opening of the *sperm duct*; and (b) tapers into the flagellum. The flagellum is elastic, represents the free, distal end of the spermatophore, and in some species can presumably be stretched to 40 times its length (Bücherl 1956).
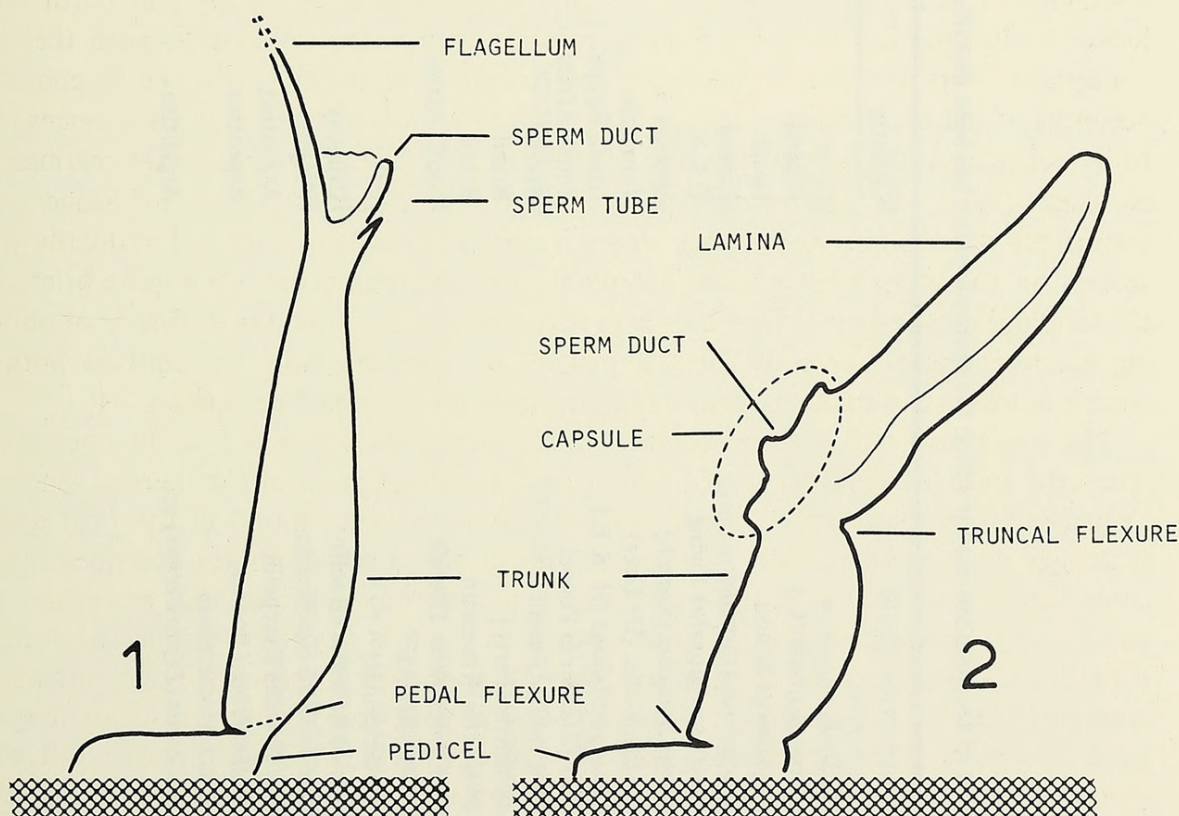
Figs. 1-2.—Diagrammatic comparison of scorpion spermatophores indicating the various structures and terminology used in the text: 1, flagelliform spermatophore; 2, lamelliform spermatophore.

Table 1.–List of scorpion species for which the spermatophore has been described.

	Country	References
FAMILY BUTHIDAE		
Androctonus australis (L.)	Algeria	Auber-Thomay 1974
Buthotus judaicus Simon	Israel	Shulov and Amitai 1958, 1959; Shulov 1958
Buthus occitanus Amoreux	France	Auber 1963
Centruroides sculpturatus Ewing	U.S.A.	Francke (this study)
Centruroides limpidus (Karsch)	Mexico	Mazzotti 1963
Isometrus maculatus (De Geer)	Tanzania	Probst 1972
Leiurus quinquestriatus (H. & E.)	Israel, Egypt	Shulov and Amitai 1958, 1959; Shulov 1958; Abushama 1968
Parabuthus planicauda Pocock	South Africa	Alexander 1959
Rhopalurus rochai Borelli	Brazil	Matthiesen 1968
Tityus bahiensis (Perty)	Brazil	Bücherl 1956; Matthiesen 1976
Tityus trivittatus Kraepelin	Brazil	Bücherl 1956
Uroplectes triangulifer Thorell	South Africa	Alexander 1959
FAMILY BOTHRIURIDAE		
Subfamily Bothriurinae		
Bothriurus bonariensis (Koch)	Uruguay	Zolessi 1956
Bothriurus bucherli San Martin	Uruguay	San Martin and Gambardella 1967
Bothriurus flavidus Kraepelin	Argentina	Abalos and Hominal 1974
Urophonius iheringii Pocock	Argentina	Maury 1968
Subfamily Brachistosterninae		
Brachistosternus (*Leptosternus*) sp.	Argentina	Maury 1975

	Country	Reference
FAMILY CHACTIDAE		
Subfamily Euscorpioninae		
Euscorpius carpathicus (L.)	Italy	Angermann 1957
Euscorpius flavicaudis (De Geer)	Italy	Angermann 1957
Euscorpius italicus (Herbst)	Italy	Angermann 1955, 1957; Angermann and Schaller 1956
Subfamily Superstitioninae		
Superstitionia donensis Stahnke	U.S.A.	Francke (this study)
FAMILY SCORPIONIDAE		
Subfamily Scorpioninae		
Opisthophthalmus latimanus (Koch)	South Africa	Alexander 1956, 1957
FAMILY DIPLOCENTRIDAE		
Subfamily Nebinae		
Nebo hierichonticus (Simon)	Israel	Rosin and Shulov 1963; Shulov and Amitai 1958
Subfamily Diplocentrinae		
Didymocentrus comondae (Stahnke)	Mexico	Francke (this study)
FAMILY VAEJOVIDAE		
Subfamily Vaejovinae		
Vaejovis confusus Stahnke	U.S.A.	Francke (this stydy)
Subfamily Hadrurinae		
Hadrurus arizonensis Ewing	U.S.A.	Francke (this study)

Lamelliform spermatophores.—The spermatophores of other scorpion families studied thus far (Table 1) are lamellate "knife-like" structures having three, and occasionally four, basic parts: (a) the pedicel, (b) the trunk, (c) the *lamella*, and occasionally (d) the *capsule* (Fig. 2). The pedicel is attached to the substrate, and connects with the trunk at the pedal flexure. The trunk is usually subcircular in cross-section, about three to five times longer than its diameter, and widens gradually away from the pedicel. The trunk houses the sperm vesicle and the capsule when one is present. The capsule is a sclerotized structure ornamented with lobes, hooks, spines, or apophyses, is traversed by the sperm duct, and is everted into the genital opening of the female during insemination. Distally the trunk (a) may be ornamented with ridges, tubercles, or apophyses of importance for emptying the contents of the sperm vesicle during insemination, and (b) connects to the lamella at the *truncal flexure*. The lamella is about as long as the trunk and is blade-like, with a "blunt" and a "sharp" edge. The blunt edge faces the substrate in the pre-insemination spermatophore and is always entire, while the sharp edge faces away from the substrate and may be notched basally. The sides of the lamella can be smooth, or have longitudinal ridges somewhere along the length.

In the descriptions that follow, the orientation of the spermatophore is given with respect to the orientation of the male: $0°$ is parallel to the substrate, with the free, distal end directed anteriorly (pedicel posterior), while $180°$ is also parallel to the substrate, but with the free, distal end directed posteriorly.

SPERMATOPHORE FORM AND FUNCTION

Centruroides sculpturatus Ewing (Buthidae)
Figs. 3-4

Spermatophore flagelliform. Pedicel very flat, 1.2-1.4 mm long, 0.7-0.8 mm wide. Trunk 4.6-4.8 mm long, 0.2 mm wide, 0.6-0.7 mm deep (Fig. 3). Trunk with short, narrow, distal sperm tube opposite flagellum base, connected to it by a thin, partially
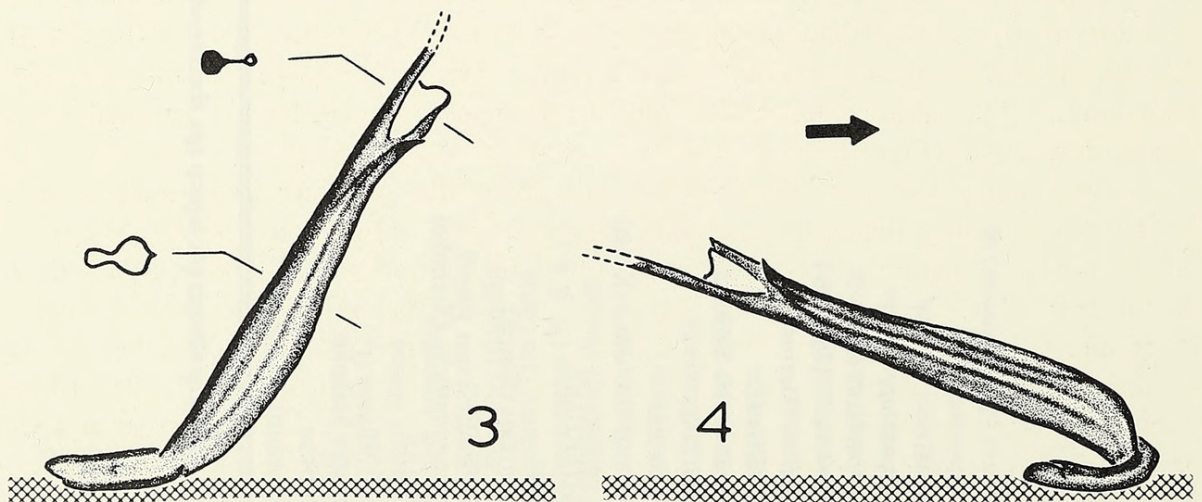
Figs. 3-4.—Spermatophore of *Centruroides sculpturatus* Ewing, from Maricopa Co., Arizona: 3, lateral aspect of pre-insemination spermatophore; 4, lateral view of post-insemination spermatophore. The flagellum is not shown. Arrow indicates direction faced by male.

sclerotized membrane. Sperm tube basally with paired, strongly sclerotized *subdistal hooks*. Flagellum subcircular in cross-section, diameter about 0.1 mm, length unknown.

During mating the male lowers himself to the substrate and attaches the pedicel. The body is then raised, pulling out the spermatophore trunk which forms an angle of 55°. At this stage the subdistal hooks are directed prolaterally (Fig. 3), and incapable of engaging the genital operculi of the female. The male retreats slowly backwards (pulling the female along), and throughout this backward motion the flagellum remains partially inside the genital opening of the male, pulling the trunk of the spermatophore and forcing it to bend over backwards at the pedal flexure (Fig. 4). Rotation of the trunk brings the subdistal hooks into an upward facing position favorable for insemination. Simultaneously the male pulls and guides the female over the spermatophore so that her genital operculi are eventually positioned above, or slightly beyond, the subdistal hooks. The male rocks the female so that her genital operculi engage the subdistal hooks, and are forced open, allowing the sperm tube of the spermatophore to be inserted into the genital opening. Continued rocking of the female by the male produces longitudinal compressional stresses on the trunk of the spermatophore, forcing sperm through the sperm duct and into the genital opening of the female.

Immediately after insemination the male releases the female and moves away, breaking the flagellum somewhere along its length (although the break usually occurs near the base). The post-insemination spermatophore does not spring back to its original position, but rather remains bent along the pedal flexure at an angle of about 160° (Fig. 4).

Didymocentrus comondae Stahnke (Diplocentridae)
Figs. 5-7

Spermatophore lamelliform. Pedicel 0.7-1.0 mm long, 0.4-0.5 mm wide. Pedal flexure very distinct. Trunk 1.4-1.5 mm long, subcircular in cross-section with median diameter 0.9-1.1 mm. Truncal flexure marked ventrally by sharp infolding, laterally by paired symmetrical inflections (representing most heavily sclerotized areas of spermatophore), and dorsally by broad median lobe projecting distally over sperm duct opening (Figs. 5-6). Capsule simple, consisting of symmetrically folded invagination (Fig. 7). Lamella 2.7-3.0 mm long, 0.3-0.4 mm wide, 0.5-0.6 mm deep; appears rather flexible terminally and curves downwards (Figs. 5, 7).

During mating the male attaches the pedicel to the substrate and slowly retreats backwards, expelling the entire spermatophore while pulling the female over it. The trunk of the pre-insemination spermatophore forms an angle of about 130°, and the lamella of about 140° (Fig. 5), and is already properly oriented for insemination with the sperm duct directed upward. As the female moves over the spermatophore, and her genital opening is above or slightly beyond it, the sharp (dorsal) edge of the lamella fits into the groove between her genital operculi. The male pushes the female backwards, and the lamella forces her genital operculi to open, guiding them into the respective lateral inflections of the truncal fexure. The backward thrust of the genital operculi on the spermatophore tends to bend the spermatophore forward along the pedal flexure. As this bending motion is initiated the lamella collides against the venter of the female, so that the spermatophore is folded upon itself. As the spermatophore is folded, the pedicel

exerts pressures upon the dorsal side of the trunk and the blunt (ventral) edge of the lamella exerts pressures upon the ventral side of the trunk, resulting in the eversion of the capsule and the ejection of the sperm mass into the exposed genital opening of the female.
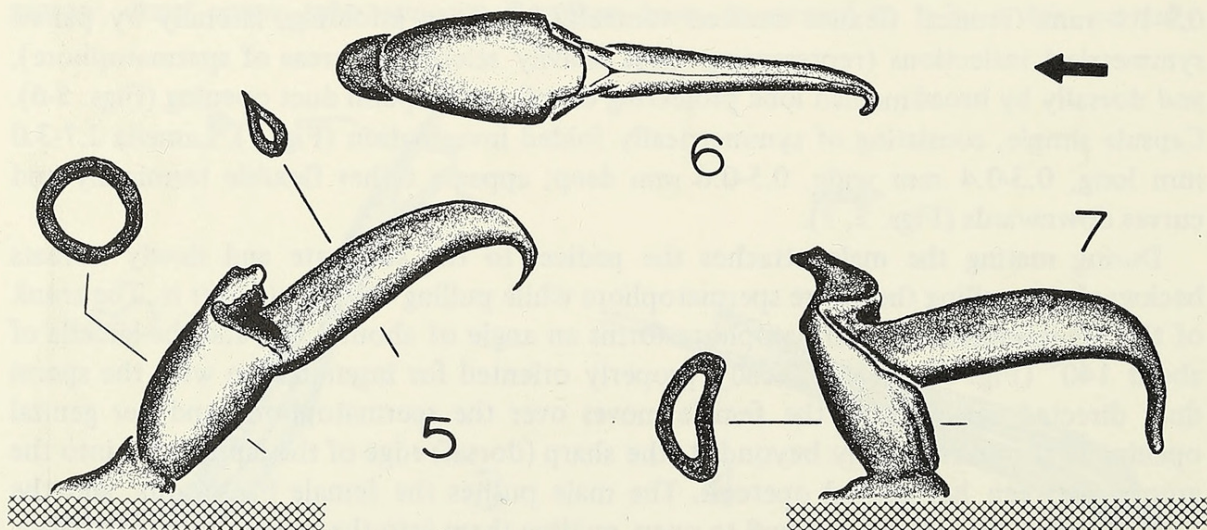
The post-insemination spermatophore does not resume its original position. The trunk, having been bent forward, now forms an angle of 70°; the lamella, having been bent downward, forms an angle of 170°; and the capsule remains in the everted position (Fig. 7).

Superstitionia donensis Stahnke (Chactidae)
Figs. 8-9

Spermatophore lamelliform. Pedicel 1.2 mm long, 0.6 mm wide. Trunk about 1.2 mm long, 0.6 mm wide, distally bearing paired small dorsal spiniform processes, medially directed, which project slightly over sperm duct opening (Fig. 9). Capsule absent. Lamella 1.8 mm long, width varies from 0.35 to 0.50 mm, depth from 0.30 to 0.40 mm; resembling "T" - beam in cross-section. Dorsal edge of lamella asymmetrically sigmoid in profile. Right and left halves (hemispermatophore lamellae) curl outwards ventrally, producing "T" - beam effect on lamella (Fig. 8). Curl extends ventrally from tip to base of lamella, across truncal flexure, ending dorsally in paired recurved hooks slightly distal to sperm duct opening (Fig. 9).

The pre-insemination spermatophore of *S. donensis* is unknown, and the events leading to insemination can not be reconstructed. In the post-insemination spermatophore the trunk forms an angle of about 130°, and the lamella of about 185° with the ventromedian edges of its two halves spread apart subdistally (Fig. 8). There appears to be no bending at the pedal flexure, and sperm ejection may be accomplished solely by bending along the truncal flexure.


Figs. 5-7.—Spermatophore of *Didymocentrus comondae* (Stahnke), from Baja California Sur, Mexico: 5, lateral aspect of pre-insemination spermatophore; 6, dorsal aspect of pre-insemination spermatophore; 7, lateral aspect of post-insemination spermatophore. Arrow indicates direction faced by male.

Vaejovis confusus Stahnke (Vaejovidae)
Figs. 10-14

Spermatophore lamelliform. Pedicel 1.1-1.2 mm long, 0.8-1.1 mm wide. Pedal flexure well defined (Figs. 10, 11). Trunk 1.9-2.0 mm long, subcircular in cross-section with median diameter 1.1-1.2 mm (diameter increases distally to accomodate capsule). Truncal flexure marked ventrally by moderate transverse fold, laterally by paired symmetrical inflections, dorsally by capsule (Figs. 10, 11). Transverse ridges marking beginning of lateral inflections extend ventrally along blunt edge of the lamella, and dorsally along base of lamella for short distance before ending abruptly in paired, heavily sclerotized recurved hooks (Figs. 10, 13, 14). Lamella 3.5-3.8 mm long; cuneiform in cross-section, median width 0.20-0.25 mm, median depth 0.5-0.6 mm.

During mating the male attaches the pedicel to the substrate and backs away slowly, expelling the entire spermatophore. The trunk of the pre-insemination spermatophore forms an angle of about 130°, and the lamella of about 145° (Fig. 10), with the sperm duct opening directed upward. As the female moves over the spermatophore, the lamella fits into the groove between her genital operculi and acts as a guide. The female is rocked by the male, and during one of the backward strokes her genital operculi slide into the lateral inflections at the truncal flexure, forcing the operculi to open and engage the dorsal hooks of the spermatophore. Simultaneously the spermatophore bends along the pedal and truncal flexures (Figs. 13, 14), the capsule is everted along its basal hinge, and the sperm mass is ejected into the exposed genital opening of the female.
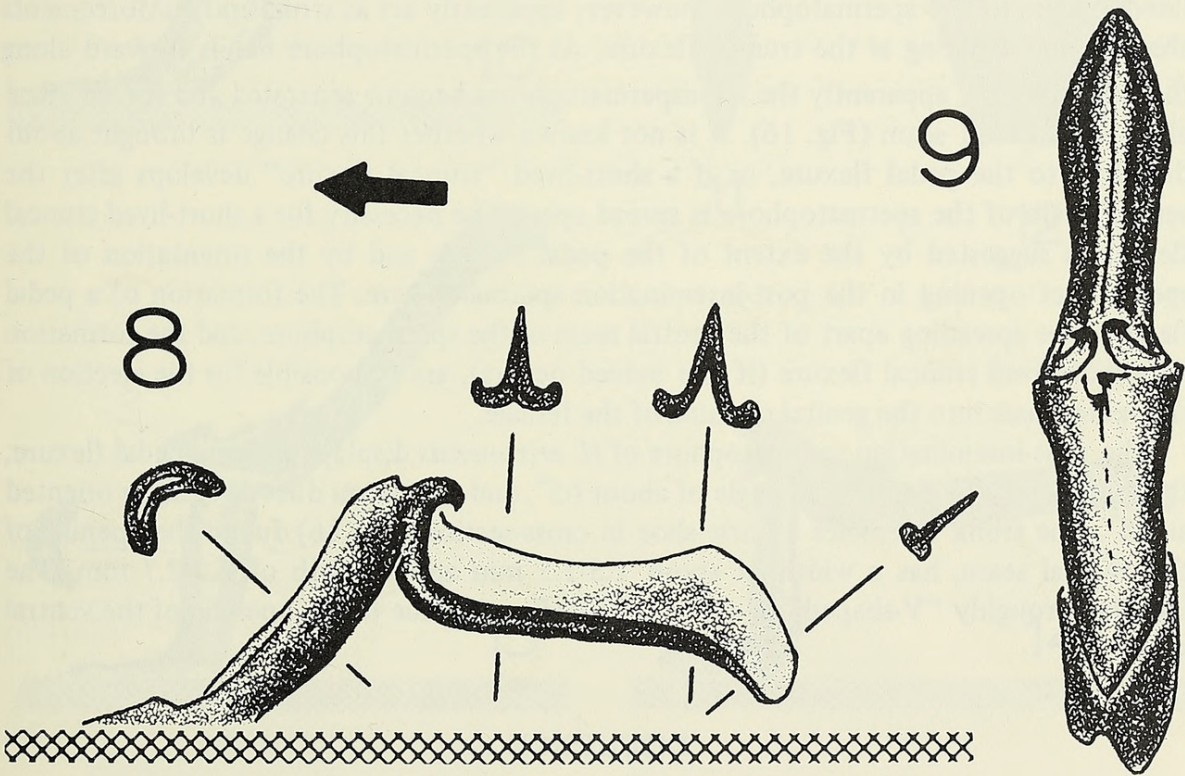
Figs. 8-9.—Post-insemination spermatophore of *Superstitionia donensis* Stahnke, from Cochise Co., Arizona: 8, lateral aspect; 9, dorsal aspect. Arrow indicates direction faced by male.

The post-insemination spermatophore remains somewhat folded upon itslef, with the trunk forming an angle of about 90°, the lamella of about 180°, and the capsule remains everted.

Hadrurus arizonensis Ewing (Vaejovidae)
Figs. 15-16

Spermatophore lamelliform. Pedicel quite massive, 4.0-5.0 mm long, 2.2-2.6 mm wide. Pedal flexure very conspicuous. Trunk 4.0-5.0 mm long, 1.0-1.3 mm wide, 2.0-2.3 mm deep, deviating considerably from subcircular cross-sectional plan previously encountered. Trunk characterized anterodorsally by sharp longitudinal ridge along hemis-permatophore-seam, posteroventrally by paired longitudinal flanges and median longitu-dinal depression (Fig. 15). Truncal flexure marked ventrally by feeble transverse fold, dorsally by sperm tube, laterally by two pairs of heavily sclerotized longitudinal ridges: mediolateral ridges straight, ending gradually along lamella; dorsolateral ridges curve dis-tally, ending near sperm duct opening (Fig. 15). Lamella 4.0-4.5 mm long, 1.0-1.5 mm wide, 2.3-2.7 mm deep, with posteroventral edge weakly flanged.

In the recently deposited spermatophore both trunk and lamella form an angle of about 150°. During mating the anterodorsal edge of the lamella functions as a guide in the same manner previously described for other lamelliform spermatophores. When the female is pushed backward her genital operculi slide into the grooves located between the paired ridges of the spermatophore, and continued backward pressure eventually forces the genital operculi to open and the spermatophore to bend along the pedal flexure. The lateral ridges of the spermatophore, however, apparently act as structural reinforcements that prevent bending at the truncal flexure. As the spermatophore bends forward along the pedal flexure, apparently the hemispermatophores become separated and spread apart along the ventral seam (Fig. 16). It is not known whether this change is brought about due only to the pedal flexure, or if a short-lived "truncal flexure" develops after the ventral seam of the spermatophore is spread apart. The necessity for a short-lived truncal flexure is suggested by the extent of the pedal flexure and by the orientation of the sperm duct opening in the post-insemination spermatophore. The formation of a pedal flexure, the spreading apart of the ventral seam of the spermatophore, and the formation of a short-lived truncal flexure (if one indeed occurs), are responsible for the ejection of the sperm mass into the genital opening of the female.

The post-insemination spermatophore of *H. arizonensis* displays a strong pedal flexure, the trunk and lamella form an angle of about 65°, and the sperm duct opening is oriented at 15°. The trunk resembles a horse-shoe in cross-section (Fig. 16) due to the opening of the ventral seam, has a width of about 1.3-1.5 mm and a depth of 2.3-2.7 mm. The lamella is roughly "V-shaped" in cross-section (Fig. 16) due to the opening of the ventral seam.

DISCUSSION

Indirect sperm transfer by means of spermatophores occurs in six Recent orders of arachnids: scorpions, pseudoscorpions, uropygids, schizomids, amblypygids, and acarines (Weygoldt 1975). Scorpion flagelliform spermatophores do not resemble, either morpho-logically or functionally, any other arachnid spermatophores. Scorpion lamelliform sper-

matophores, however, show strong morphological and functional similarities with those of atemnid pseudoscorpions (Cheliferoidea, Atemnidae). Although pseudoscorpion spermatophores are diverse (Weygoldt 1969, 1975), those of *Atemnus politus* (Simon) have: (a) a distinct pedicel and trunk connected by a well marked pedal flexure; (b) "paired, wing-like structures under the sperm package" (Weygoldt 1969:63) that closely resemble the lamella of scorpion spermatophores, and may be homologous to them; (c) a distinct truncal flexure and an eversible capsule; and (d) insemination apparently proceeds in a similar way to that described above for *Vaejovis confusus*, as suggested by examination of
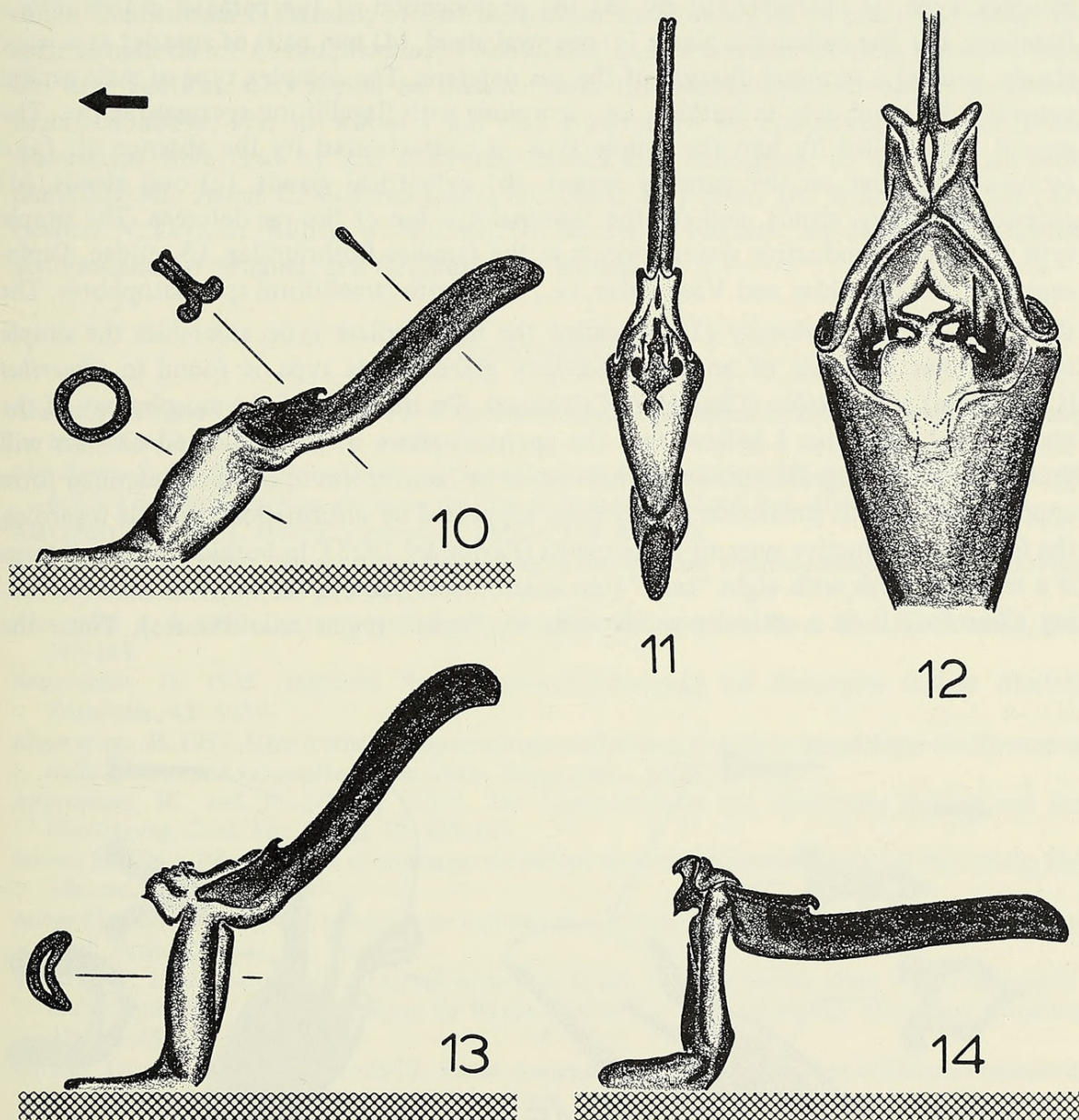
Figs. 10-14.—Spermatophore of *Vaejovis confusus* Stahnke, from Maricopa Co., Arizona: 10, lateral aspect of pre-insemination spermatophore; 11, dorsal aspect of pre-insemination spermatophore; 12, detail of dorsal aspect showing the infolded capsule; 13, lateral view of spermatophore during initial stages of insemination showing the partial eversion of the capsule; 14, lateral aspect of post-insemination spermatophore. Arrow indicates direction faced by male.

its pre-insemination and post-insemination states (Weygoldt 1969:63, fig. 57). The impli-cations of this apparent homology in spermatophores of scorpions and pseudoscorpions with respect to their phylogenetic relationships and the classification of the Arachnida will be explored elsewhere.

The spermatophores of representatives of six of the seven currently recognized families of Recent scorpions are known. The family Buthidae is characterized by flagelliform spermatophores, and the families Bothriuridae, Chactidae, Diplocentridae, Scorpionidae and Vaejovidae by lamelliform spermatophores.

Pavlovsky (1924) studied the male genital apparatus of 28 genera of scorpions and found three distinct morphological types among them. The first type, which he called the complex type, is characterized by (a) the prolongation of the paraxial organs into a flagellum, (b) one cylindrical gland, (c) one oval gland, (d) two pairs of anterior accessory glands, and (e) a terminal dilation of the vas deferens. The complex type of male genital apparatus is found only in buthids, i.e., scorpions with flagelliform spermatophores. The second type, called by him the simple type, is characterized by the absence of: (a) a terminal flagellum on the paraxial organs, (b) cylindrical glands, (c) oval glands, (d) anterior accessory glands, and (e) the terminal dilation of the vas deferens. The simple type of male reproductive system occurs in the families Bothriuridae, Chactidae, Diplo-centridae, Scorpionidae and Vaejovidae, i.e., those with lamelliform spermatophores. The third type, which Pavlovsky (1924) called the intermediate type, resembles the simple type but has one pair of anterior accessory glands. This type is found in *Chaerilus* (Chaerilidae) and *Calchas* (Chactidae, Calchinae). On the basis of the morphology of the male genital apparatus I believe that the spermatophore of *Chaerilus* and *Calchas* will probably not be flagelliform, but rather should be lamelliform or of an undescribed form approaching it. This prediction is indirectly supported by information available regarding the female reproductive systems in scorpions (Pavlovsky 1925). In buthids the ovariuterus is a reticular mesh with eight "cells" (ten anastomoses), and in the other families (includ-ing *Chaerilus*) it is a reticular mesh with six "cells" (eight anastomoses). Thus, the
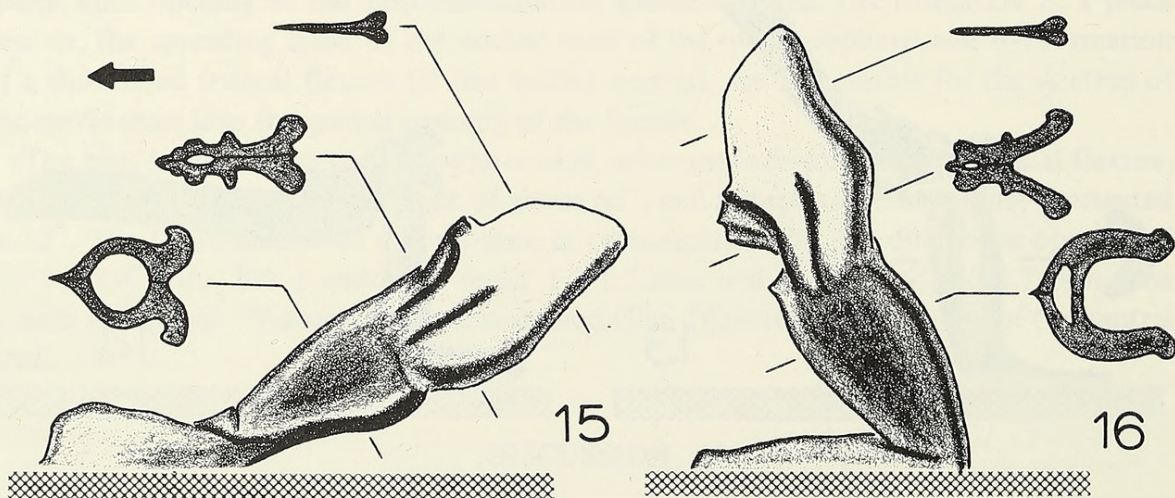
Figs. 15-16.—Spermatophore of *Hadrurus arizonensis* Ewing, from Maricopa Co., Arizona: 15, lateral aspect of pre-insemination spermatophore; 16, lateral aspect of post-insemination spermato-phore. Arrow indicates direction faced by male.

Chaerilidae appear to be more closely related to those scorpions with lamelliform spermatophores than they are to those with flagelliform spermatophores. The significance of these findings regarding the phylogeny and classification of the order will be discussed in a future contribution.

ACKNOWLEDGEMENTS

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