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THE TEXAN KÆNENIA.¹

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THIS most interesting microthelyphonid was discovered last May in the neighborhood of Shoal Creek, near Austin, Texas, under stones in company with Campodea, Japyx, and Scolopendrella. A short description of it was given by Dr. W. M. Wheeler in the November *Naturalist*, under the title "A Singular Arachnid (*Kænenia mirabilis* Grassi) occurring in Texas." The writer believed the Texas species to be identical with the Sicilian one figured and described by Drs. Hansen and Sorensen, and therefore wrote of it under that name. A number of specimens have since been examined *in toto* and in sections, and some interesting results have been obtained. It did not seem probable that the Texan *Kænenia* had been imported, yet it seemed less probable, though our climate is much like that of southern Europe, that the two species were identical. Close microscopic examination has shown them to be two distinct species of the family *Kæneniidæ*.

Kænenia has since been found in Siam and Paraguay and, like all archaic types, it will doubtless be found to be cosmopolitan

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in its distribution. A young Danish zoölogist has recently found in Siam a distinct species of *Kœnenia* which Dr. Hansen is to describe. Dr. Silvestri, the discoverer of the species from Paraguay (*K. grassii*), has promised me a few of his specimens in return for the Texan species, which I hoped to have for comparison before this paper was finished. I have likewise been unable to collect any *K. parvula*,¹ of which species Dr. Wheeler has found a single specimen, which he has briefly described in his paper (p. 233). When descriptions of these species are published a more correct idea can be framed of the valuable taxonomic characters of the hitherto unknown order.

Kœnenia wheeleri n. sp.

I desire now to name our principal Texan form after its discoverer, Dr. Wheeler, and to give along with its internal structure a short description of the characteristics which set it apart as a new and distinct species.

In the beginning I may say we have been more fortunate than Drs. Hansen and Sorensen in being able to distinguish the two sexes. It hardly seems possible that the males of Grassi's species could be so rare when they are so abundant in our species. In fact, in the material collected in the fall, the males predominated. Very few females were to be had then, and those few were so small and insignificant that it was thought they were the males. The criterion taken for distinguishing the sexes in this material was the opaque glistening body in the second abdominal segment of the female, the receptaculum seminis of Hansen. Unfortunately the seminal vesicles of the male are situated in the same region and have much the same appearance; hence Dr. Wheeler, in his interesting paper, was misled into thinking that the male was of the other sex. It was not until fresh material was collected this spring and sections made that the mistake was discovered. In size and general form the sexes are alike, and it was only after examining sections that one could say for the first time that the animal possessing the more complex reproductive appendages is the male.

¹ I have the pleasure also of giving this species its name.

External Anatomy.

On comparing *K. wheeleri* with the figures and descriptions of Drs. Hansen and Sorensen for *K. mirabilis* the following differences are apparent: (1) the number and position of the hairs of the body; (2) the appendages of the reproductive orifice situated between the second and third segments of the abdomen; (3) the three pairs of prominent orifices on the ventral surface of segments four, five, and six, through which the lung sacs are everted; (4) the lateral sense organs of the cephalothorax; (5) the number of teeth on the two last joints of the chelicerae.

The hairs over the ventral surface of the abdomen of the Texan species are more numerous and are distributed in a manner quite different from those over the abdomen of the old-world form. In the second segment of the female there are three rows of plumulose setæ. The first row of six runs across the ventral surface anterior to the middle line and is continuous with the hairs of the dorsal surface. These form a belt around the second segment. The second row of six arises along the base of the triangular flap of the reproductive orifice. The third row is so irregular that it can scarcely be called a row. Here the hairs follow in a fashion the other two sides of the triangular appendage. Fig. 2 is a camera drawing of this portion of a specimen which has been treated with potassium hydrate. The figure clearly shows the arrangement of hairs over this region of the female. The dotted lines of the figure represent the portion of the organ which can be seen only by focusing through the triangular appendage.

In segment two of the male there are three primary rows of plumulose hairs. The first row, consisting of from four to six small setæ, runs across the ventral surface at about the middle of the segment and continues dorsally to form the circular row



FIG. 1.—Ventral surface of the abdomen of male *K. wheeleri*.

of setæ. This second row of four small setæ extends across the middle of the shield-shaped appendage of the reproductive organs. The third set consists of two secondary groups, the first of which, containing eight hairs, runs across a sort of hem attached to the lower margin of the shield-shaped organ. The second set is made up of large plumulose spines arising from the tips of ten papillæ, four of which spring from the edge and six from under the edge of the hem. Fig. 3 is a careful camera drawing of this region of the male. The first row of setæ not on the reproductive appendage is not figured.

Segment three in both male and female has on the two blades of the reproductive appendages irregularly placed hairs which are of varying lengths. In a line posterior to the middle of the segment are eight other setæ in a row continuing with those of the dorsal surface to form the setigerous belt of segment three.

Most remarkable are the differences between segments four, five, and six of *K. wheeleri* and the corresponding segments of *K. mirabilis*. Concerning the fourth segment of Grassi's species, Drs. Hansen and Sorensen have written, "Provided on the ventral side in front of the middle with a wart-like protuberance which bears six stiff setæ, almost spines (*aculei*), arranged in two transverse rows, the foremost of which is arched and has four spines. Grassi seems to consider these spines sensory organs, an opinion we by no means share." In *K. wheeleri* segment four is provided on its ventral side with three pairs of hair groups. The first pair consists of three long backward-pointing setæ on each side of and near the midventral line. These setæ are situated on delicate chitinous flaps of the integument which arise in front of the middle of the segment. The second pair is made up of four much shorter backward-curving hairs arranged in an arched transverse row near the middle of the segment to the right and left, respectively, of the first pair. These hairs are most evidently for the protection of the delicate lung sacs when they are ejected, and for protection of their orifices when they are drawn in. The third pair consists of two small setæ in the same line and lateral to those of the second group. The former are continuous with the belt of setæ encircling the whole segment.

Of the fifth segment nothing is said concerning *K. mirabilis*, while the figures show it to be like segment seven. This is decidedly not the case in our species. The fifth segment is — as far as the setæ are concerned — a facsimile of the fourth.

Again, concerning the sixth segment of the Sicilian species, the Danish investigators write, "It is furnished on its ventral side with a rather strongly protruding wart, bearing a somewhat arched transverse row of six forward-curving setæ. We do not think these to be sensory organs either." In *K. wheeleri* the ventral surface of the sixth segment is in reality less prominent than that of the two preceding segments, for it is lacking in the first group of large hairs situated on the flaps on each side of the midventral line; the flaps, however, are retained. Fig. 1 is a ventral view of the abdominal exoskeleton of a male *Kœnenia*, which has been thoroughly cleaned of its cellular contents in KOH. In this specimen all six of the sacs are thrown out, and the protective function of the groups of four hairs is quite evident. All the setæ shown in this figure are plumulose; but under a magnification of about 120 diameters they barely appear to be so, and I did not attempt to represent this condition in the drawing.

It was only after repeated attempts that I succeeded in obtaining clear views of the reproductive appendages. In both sexes, segments two and three are conspicuous for their relatively enormous appendages. In the female the midventral surface of the second segment projects downward and backward into a triangular appendage, which is not emarginate at its apex, as in *K. mirabilis*. This projection almost covers a couple of heavily chitinized downward projections of the third segment.

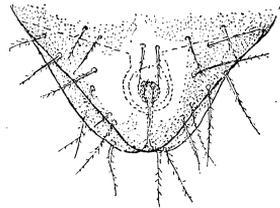


FIG. 2. — Reproductive appendages of female *K. wheeleri*. The round sac in the center of the figure is the receptaculum seminis.

The receptaculum seminis opens between these two appendages, while the reproductive organs open further forward into the vagina formed by the three appendages. Fig. 2 shows what I take to be the receptaculum seminis, while the reproductive orifice only shows in section. The male appendages are very

complex and difficult to explain. Fig. 3 will aid in making the account clear. The appendage of the second segment represents in surface view a truncated conical flap having at its base a hem which is notched in the midventral line. The hem near the outer sides of the flap projects into two papillæ, each of

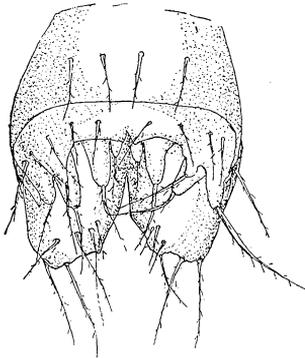


FIG. 3.—Reproductive appendages of male *K. wheeleri*.

which terminates in a heavy spine. Projecting from the under surface of the hem are two pairs of large and one pair of small papillæ, with their corresponding spines. This papillate appendage partially conceals two trowel-shaped, strongly chitinized, downward and backward directed projections of the third segment. The accessory glands and vasa deferentia open near together, in the median line, where the posterior surface of the unpaired appendage is continuous with the anterior surfaces of the paired appendages.

Another important specific difference seems to be in respect to the lung sacs, organs which are evidently much more prominent in the Texan species. These organs must, in fact, be entirely lacking in *K. mirabilis*, for such careful observers as Drs. Hansen and Sorensen could not have entirely overlooked them. On examination of a few of our specimens, one cannot fail to observe peculiar little sacs projecting from the ventral surface sometimes of the fourth, sometimes of the fifth, sometimes of the sixth, and occasionally from all three segments. Again a specimen may be found in which all six sacs are invaginated, giving it the appearance of possessing three pairs of stigmatic apertures. Of these organs Dr. Wheeler writes: "In many specimens a delicate sac may be found evaginated from under a flap on all three segments. These sacs are in all probability lung books. They appear to be the only respiratory organs of *Koenenia* apart from the delicate integument, which in so small an animal must of itself nearly suffice for respiratory purposes. If I am correct in regarding the above-described

sacs as lung books, they must represent those organs in an extremely simple form, in a form, moreover, which strongly suggests their origin from invaginated appendages serially homologous with those of the cephalic and thoracic segments."

The two anterior sensory organs do not appear different in any respect from the same organs of *K. mirabilis*. The lateral organs, however, though situated in about the same place, consist of three sensory rods each, instead of the two blades. These are short-pointed rods pressed close together and projecting, when at rest, forwards and outward. Fig. 4 is a camera drawing of these lateral sensory hairs, under a high magnification. In cross-section the hairs appear as three rings in contact with one another. I am unable to make out on the surface of these organs anything more than the minute projections which are found over the entire surface of the animal's body.

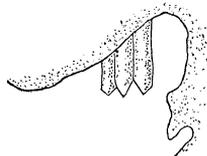


FIG. 4. — Lateral sense hairs.

The second and third joints of the chelicerae, which form pinchers, in specimens examined for this special purpose, were found to be each provided with eight teeth. The teeth of the fixed portion are long and very acute, with barbs at the base; while the teeth of the movable joint are short, broad, and blunt.

The above are the most evident differences of the two species of *Koenenia*, unless it be that there are more segments in the caudal flagellum of one than of the other. I have examined a number of complete specimens of both males and females, and find in every case that the tail is made up of fifteen segments. Grassi states for his species, which has been redescribed for all other points except this, that it possesses thirteen or fourteen joints.

Internal Anatomy.

In considering the internal anatomy of this minute animal, several difficulties have arisen which I fear I have not entirely surmounted. The extreme minuteness of the cells of the very delicate tissue enclosed in the comparatively heavy chitinous case makes microscopic study rather unsatisfactory.

Integument.— Drs. Hansen and Sorensen state, “As a peculiarity in *Kœnenia*, we think right to emphasize at once that its skin is but slightly chitinized, especially on the abdomen, where, consequently, there is no distinction between the (dorsal and ventral) plates and the pleura; so the expansion, which the abdomen must be capable of allowing, probably depends on the elasticity of this thin chitin itself.” I think had these gentlemen attempted to section *Kœnenia* they would not have been so emphatic about the thinness of its exoskeleton. The chitinous cuticle, which rests on a delicate hypodermis, corresponds more nearly to that of most spiders, in that over the expanded abdomen it does not appear to form special plates. It also corresponds to spiders, in that it is a flexible or accordion-plaited covering, the folds of which run parallel with the long axis of the body. This arrangement thus allows of great expansion of the abdomen, its function being evidently the same as the folds in the late integument of the abdomen of *Thelyphonus*. Over the chelicerae labrum-hypostome and reproductive appendages the chitin is thick and yellow, while between the joints it is very thin. In the floor of the mouth the chitin is thrown into folds, running at right angles to the long axis of the body. This, in sagittal sections of the animal, gives it the appearance of possessing teeth. The entire chitinous surface of the animal is not smooth, but under high magnification appears to be covered with small dot-like elevations.

Kœnenia wheeleri is remarkable for the comparatively thick covering of hairs arising from its flexible cuticle. The smallest hairs are like down, covering the anterior surface of the labrum and the under surface of the hypostome. The longest and most delicate are the tactile hairs of the sixth, seventh, and eighth segments of the third pair of appendages. The broadest and heaviest spines are situated on the underside of the proximal joint of the chelicerae; otherwise the setae are distributed as Dr. Wheeler has already shown. All the hairs over the body of *Kœnenia*, with the exception of the tactile and the very minute ones on the mouth appendages which are too delicate to be made out, are microscopically plumulose.

The muscles of *Kœenenia* are decidedly striated, like those of insects. They represent a condition of musculature which would be expected in so small and primitive an animal. Worthy of note are the two pairs of simple dorsal and ventral muscles of the abdomen and thorax. Other important muscles are those running from the roof and side of the thorax to the chelicerae. The muscles of the appendages need not be described, with the exception of those extending from the side of the thorax to be inserted on the thoracic appendages. These muscles arise on the sides of the thorax, opposite to their corresponding legs, and, crossing over just above the subœsophageal ganglion, become inserted on their proximal joints. The only other muscles that need to be mentioned are the primitive dorso-ventral muscles of the thorax and abdomen. These are decidedly a very striking feature in the abdomens of arachnids.

Nervous System.—One of the most singular things about *Kœenenia* is its large proportion of concentrated nervous substance. The concentration of the ganglia is almost equal to that of the *Araneidæ*. In this respect *Kœenenia* is even more specialized than *Thelyphonus*. There seems to be no reduction of nervous element here due to the absence of eyes, but, like all primitive types, it retains its cephalothoracic ganglia unmodified. The brain and subœsophageal ganglion unite to form one large mass perforated by the small œsophagus. The brain is enormous, occupying the entire dorsal portion of the head above the level of the œsophagus. It innervates the median and lateral sense organs, the labrum, and chelicerae. The subœsophageal ganglion covers the entire floor of the head and thorax, and shows in section swellings corresponding to each of the five pairs of appendages. With a slight constriction at the waist, the subœsophageal ganglion connects with a single abdominal ganglion which is situated in segments two and three, dorsal to the reproductive orifice. From this ganglion, nerves run to all parts of the abdomen and tail. In its nervous system *Kœenenia* is thus very unlike the *Scorpionidea* and differs from *Thelyphonus* in the relative size of the cephalothoracic ganglion and in the situation of the

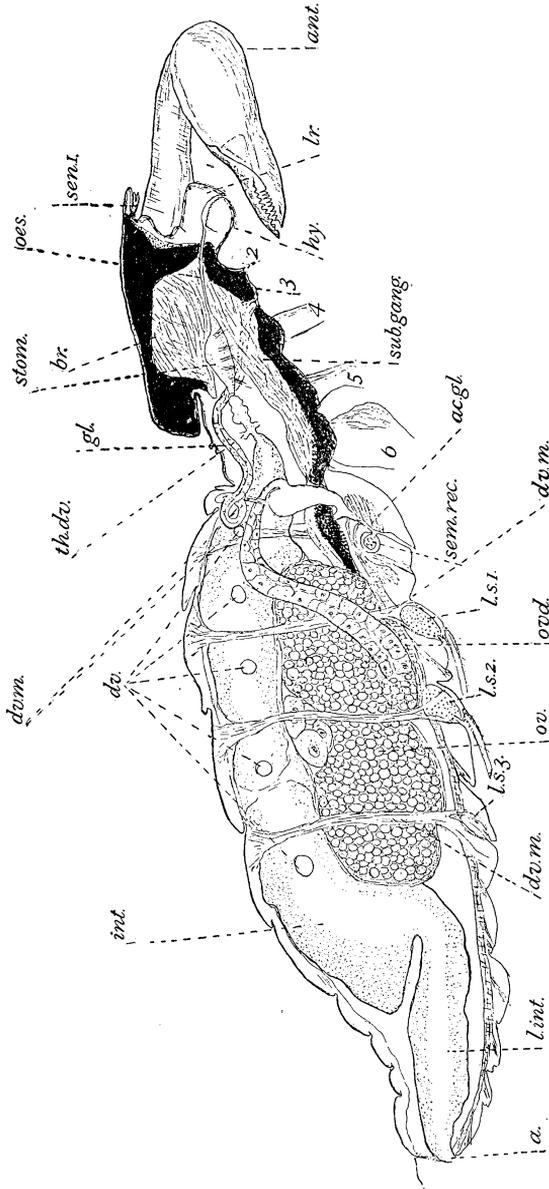


FIG. 5.—Diagrammatic sagittal section of a female *K. wheeleri*. *ant.*, chelicere; *ac.gl.*, accessory gland; *a.*, anus; *br.*, brain; *sub.gang.*, sub-oesophageal ganglion; *dv.*, diverticula; *dv.m.*, dorso-ventral muscles; *th.dv.*, thoracic diverticulum; *gl.*, coxal gland; *ly.*, hypostome; *br.*, labrum; *int.*, intestine; *l.s.1, 2, 3*, lung sacs; *ovs.*, oesophagus; *ov.*, ovary; *ovd.*, oviduct; *sem.rec.*, seminal receptacle; *sens.*, anterior sensory hairs; *stom.*, stomach.

abdominal ganglion, which has not been drawn up toward the head in the latter, but remains in the eighth segment.

Digestive System. — The downward-curved, crescentic mouth leads into a strongly chitin-lined pharynx. This in turn runs into a very delicate œsophagus which penetrates the cephalothoracic nerve mass, only to dilate immediately into a pouch-like sucking stomach. This stomach is roofed over by the brain, while underneath it the subœsophageal ganglion extends. At the sides the brain is not continuous with the subœsophageal ganglion, thus leaving a passageway for muscles arising from the sides of the cephalothorax to enter and attach themselves to the stomach. When expanded to its utmost the stomach fits snugly in between the two ganglia, but when pulled on by the muscles it is flattened dorso-ventrally. The comparatively thick-walled stomach opens through a valve-like constriction into the exceedingly thin-walled intestine. The intestine, before it leaves the thorax, gives off a pair of small diverticula. It then passes into the abdomen, becoming much dilated, and giving off five shallow metameric pairs of diverticula, from the third to the seventh segments inclusive. These diverticula are very diagrammatically represented in Figs. 5 and 6, as are all the other organs, save the brain and the anterior portion of the digestive tract as far back as to the first pair of diverticula. At about the eighth segment the thick-walled large intestine begins. Unlike *Thelyphonus*, no Malpighian tubules are present, opening into the hind gut, before it terminates at the anus. On this point *Kœenenia* is most primitive, since it seems not yet to have reached the stage in which intestinal diverticula become modified as excretory organs. There are also no salivary glands present; these would hardly be of any use to an animal living under such simple conditions. The intestine and diverticula are invariably filled with food particles, which have the appearance of yolk granules. Strange to say, — because of the conditions under which *Kœenenia* is found, — throughout the entire digestive tract no dirt ever appears. This goes to prove that the food is probably derived, as Dr. Wheeler has already suggested, from the eggs of animals with which it associates. The

digestive tract is thus admirably constructed for such an illegitimate practice as egg-sucking.

Excretory System. — I have succeeded in tracing the pair of tubular glands, “*tappezzata d’ un semplice strato di cellule epiteliali,*” of which Grassi speaks. According to him, these glands extend through a large part of the cephalothorax, and perhaps have their orifice in front of the third pair of limbs. These excretory organs in reality arise in the second segment of the abdomen, and after forming one or two convolutions run into and straight through the thorax, to terminate between the second and third pair of appendages. There being no Malpighian tubules in the small animal, this simple pair of coxal glands would seem to represent the only excretory organs, unless, indeed, the glandular cells around the respiratory sacs can be considered as possessing excretory functions. If this be the case, the eversible sacs will then have a double function of respiration and excretion like the vertebrate allantois. These cells are not represented in the drawings.

Respiratory Organs. — Respiration in so small an animal as *Kœnenia* must necessarily be very simple, and, if I have rightly interpreted the facts, we have in this minute Palpigrade the most primitive form of respiratory organs. These organs consist of the three pairs of lung sacs which are situated in segments four, five, and six, with their corresponding orifices on the ventral surface. They are evidently evaginated through the internal blood pressure. For each pair of sacs there is a pair of dorso-ventral muscles, corresponding to the dorso-ventral muscles of *Thelyphonus*, which have the function in *Kœnenia* of drawing in the everted sac appendages. These lung sacs possess on their inner surface (inner when they are evaginated) granular bodies which stain a deep blue with alcoholic carmen if they happen to be invaginated, but which take on a normal red stain when the sacs are thrown out. Often, in examining sections through the inverted sacs, one can hardly refrain from calling them tracheæ, so very much do they look like simple tubes. In truth, according to whether the sacs are pulled in by muscles, remaining contracted, or whether they have been pulled in by muscles that have immediately become

relaxed, allowing the sac to flatten dorso-ventrally and wrinkle, do we obtain diminutive tracheæ or simple lung books. After examining a great number of sections one cannot refrain from believing that simple sac tracheæ like those of Kœenenia may have given rise to both lung books and tracheæ in other arachnids. If this be the case, we may hold that Kœenenia, which possesses the simplest phase of these organs, the lung tracheæ (which are in reality abdominal appendages belonging to distinct body segments), is the most primitive of all Arachnoidea.

Circulatory System.—As to the circulatory system, the simplest condition possible exists. A definite heart has not yet made its appearance. The blood can have no regular course through the lacunæ and sinuses, and it probably makes its exchange of gases in the neighborhood of the lung sacs. There must be some definite region for the interchange of oxygen and carbon dioxide, for though Kœenenia is small, its exoskeleton is rather too thick to allow of a general surface respiration. I do not think that the dots over the entire surface of the chitin can be minute pores, which the spiders alone of all the arachnids possess, over the skin of the abdomen.

Reproductive System.—In the female the unpaired ovary begins as a blind tube in the seventh or eighth segment and extends into the third. From each side near the anterior end it is prolonged into two oviducts, consisting, for the greater part of their length, of large glandular cells—the largest cells, in fact, of the body. These ducts run forward and upward, becoming very small and thin-walled; probably the last portion, for a short distance, being chitin-lined, as in Galeodes. In the second abdominal segment they become very much swollen, forming a sort of pouch on each side, filled with a gelatinous secretion, evidently derived from the gland cells of the oviduct. The duct continuing from each pouch or vesicle runs backward and downward to meet at the place of entrance in the vagina. It is this portion of the reproductive organ, the vitelline vesicles and their terminal ducts, of which Hansen and Sorensen write: “In the second abdominal segment there is an organ which shows the same peculiar luster and refraction of light which one of us knows so well for the

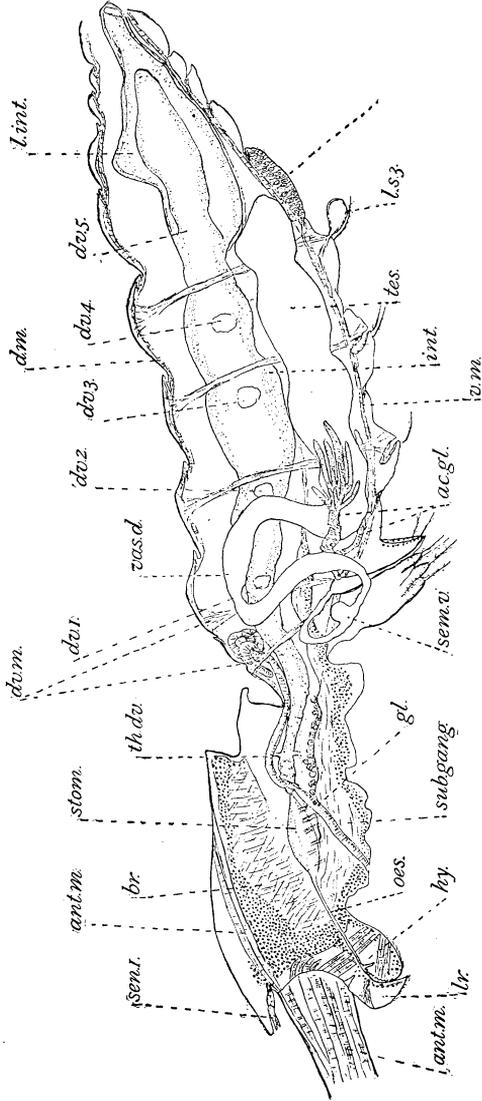


FIG. 6.—Diagrammatic sagittal section of the male of *K. wheeleri*. Lettering the same as in Fig. 5. *ant.m.*, muscles of chelicera; *tes.*, testis; *vas.d.*, vas deferens; *ac.gl.*, accessory glands; *sem.v.*, seminal vesicle; *d.m.*, dorsal muscle; *v.m.*, ventral muscle.

receptaculum seminis of small crustacea." In all of my sections I have never been able to see any sign of spermatozoa in the vesicle, which is always full of a non-granular, gelatinous secretion. Just posterior to the outlet of the oviducts, and between the two lateral appendages of this region, is the outlet of the small flask-shaped receptaculum seminis. The accessory glands are small and insignificant, and in the lateral anterior portion of the abdomen they empty into the vagina. The ovary, which fills almost the entire lower portion of the abdomen, does not show its primitive paired condition. Although the muscular walls of the pouch-like ovary are bulged out with what appear to be cells, only a few of these become the eggs, while the remaining seem to be the nurse cells, and are consumed by the growing ova, which early in the spring lie in the upper portion of the organ. Later in the season a few of the eggs fill the entire ovary, while most of the small bodies have disappeared, and in their place a few oil drops remain. These oil drops are seen at this stage in the lumen of the oviducts. Fig. 5 is, for the most part, a diagrammatic sagittal section through a female *Koenenia*. The ovary, however, is an exact camera drawing which shows the proportion between the true eggs and the food bodies, and their corresponding position in the ovary of an animal taken early in the spring. In *Koenenia* the egg is evidently not fertilized until it reaches the vagina, and all the food that it receives before its fertilization is a product of the ovary and oviduct. The latter must also necessarily furnish the membrane of the egg. Just as there is a pair of dorso-ventral muscles for each pair of lung sacs, there is also a corresponding pair for the reproductive appendages of each segment. These, together with special muscles, undoubtedly cause a slight protrusion and retraction of these organs.

In the male the primitive paired condition of the generative organs is retained. The testes consist of two equally swollen tubes, beginning in the seventh or eighth segment and extending along the floor of the abdomen, to be continued anteriorly into the vas deferens of each side. The vasa deferentia are very much coiled, and fill — at certain times of the year — all

the space in segments two and three of the abdomen, before descending on each side to swell and form the seminal vesicles. From these vesicles the ducts run slightly up and back to a common opening situated between the points of attachment of the two pairs of the dorso-ventral muscles of these appendages. The accessory glands, which are larger in the male than in the female, appear to open into the atrium at a point just posterior to the orifice of the vasa deferentia. The exact courses of the vasa deferentia and the accessory glands are extremely difficult to follow. In places the walls of the ducts entirely disappear, leaving only as a guide, in the case of the vasa deferentia, the contained spermatophores. In some specimens the whole anterior portion of the abdomen is packed with spermatophores. Fig. 6 is a diagrammatic drawing of a longitudinal section through a male *Kœenia*, taken to one side of the sagittal plane. Only the testis and vas deferens, with the accompanying accessory glands of one side, are shown. There are, evidently, delicate muscles in the walls of the testes. In the posterior ends of the testes are numerous cells which are undoubtedly sperm mother-cells, while the anterior portion appears to be crowded with small dotted packets. These dots, which must necessarily be the spermatozoa, glisten under transmitted light and rarely show a stain, even with iron-hæmatoxylin. Nowhere throughout the whole course of these organs is there any trace of spermatozoa possessing flagella. It must be that, in *Kœenia*, the condition is retained which is found in most crustacea, which possess non-motal spermatozoa often imbedded in gelatinous spermatophores. It is probably due to this spermatophore secretion that the sperm cells almost entirely refuse to take on the stain.

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May 23, 1901.