The Sense Organs Involved in the Courtship of Storeria, Thamnophis and other Snakes

By G. K. Noble

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Plates VIII to X; Figures 1 to 8

THE PROBLEM

It has recently been shown that the courtship of salamanders (Noble, 1931) and lizards (Noble and Bradley, 1933) is a very stereotyped performance. Related groups of species and even genera frequently exhibit the same pattern of behavior which has therefore changed more slowly in evolution than have many morphological features. More recently I have observed the brown snake, *Storeria dekayi*, mating in the laboratory and have noted the close similarity between the courtship pattern of this form and that of two species of garter snake, *Thamnophis*, to which *Storeria* is closely related. Snakes differ remarkably from most lizards in usually lacking any sexual difference in color. In the frogs, another group of vertebrates exhibiting little sexual dichromatism, it has been shown that vision plays only a subordinate rôle in sex discrimination (Noble and Farris, 1929). The rôle of vision and of other sensory modalities in the sex recognition of serpents has not been adequately determined although the importance of olfaction in this regard has been clearly indicated in the experiments of Noble and Clausen (1936). In view of the large number of unexplained sexual differences in snakes it has seemed desirable to undertake a study of the method of sex discrimination in this group. Some attempt has also been made to trace the progressive modification of the courtship pattern in phylogeny but this has proved to be less satisfactory than previous attempts for salamanders or lizards chiefly because less is known of the courtship patterns of snakes. After these notes had been prepared for publication a paper by Davis (1936) appeared reviewing much of the literature and similarly attempting a phylogeny of courtship in this group. Our interpretation of the same data is often so surprisingly different that it has seemed desirable to retain much of the historical treatment in the present paper.

THE MATING BEHAVIOR OF *STORERIA DEKAYI*

Although *Storeria dekayi* is one of the commoner species of snakes in eastern United States its courtship has not been previously described. During April, 1932, I had more than 50 adults under observation and from April 12 to 22 some courtship activity occurred nearly every day. Courtship could be stimulated during this period by temperature change. Leaving the snakes in an ice-box at 7° C. and then moving the cages to a well-illuminated room at approximately 25° C. seldom failed to induce some response. Thus, on April 22, after the snakes had been left over night in the ice-box, five pairs were observed courting at one time. *Storeria* is generally assumed to be nocturnal. Both adults and immatures prowl about their cages at night but also during the day. All the courtship in our series occurred during the daytime and usually in the morning after 9 o'clock. Although cages with courting snakes were left in the warm rooms throughout the night and observed at intervals until 9 P.M., no courtships were recorded. Most of our courtships occurred in cages placed behind a pane of frosted glass which cut out the direct sun rays but allowed a gradual heating up of the cages during the morning hours. Snakes placed in cages having a dry gravel floor responded more quickly than did those on a dampened floor. Since the cage size was the same throughout these observations and the methods of handling the same, the different results obtained at different temperatures and humidities appear to be significant. During the breeding season a rising temperature tends to induce courtship and, since this is more apt to occur in the morning hours in a state of nature, courtship presumably occurs at that time.

Courtship occurs in early spring when numbers of individuals are found together near the entrance of hibernation dens. All of the specimens which courted in the laboratory had recently been collected near some holes which were known to harbor numbers of hibernating *S. dekayi* during at least two winters. Lots of 10 to 20 adults were placed in cages 42 × 49 × 63 cm. During the period of observation all moss, sticks or other débris were removed from the cages in order to secure an unobstructed view. This clearing away of the cover apparently had no effect on either the speed or mode of courtship.

The first sign of courtship is disclosed by the male which twitches the tip of his tail nervously but slowly from side to side. The movement is much slower than the tail vibrations many snakes practice when frightened. The male flickers his tongue rapidly in several directions and moves away toward other active snakes. The male soon singles out an individual which later cloacal examination reveals to be a female and attempts to run his chin along her back. In moving forward along her back he flickers his tongue first on one side of the mid-line of her back and then on the other. In doing this he turns his head slightly from side to side and often brings his tongue in contact with her skin. The female is usually approached from the side and as she almost invariably moves away from the advances of the male, the bodies of the two snakes soon come to be parallel. If two or three males begin to court the same female there is always considerable jockeying for the dorsal position. Such rivalry frequently puts the female to flight and as she glides rapidly away the males follow neck to neck like so many hounds on a hot trail. The first to make contact with the female slides rapidly along to bring his chin in contact with her neck, that is, with the skin on the dorsal surface of her body immediately behind the occiput. There is never any hesitation in the region of the cloaca, and if a male slides too far forward onto the occipital shields he soon works back to the neck.

Although the males are usually smaller than the females, there is considerable variation. Several of our courting males were as large or larger than the females they pursued. Nevertheless, the males have little difficulty in rapidly identifying sex. If a female is quickly removed from the cage when being followed by two males, the latter start flickering their tongues at one another but make no attempt to court. Again, when two or more males are courting the same female one may be crowded out from immediate contact with the body of the female. Such a male frequently persists and may run his chin along the back of another male but will never continue courting one of his own sex.

Although the males recognize sex within a few moments there is never any antagonism among them. In endeavoring to secure a position on the back of a female they may crowd a rival off but their movements against one of their own sex are never more violent than toward an inanimate obstruction. In following the trail of a rapidly disappearing female a male makes no attempt to drive his rivals away. These observations repeated many times lead to the conclusion that while the female sex attracts, the male sex does not repel the sexually active male.

In the confines of the laboratory cage the female's flight may be blocked or she may double back on her trail sometimes to the confusion of the male. In either event the male may start to work toward the tail instead of toward the head of the female. When he reaches the tail base, he presumably recognizes the mistake because he almost invariably turns and works back toward the head.

As soon as the male has reached a position approximately a centimeter behind the occiput of the female he attempts to encircle the female with the posterior part of his body. While the head and neck of the male come to lie above the female the greater part of his body usually falls to one side or the other. If the middle section of the male's body chances to lie on one side, the region immediately anterior to his cloaca is thrown across the back of the female and the section including the cloaca bent under her body in the form of a sharp turn or wedge. A firm grip on the female's tail is secured by one or more twists of the male's tail. Then as the cloacal section of the male's body is pried under the cloacal region of the female, the male's body begins to writhe. These violent lateral movements are soon replaced by a series of caudocephalic waves of the body which may begin simultaneously in two different parts of the male and run rapidly forward. The waves may begin near the center of the tail and, closely resembling a series of antiperistaltic ripples, run the full length of the body to the head. The male endeavors to keep his chin on the neck of the female, even when these caudocephalic waves are again replaced by more violent movements. Both the body waves and the writhing serve the purpose of tapping many parts of the female's body. As the movements continue the wedge-like turn of the male's body lifts the cloacal region of the female two or three centimeters from the ground. The base of the hemipenis on the side in contact with the female's body is slightly protruded and the prominence brought close to the cloacal slit of the female.

The courtship behavior described above was witnessed many times in a series of individuals. But only twice while the observer was present did copulation follow. In one of these cases two males were following the same female. Within five minutes after being placed in the observation cage, one male had inserted his right hemipenis into the cloaca of the female. He then no longer made an effort to keep his chin on her dorsum but allowed himself to be dragged about the cage by the female, which continued her progress about the cage. It seemed remarkable that the other male which had been courting the female immediately left the pair even though he, like other courting males, is usually attracted by movement. As soon as the first male had become attached by his hemipenis to the moving body of the female, his cloacal region and tail began to jerk spasmodically. Each movement of these regions was essentially a forward thrust. There were two or three rapid thrusts followed by a pause of two seconds. These movements were continued even when the male had been dragged about until his head pointed in the opposite direction from that of the female and his cloacal region was bent sharply back on itself. The thrusts were readily distinguished from the caudocephalic waves of courtship both in their tempo and in the fact that they did not extend anterior to the cloaca.

The female's cloaca was greatly distended by the single hemipenis of the male and the cloacal lips at the point of juncture were wet with lymph and a little blood. When another male happened to cross the path of the pair the male rolled over and over carrying the female across with him. These actions did not free him from the female and he began other, more vigorous movements. In an attempt to pull himself loose, he wound himself tightly around the female making three complete coils anterior to her cloaca. The violent struggling which followed did not serve to free the hemipenis. Once more he relaxed and allowed himself to be dragged. Finally at 10:22 A.M., just 24 minutes after beginning the copulation, the male gained his freedom.

Copulation in the second pair proceeded like that in the first. Again other courting males paid no attention to the pair *in copulo* although they had been following the female a moment before. Again the male allowed himself to be dragged, giving the impression that he was entirely helpless in the matter. As in the preceding case it was only one hemipenis, the right, which became attached.

In view of the male's apparently helpless condition, I attempted by manipulation to determine how firm was the attachment. After copulation had continued a few minutes, I picked up the pair and pressed down on the base of the everted hemipenis with my thumb. This and other squeezing movements did not free the male. His cloaca was next thrust forward and the spines unhooked from the lining of the female's cloaca. When entirely free the hemipenis still remained everted and it was more than a minute before it began to be withdrawn into its sheath. These observations indicate that once the hemipenis is everted it cannot be readily withdrawn even though an irritated male may seek in every possible way to free himself. The spines on the hemipenis do not help a male maintain his position in struggles with rival males but rather they insure the continuing of copulation by males which otherwise would be rubbed off by their active partners.

COMPARISON WITH *THAMNOPHIS*

The courtship of *Thamnophis* is better known than that of any other North American snake and, consequently, invites a comparison with that of *Storeria.* Ruthven (1908) observed a pair of *T. sirtalis* mate in captivity. Brennan (1924), Bishop and Alexander (1927), and Truitt (1927) have described certain features of the courtship or mating of the same species which they observed in the field. Blanchard (1931) has published a photograph of a mating pair of *T. radix.* The courtship of *T. butleri* has been described by Ruthven (1912) and compared with that of *T. sirtalis.* Recently Davis (1936) has reported in great detail the observations of Weed on *T. radix* but his interpretation of the events is at variance with the conclusions reached by observers of other species of *Thamnophis.* During the last four years I have observed a large series of both *T. sirtalis sirtalis* and *T. butleri* courting in the laboratory and have been able to work out certain additional details in the behavior of both forms.

The courtship of *Thamnophis* is essentially the same as that of *Storeria* as described above. There are, however, certain differences which may prove to be more specific than generic. Thus the courtship of *T. butleri* is not exactly the same as that of *T. sirtalis* as Ruthven (1912) infers. In certain details it resembles the courtship of *S. dekayi* more than it does that of *T. sirtalis.* In both species of *Thamnophis,* as in *Storeria,* two or more males may pursue the same female without fighting or even jostling one another except when endeavoring to secure the dorsal position. The males attempt to run their chins along the back of the female until they reach the neck region. The tongue is frequently protruded, often to make contact with the female's back during this process. In neither species of *Thamnophis* is the head turned from side to side as the male progresses along the female's back. However, in both species the cloacal region is thrust under the female in the manner of *Storeria.* Frequently when the male finally comes to rest his body will lie with several turns across the female's back. Before his cloaca is thrust under the female, the region immediately anterior to the cloaca is thrown across her back and his cloacal region, bent in the form of a wedge, is forced under her body from the side opposite to that on which the most posterior section of his body lies. In both species of *Thamnophis,* the whole body and tail are thrown into a series of rhythmical, caudocephalic waves which are much more regular than in *Storeria.* They may arise simultaneously in two different parts of the body but they may also follow one another in regular sequence along most of the tail and all of the body except for a small part of the neck. The frequency of the waves is greater in *T. butleri* than in *T. sirtalis.* Several males of the latter species began a wave once every two seconds and after three to six of these waves rested ten seconds before beginning another series. In *T. butleri,* as in *S. dekayi,* the waves may come with a frequency of less than a second. There is, however, considerable variation. At the height of the courtship certain individuals of *T. sirtalis* increased the frequency of their waves to a little less than a second apart.

It is noteworthy that it is the two small species, *T. butleri* and *S. dekayi,* which have the greatest frequency in their caudocephalic waves. Moreover, it is the two small species which have the greatest amplitude of each wave. That is, the crest of each undulation when compared with the total length of the snake is lifted a greater distance from the body of the female of these species than in the case of *T. sirtalis.* In correlation with this greater vigor of the caudocephalic waves in the small species the cloacal region of the female is lifted a greater distance from the ground by the wedge-like loop of the male's cloacal region, Pl. VIII. In *T. sirtalis,* many of the males are markedly smaller than the female. These small individuals soon slide caudally along the female's back until their cloacas are near that of the female. If the cloacal loop is adjusted under the female's cloaca while the small male is moving forward along the female's back his chin may never reach her neck region. In both species of *Thamnophis,* as in *Storeria,* the cloacal region of the male is not laid flat against that of the female but only one side of the ventral surface is so adjusted. As the body undulations continue the base of the hemipenis on that side is slightly protruded to form a low eminence.

Although the courtship, including the caudocephalic waves, may continue with interruptions for days, there appears to be no correlation between the amount of time consumed and the success of the procedure. At least many of the most persistent male *Thamnophis* never copulated. On the other hand, three male *T. butleri* became attached by their hemipenes within a few minutes after they had begun the caudocephalic waves. After attachment there are no rhythmical thrusts of the tail base in this species as in *Storeria*. In one mating of *T. butleri* which was allowed to continue without disturbance, a rhythmical pulsation of the sides of the female's body immediately anterior to the cloaca was noted. There was one beat approximately every three seconds. Apparently this pulsating was due to rhythmical movements in the male's hemipenis. As in all snakes, only one hemipenis was inserted at a time and in *T. butleri*, as in *Storeria*, this not only filled the cloaca but greatly dilated it. As copulation continued in *T. butleri* the cloacal lips became moistened with considerable lymph and a little blood.

In the pair of *T. butleri* which was left undisturbed until the completion of copulation the male had inserted his left hemipenis. The female which as usual during courtship had been moving unconcernedly about the cage, continued to move after the male's hemipenis had been inserted. Immediately after attachment the male let his chin slip off the female and permitted himself to be dragged about. A moment later the male had been turned upside down. Five minutes later the male had regained his position alongside the body of the female and his body gave a few twitches. Fifteen minutes after beginning of copulation the pulsation of the female's body anterior to the cloaca became very feeble. At 18 minutes the male moved his chin along the back of the female's neck and his body was thrown into the typical caudocephalic waves. A moment later the female moved on, dragging the male passively along. At 22 minutes she began to dig with her snout. Forty minutes after the beginning of copulation the male, after considerable writhing, broke loose. Since the pair had not been disturbed the male's violent efforts to free himself had not been induced by the observer. Apparently in *Thamnophis*, as in *Storeria*, the withdrawal of the hemipenis once it has been hooked into the cloaca of the female is accomplished only with difficulty.

Davis (1936), in reporting the observations made by Weed on *T. radix*, considers the caudocephalic waves, which he describes as a quivering, "as indicating the actual orgasm." The fact that the male under observation quickly changed the position of his cloaca from one side to the other of the female may be taken as proof that his hemipenis was not actually inserted into the cloaca of the female. As stated above, the courting male throws a loop over the back of the female immediately cephalad to the cloaca and slightly protrudes the hemipenis adjacent to the female. When the male changes his position relative to the female, the tail wedge is also reversed and the opposite hemipenis is slightly protruded. This is not copulation as one may readily verify by gently lifting the entwined tails of the courting pair.

During courtship there is no extrusion of cloacal gland secretion by either sex although defecation frequently occurs. Males differ enormously in the intensity of their sexual ardor but since they do not compete with one another, except when two or more happen to start for one female at the same moment, it can hardly be said that one is dominant over the other.

COMPARISON WITH *COLUBER CONSTRICTOR CONSTRICTOR* AND *ELAPHE OBSOLETA OBSOLETA*

Although the black snake, *Coluber constrictor constrictor*, is another common snake in eastern United States its courtship has never been described except in very general terms from observations made long ago (Brons, 1882). During April, May and June, 1934, I had a large number of black snakes under observation in a cage 1.1 × 2.5 meters at its base. These were placed in a cold room held at 7° C. every evening and kept there on cloudy days. On frequent occasions when the sun was shining the snakes were placed in a greenhouse having a helioglass roof, that is, one which passes a considerable amount of ultraviolet. Under these circumstances, courtship was frequently observed although on only two occasions did this lead to copulation.

The courtship of *C. constrictor* resembles that of Dekay's and the garter snake in its general pattern. The male attempts to run his chin along the back of the female while at the same time undulations run forward along the side of the body. The chin is not, however, pressed tightly against the back of the female as in the case of the garter snake and the tongue is less frequently extended. The behavior immediately preceding this trailing finds no parallel in either the garter snake or Dekay's snake. As the black snakes warmed up after their stay in the cold room, one individual would suddenly dash madly across the cage and this would start many of the others dashing back and forth. These unexpected rushes usually resulted in one or more males settling down to a steady pursuit of one female. As in the case of the other snakes discussed above there is no rivalry among the males except for the slight pushing when two males follow the same female. The dashing about appears to be a normal phase in the courtship of the black snake. It obviously stimulates the whole group to greater sexual activity.

Later phases of the courtship differ in detail from that of Dekay's snake or the garter snake. A wedge is made of the cloacal portion of the body and thrown over the body of the female to the side opposite from that where most of the male's body lies. But the male does not twist his tail firmly around that of the female as in the case of these snakes. While lifting with his cloacal wedge the male gives one or more rapid jerks and fully everts the hemipenis lying adjacent to the female. This frequent protrusion of a hemipenis before the cloacas are in contact distinguishes the breeding behavior of the black snake sharply from that of Dekay's or the garter snake.

In both cases when copulation was effected, the hemipenis did not show because the bodies of the two snakes were too close together. As soon as the hemipenis was engaged the male made no further attempt to keep his chin on the neck of the female. The male continued to give forward thrusts with his cloacal region and bubbles of mucus appeared about the base of the hemipenis. In one case the male twisted and disengaged himself in less than a minute but in the second case copulation continued for approximately five minutes. The female dragged the male about the cage while his hemipenis was pulled half out of her cloaca. The male turned over and over in his attempt to dislodge himself. The base of the hemipenis was swollen to nearly the diameter of the tail at its midpoint.

I have observed only two instances of courtship of the black snake in the field. Both of these occurred on the snake's hibernation area in the water supply reservation at Hartford, Connecticut. Great numbers of black snakes hibernate each year on a steep slope of broken trap rock facing east. The snakes hibernate among the interstices of the loose rock in the same way I have observed them hibernating on a slope at Stony Point, New York. There is no central den but the snakes are distributed over an area several hundred yards in length. On May 1 and 2, 1937, there were large numbers of both sexes of black snakes scattered over this hibernation area. One male courted two different females within a five-minute period. In both cases he ran his chin along her back and attempted to encircle her tail with his own. Both females disappeared down crevices before the male could begin the quivering behavior observed in the laboratory. A second male watched the procedure at a distance of 30 feet. During the course of the day two other snakes crossed this particular courting area. There was no rivalry among the males and no marking out of territories.

A second pair was observed with tails loosely entwined at the mouth of another crevice approximately a hundred yards distant. Again the female disappeared down the crevice before the male developed the courtship movements seen in the laboratory. Releasing a snake over the first courtship area induced a second snake to appear, apparently attracted by the movements of the escaping individual. This glimpse of the courtship of the black snake in the field, although obviously incomplete, indicates clearly that the species courts soon after appearance from hibernation. No territories are marked out in this region but the males move about actively in search of females. No "snake balls" are formed because the hibernation area is diffused. Different females appear at widely separated spots and attract males which happen to be in that region at the moment. Several males were seen traveling over large sections of this hibernating area, indicating clearly that they do not restrict their searching to some particular spot.

In the laboratory a warm atmosphere was found essential to courtship. The body temperature of eight of the snakes captured on the hibernating area was taken with a cloacal thermometer. The usual precautions to prevent the heat of the hand from modifying the readings were observed. It was found that the cloacal temperature of these eight snakes averaged 30.8° C., maximum 33.3°, minimum 28.2°, while the temperature of the air in direct sunlight at the point of capture averaged 20.7° C., maximum 24.4°, minimum 14.2°. One male which had its tail under the rock and head out was found to have a cloacal temperature of 24.5° C., while the temperature of the rock, in direct sunlight was 21.5° C. A female which had her tail and body in one of the crevices, but her head out, had a cloacal temperature of 16.2° C., while the air at the immediate entrance to the burrow was 19.2° C. in direct sunlight. This indicates that the heating of the snake's body is localized to the point where the sun strikes it. The male snakes, therefore, while waiting for the females to appear, increase their body temperatures about 10° C. by the direct action of the sun. The females also increase their body temperature before they move about. Doubtlessly, the black pigment of the skin augments this absorption of heat.

Although there appears to be no rivalry in the courtship of the black snake, certain individuals may become vicious at this season. Mr.

Lewis H. Babbitt, who showed me the Hartford hibernation area, informs me that once he saw a black snake bite the black rubber laced hiking boots of one of his friends who stayed perfectly still while the snake approached him. On another occasion he saw one snake in a group of three bite another. Whether this was the female retaliating against the male, or a male biting another male, was not entirely clear. Mr. Babbitt has seen as many as thirteen black snakes together in early April. Three or four snakes together is not a rare sight. In brief, the black snake, like Dekay's snake and the garter snake, courts on its hibernation ground, but since this may be a large area there may be little mass courtship in this species.

From June 2 to July 1, 1934, I had under observation a pair of mountain black snakes, *Elaphe obsoleta obsoleta*, which for two weeks previously had shown some courtship behavior. The male was considerably longer than the female, being 187.9 cm. in total length in contrast to the 149.8 cm. of the female and possibly this difference may account for the fact that a union was never effected. Nevertheless the courtship which was frequently observed between these dates was presumably typical and of especial interest when compared with that of *Coluber constrictor*. As in that species, there were caudocephalic undulations but these rarely involved the whole body but were mere waves of pulsation in the sides of the body. Such pulsations would frequently begin simultaneously in two different parts of the snake's body and pass rapidly forward. Sometimes the pulsation would include only the ventral part of the body wall in any one area.

Elaphe obsoleta resembled *C. constrictor* and differed from the other species considered above in that the male did not twist his tail tightly about that of the female. At the height of courtship his tail vibrated with excitement while holding loosely that of the female. At the same moment a hemipenis was suddenly protruded its full length even when the cloacas were several centimeters apart. In this eversion of a hemipenis before cloacal adjustment as well as in the reduction of the tongue protrusions while trailing the female, the mountain black snake resembled the black snake closely. The most important difference in their courtships occurred at the very beginning of the performance. When the male first touched the side of the female's body with his snout she would begin to give a series of spasmodic twitches, about one a second, involving a large part of her whole body. These twitches were not caudocephalic undulations but rapid contractions of various muscle groups. They were not continuous but in a series of twenty or more interspaced by rest periods of 10 or 15 seconds. These twitches ceased as soon as the male's courtship activities became more vigorous or died away entirely. Hence, they probably functioned the same as the preliminary rushes of the black snake courtship, that is, to raise the emotional level of the pairing group.

COURTSHIP PATTERNS IN OTHER SNAKES

The garter snakes have been derived from *Natrix* and it is not surprising to find that their courtship is essentially the same. The courtship of some of the European species of *Natrix* is well known. Aggregations are found in the spring soon after the snakes appear from hibernation. The male, after flickering his tongue, runs his chin along the back of the female apparently exactly the same as in *Thamnophis*. He encircles her cloacal region with his tail and begins the same rhythmical movements of the body musculature. Klingelhöffer (1931) has compared these movements in *N. viperina* to those made in a rubber tube when squeezed at the hind end. Apparently the muscular waves pass forward along the body exactly as in *Thamnophis*. Stein (1924) has recorded that in *N. natrix* the male nods his head in a jerky fashion. In *N. viperina* there are also jerky movements of the head. I have observed very sudden nodding movements of the head in the American *N. cyclopion* and *N. sipedon pictiventris* during courtship. Unfortunately, neither of these courtships ended in copulation. Nevertheless, it appears highly probable that the courtship of *Natrix* is practically identical to that of *Thamnophis* except that the male not only rubs his chin along the female's back but practices jerky nodding movements of the head while in position on her back. Both Stein and Klingelhöffer make it clear that there is no rivalry among the males. Two males may pursue the same female without fighting exactly as in the case of *Thamnophis*. *Storeria* differs from *Thamnophis* in the use of its head during courtship. But the head movements of the male *Storeria* are lateral and not vertical as in *Natrix*. Unfortunately, the mating behavior of no American species of *Natrix* is known in full although Evermann and Clark (1920) described the early spring aggregations and Perry (1920) witnessed the "periodic spasms" of the courtship of the same species in the field.

The courtship of the natricine snakes is apparently the most widespread type of behavior pattern found throughout the suborder. Moreover, the viperid snakes, which are usually considered the most advanced group among the serpents, have retained this pattern in a modified form. In *Crotalus* there are head movements of the male which have been regarded as caresses (Wiley, 1929). In the related *Sistrurus* the head of the male is "thrust about above the body of the female" (Guthrie, 1927) during the courtship. The male encircles the cloacal region of the female with his tail and engages in "a sort of spasmodic twitching, mainly of the posterior half but sometimes of the entire body." The courtship of *Crotalus basiliscus* has been observed by Perkins in the St. Louis Zoo. As reported by Davis (1936), the "male nudges the female and rubs the side of his head against her body."

Exactly how these movements differ from those of *Thamnophis* cannot be determined from these descriptions. Fortunately, I have had a series of *Crotalus viridis viridis* under observation for some months and although males frequently courted no copulation occurred during the period of observation. A series of 80 adults and half-grown young were secured from a single hibernation den, April 15. Although these snakes were fed and given a cage with southern exposure no courtship began until July 8 of that year (1935). In courting, the male moves forward with chin pressed to the back of the female and tongue frequently flickering. His head and sometimes a third or half of his body give a series of short, forward jerks. At other times the male's body may stay in one position but twitch. The ventral muscles are carried upward and backward by each spasm with the result that the back is carried forward slightly. As the ventral muscles relax after each twitch the back returns to its original position. The twitches occur at intervals of approximately one a second.

There are no undulations of the body in *Crotalus viridis* as in *Thamnophis*. The male throws his tail once around that of the female. It grips the cloacal region of the female in the manner of a shepherd's crook. There is no loop thrown over the dorsal surface of the tail in the cloacal region of the female as in the case of garter snakes. The tails are not twisted together as in that group. The modification of the tail of *Crotalus* into a rattling device would account for the loss of tail twisting in that group but the degeneration of the body undulations to a series of twitches or forward jerks is not correlated with any external specialization.

At the height of the courtship the male brings his cloaca close to that of the female with the result that a considerable portion of his tail remains ventral side uppermost. Since this occurred at 6:15 P.M., July 21, in the case of one male, it is probable that copulation may occur during the night.

Future work will probably disclose that there are constant differences between the courtship patterns of the various genera of Crotalidae. Perkins has not noted any forward jerking of the body of the male *Agkistrodon piscivorus* in the St. Louis Zoo although copulation frequently occurred (Davis, 1936). The courting snakes seem to raise the anterior parts of the body much more than in *Crotalus* and "each snake pushes and rubs vigorously against its mate." It is interesting that the courtship of *Crotalus* and *Sistrurus* should be so much alike and yet different from that of *A. piscivorus.* It would be important to know how closely the copperhead and water moccasin agree in their courtship.

Few snakes show any sexual dichromatism. The two European vipers, *V. aspis* and *V. berus,* form a notable exception for the males are usually lighter and more conspicuously colored than the females. The tongue movements and head nods of *Sistrurus* form a conspicuous part of the courtship of both species. There are also twitching movements of the body (Klingelhöffer, 1931) which are presumably similar to those of *Crotalus* and *Sistrurus.* When following the trail of a female, *V. aspis* raises its tail and opens his cloaca from time to time (Baumann, 1929). This habit is apparently correlated with the use of the cloacal secretions in trailing. A fundamental difference between the courtship of these vipers and the snakes showing no sexual dichromatism is that the males fight actively among themselves during the breeding season. This has been well shown for *V. berus* by Reuss (1923) and for *V. aspis* by Baumann (1929) and by Köster (1932). The rivalry of male adders has been observed in some detail in the field (Prior, 1933) where they opposed one another in a vigorous "dance" which finally led to the driving away of one of the males from the female. In lizards, bright colors aid the males in intimidating rivals (Noble and Bradley, 1933) and it would seem to follow that the differential colors may aid these vipers in sex recognition. The relative importance of odor as contrasted to vision in sex recognition has not been shown for *Vipera* or for any other snake.

One other comparison between *Vipera* and lizards may be made. Although the male vipers, like some male lizards, usually appear earlier in the spring than do the females (Leighton, 1902; Vainio, 1932) they do not mark out definite territories which they defend against other males. At least aggregations of breeding vipers have been frequently seen (Klingelhöffer, 1931). At present it is not known whether this formation of assemblages is due to a true aggregation response such as occurs in *Storeria* (Noble and Clausen, 1936) or merely to the powerful attraction of the female which overrides any tendency toward isolation resulting from the fighting. In either case the fact that vipers hibernate in groups and consequently are found together early in spring would tend to produce aggregations regardless of the degree of female attractiveness or male combativeness.

Aside from the vipers there is one other species of European snake which shows a sexual dichromatism and it is the only species besides the vipers which is known to fight during the breeding season. Franke (1881), who was the first to record this behavior, did not, however, clearly distinguish it from the biting which forms a normal part of the courtship of this snake as described by Schreiber (1912). The American king snakes are closely allied to *Coronella* and it is interesting that they also exhibit the biting as part of their courtship. Meade (1932) describes the male *Lampropeltis getulus holbrooki* as biting the female's body during the preliminaries of mating which continued for half an hour. The snake "would release his hold momentarily, grasping the body at a new place after a few seconds."

Mr. Stewart Springer has observed the courtship in a pair of this race which occurred at Biloxi, Mississippi, on March 29, 1932. I quote directly from the field notes of Mr. Springer:

"A large male *L. g. holbrooki* from this vicinity was transferred from a sack to a snake box containing a female taken locally also. In about five minutes after placing the male in the box he began to follow the female about the box which was 24 by 60 in. While following he would bite the female from time to time releasing his hold almost immediately. After about 20 minutes the male seized the female just anterior to the heart region and held on undulating his own body from forward back in what was apparently an attempt to straighten out her body. The undulations were rhythmical but irregular. During the course of the next hour the male released his hold and allowed the female to coil several times but always caught her again in the same place and continued his undulations. In moving into a position for grasping the female the male proceeded by regular short pushes evidently made entirely by the ventral scales advancing about $^1/_4$ inch at intervals of one second and following the body of the female along until the point of grasping had been reached. The biting in all instances was deliberate. The body of the female examined subsequently showed no evidence of the scales or skin being torn. The female had only about an inch of tail left from an old injury. When the vent of the male came opposite that of the female one hemipenis was protruded. This happened three times, the third time the single hemipenis remained engaged for a period of fifteen minutes during which there was less movement on the part of the female. I cannot be sure separation followed some outside disturbance or not. The whole period of courtship and copulation occupied three hours and forty-five minutes. The temperature was 72° and at maximum for the day."

The courtship of *L. getulus holbrooki* which Mr. Springer witnessed was with a female having a back broken halfway between head and tail. "The posterior end responded to external stimuli such as a slight jab with a stick but was not used in locomotion." The female died the third day and Mr. Springer sent on the male to New York together with a new female. There the male began the same performance of biting the female which remained tightly coiled during this treatment. Both sexes vibrated their tails, the male more slowly than the female. The male encircled the coiled body of the female tightly but never displayed any caudocephalic undulations of his body. Unfortunately this courtship never ended in copulation although the male's cloaca was distended by the slightly protruding hemipenes when his cloaca was near that of the female. These observations although incomplete seem to indicate that the caudocephalic undulations of the natricine snakes have been replaced by a biting performance as a means of stimulating the female.

Coluber viridiflavus carbonarius appears to exhibit an intermediate type of courtship between that of *Thamnophis* and *Lampropeltis.* At least Schreiber (1912) describes the male as making forward and backward movements of the neck while holding the female in his jaws. Schreiber (*loc. cit.*) figures the tails of the pair as twisted spirally. He also states that the female may seize the male in her jaws. Male *Elaphe quatuor-lineata,* according to Schreiber (1912) and Stemmler-Morath (1935), also grips the female by the neck. Mr. O. C. Van Hyning has advised me that the male *Elaphe quadrivittata* also seizes the female's neck region in his mouth while twisting his tail about her. Since these two species of *Elaphe* are found on opposite sides of the Atlantic we have here a splendid case of the constancy of courtship pattern in related species regardless of the environment. There is also some evidence that *Elaphe vulpina* maintains a hold by gripping with the mouth although this is not very complete (Davis, 1936). Why the male *Elaphe obsoleta obsoleta* described above did not grip with his jaws during courtship is at first difficult to decide. It may be noted, however, that courtship did not result in copulation in this pair.

The Indian *Ptyas mucosus* is closely related to *Elaphe* and its courtship so far as known has many resemblances. Prater (1933) has figured but not described the body of the male as encircling the body of the female spirally. Wall (1921), reporting the observations of Frere, states in regard to a pair: "Their bodies were twined together and writhing, except for the anterior quarter. Their heads were raised from the ground for 1 foot to 18 inches and appeared to be sparring at each other like two young cockerels. Their movements were active and vigorous."

Davis (1936) would include the behavior of *Ptyas mucosus* in his "*Coluber* type" of courtship. The tight spiral formation figured by Prater has not, however, been described in any other species of snake. The tendency of the male to seize the female in his jaws distinguishes the behavior of the European *C. v. carbonarius* from that of the American *C. constrictor*. If we are to judge from courtship behavior alone the European species of *Coluber* and *Elaphe* would be considered more closely related to one another than either is to the American *C. constrictor*. It would also follow that *Coronella* and *Lampropeltis* represent a modification of the *Elaphe* type. Unfortunately much more must be known of the courtship of all these snakes before a full description of the similarities and differences can be given.

Mell (1928) makes the general statement that during courtship the anterior part of the body of not only *Ptyas* but also *Naja*, *Vipera* and some *Natrix* is raised and rubbed against the mate in what he calls sympathetic stimulation. It is highly probable, however, that not only *Ptyas* but also *Naja* have certain distinctive features in their courtships. In the case of *Naja tripudians*, Wall (1921) states: "In Mr. Hampton's vivarium coitus lasted intermittently for three days. He observed that the pair nodded their heads continually, and their bodies quivered. They did not take the slightest notice of anybody in front of their cage. They did not expand their hoods, neither did they wrap themselves around one another. Each turned the vent upwards and sideways to effect engagement." From this account it would appear that in *Naja tripudians* at least the nodding and quivering of the natricine pattern is retained while the entwining behavior has been lost.

Among the most primitive snakes the males apparently have not yet developed the habit of throwing their bodies in caudocephalic waves. Lederer (1931) found that in *Eunectes notaeus* the claw-like limbs of the male were hooked into the skin near the cloaca of the female and served to lift this part of the body up from the floor. In the natricine snakes it is a wedge-shaped loop made near the cloacal region of the male which serves the same purpose. Lederer observed this behavior several times. In *Eunectes murinus*, Mole (1924) reports that the claw-like limbs of the male "are moved quickly, and scratch the scaly sides of his mate, inducing her to crawl forward slowly until union is established." Mole and Urich (1894) attribute the same function to the claws in *Constrictor constrictor*. They state: "When about to couple, the male extends these hooks at right angles to the body and vibrates them in an extremely rapid manner, scratching, as he does so, the back and sides of his companion. The claws scratching the scales of his mate make a noise which can be distinctly heard two yards off. This habit has also been observed in *Epicrates cenchris*."

The Pythonidae are closely related to the Boidae and like them are equipped with rudimentary hind limbs in the male. Perkins, as reported by Davis (1936), has recently described the male *Python curtus* as stroking the body of the female with them during courtship. He failed to observe any lifting movement of the spurs. Under stimulation of the spur movements "the female gradually twists her cloacal region laterally and the male works his tail under hers. When her cloaca is nearly in a vertical position the female suddenly gapes it, the male inserts a hemipenis, and copulation takes place."

These data make it appear probable that the scratching movements of the rudimentary hind limbs of some male boids and pythonids have the same function as the caudocephalic waves of the garter snakes, namely, the stimulation of the female. No such waves have ever been described in any boid or pythonid and hence the limbs might assume this function. In some lizards the comb-like growths on the femurs of the males are rubbed back and forth along the back of the female to quiet her (Noble and Bradley, 1933). Further observations may show that the claw-like limbs of all boids and pythonids have the double function of both stimulating the female and lifting her cloacal region. In correlation with these habits it is the male which retains the longest hind limbs. With the loss of the limbs in all the higher snakes these two functions are assumed by other parts of the male's body.

The courtship pattern of snakes has not undergone a great change in phylogeny. What is known of the courtship of such genera as distantly related as *Dryophis* (Berg, 1902) and *Pituophis* (Fisher, 1925) agrees with that of *Thamnophis* and *Storeria* in its broad features. There has, nevertheless, been some phylogenetic change in the courtship of snakes. The primitive Boidae and Pythonidae retained the hind limbs of their saurian ancestors to serve as both stimulating and lifting devices of service only in courtship. The colubrids lost these appendages and developed caudocephalic undulations to stimulate the female and wedge-like twists of the tail to lift up the female's cloacal region. In crotalids with the development of the rattle the tail twistings were reduced to a mere crooking of the tail. The caudocephalic undulations degenerated to mere twitching. Viperids seem to depend more on smell than do crotalids for the latter are equipped with organs for detecting the body temperature of their prey (*vide infra*). In viperids, cloacal gland secretions appear to aid sex discrimination but the pattern of their courtship, except for cloacal protrusions, is essentially like that of *Crotalus*. One group of colubrids, although presumably less advanced than crotalids, has specialized in gripping with the jaws during courtship. This has led in *Coronella* and *Lampropeltis* to a loss of the body undulations. How closely this change of habit has accompanied the differentiation of genera cannot be stated from the data available. There is little evidence, however, in favor of the view expressed by Davis (1936) that the crotalid type of behavior evolved from the specialized type characteristic of *Lampropeltis*. Lederer (1931) describes the male *Agkistrodon piscivorus* as seizing his mate in his jaws during courtship and is careful to point out that the fangs were not engaged. But this was a homosexual union between two males long in captivity. If this one instance of biting during courtship is laid aside as abnormal, the courtship of both crotalids and viperids can be more readily derived from that of *Thamnophis* which represents a generalized colubrid pattern.

Movement arouses the attention of snakes and in some forms special courtship performances arise which appear to be mutually stimulating. In *Coluber constrictor* there is a wild dash preceding the trailing. In other forms, as *Ptyas*, there develop head movements of both sexes during courtship which seem to stimulate both sexes. It is noteworthy that in some of these forms the hemipenis is everted before the male's cloaca is in contact with that of the female. The head movements or "dances" are not to be confused with the jousts between rival males which occur in the sexually dichromatic species of *Vipera*. In lizards, sexual differences in color aid sex recognition and the same may be true of snakes. Sexual dichromatism has, however, developed only among those snakes in which the males fight among themselves for females. A male livery is presumably a warning to other males rather than an attraction to the female.

THE RÔLE OF VISION IN COURTSHIP

It was obvious from the beginning of the observations that movement was of considerable significance in the courtship of both *Storeria* and *Thamnophis*. When the glass-sided cages were placed beside one another courtship activity in one cage would stir up the individuals in another cage and they would attempt to pass through the glass side in the direction of their active companions. This action in itself is not sexual for sexually immature individuals respond the same way. The courtship response of the male may have this general tendency to aggregate toward movement. It is distinctive, however, in that the male continues in the direction of the movement and attempts to push his chin along the top of the moving object. In order for courtship to continue the object must have certain qualities. Frequently I had *T. sirtalis* courting in the same cage with *T. butleri* but it was not possible to secure a cross-courtship of the two species even utilizing very eager males. Once when a male *T. sirtalis* had been courting with caudocephalic waves for some time, a female *Natrix sipedon sipedon* was exchanged for the female of his own species. The male continued his body undulations for several minutes but eventually gave up.

Was this failure to court due to the lack of familiar visual cues? Since the species differ in color it seemed possible that modifying the color pattern might confuse the snakes. A series of female *T. butleri* and *T. sirtalis* were, therefore, stained with brilliant dyes. A treatment with one per cent aqueous solution of methylene blue followed by several dips in a 0.3 per cent alcoholic solution of the same stain changed the olive tones of the female to a brilliant purplish red over most of the dorsal surface and blue over the rest. Immersion in the alcoholic methylene blue stained both upper and lower surfaces blue. Various dilutions of mercurochrome gave different colors. The weaker solutions stained the dorsal surfaces a brilliant green turning to pink on the side. When these females were tested with males, their gaudy colors in no way slowed down or modified the courtship procedure. On the contrary, when females which had been actively courted were stained and placed in cages with unstained adult females with no previous record of courtship, the males went by preference to the stained females not only that day but on following days. Although two adult females may be indistinguishable to the observer in structure or behavior, courting males will select a particular female even when her appearance has been radically changed by staining with brilliant colors. The female now retains her attractiveness to the male over a period of several days and regardless of one or more changes of color.

Even though color may not enter into courtship it seemed possible that the males might use their eyes to distinguish differences in movement not recognizable to the observer. A series of male *T. sirtalis* and *T. butleri* were therefore blindfolded with caps of adhesive tape painted with India ink or with photographer's opaque. Both species usually made vigorous attempts to remove the caps by rubbing. The blindfolded males would frequently raise their heads high from the ground and flicker their tongues vigorously. Several blindfolded *T. sirtalis* settled down to a series of prowling movements on the day of blindfolding and all were tested over a period of several days.

Blindfolded males did not seek aggregations of courting individuals. But while moving about the cages if they chanced to come near a female they would frequently move toward her and begin an active courtship. In several cases a blindfolded *T. sirtalis* succeeded in displacing a courting male which had already secured a position along the back of the female This experiment, repeated many times, failed to show that a blindfolded male once in the immediate vicinity of a female was in any real disadvantage. If the male was a small individual he would rapidly assume the more posterior position on the back of a female. If started the wrong direction the blindfolded males showed themselves exactly as adept in turning about on reaching the tail base as did the controls. It was clear that the males in these experiments were not using vision to determine which end to court.

A blindfolded male once in the vicinity of a female is at no disadvantage in competing with a rival. This was found to be true both of *T. sirtalis* and of *T. butleri* except when the males were irritated by the tape. For example, on April 17 a male, which had his eyes completely covered with opaqued adhesive tape, courted a female actively for nine minutes. When at the end of that time he lost his position, the cage was in no way disturbed. Thirty seconds later he had found the female again which at that moment was being vigorously courted by a control male. For nearly two minutes the female continued to move about the cage with the blindfolded and control males side by side on her back. Both had their chins on her neck and both were giving rapid caudocephalic undulations of their bodies. A moment later the blindfolded male succeeded in introducing his right hemipenis into the cloaca of the female and the rival male immediately left the coupled pair. The attachment of the hemipenis was secured approximately 14 minutes after the blindfolded male had begun the courtship. Here was a case where a blindfolded male had won in a contest with an unhampered male. It is possible that his nine minutes of uncontested courtship had given him a certain advantage but the control male was in possession of the female when he began his second period of courtship. When the two males had assumed the dorsal position there was no noticeable difference in the vigor of their activity.

In spite of the success of this and other blindfolded garter snakes, the eyes are not functionless in courtship. When courtship activity begins at a distance from the blindfolded male he rarely moves toward the center of activity. In the course of a morning there are frequent shifts of this center and it is the blindfolded males which are usually left behind. Male *T. butleri* in seeking a mate frequently wag their heads from side to side as if to secure several views of the same object. These movements are lost in a blindfolded individual who frequently remains quiescent in one place in the cage. In general, *T. butleri* seemed to suffer more from blindfolding than did *T. sirtalis*.

THE CHEMICAL SENSES IN COURTSHIP

Experiments with blindfolded *Thamnophis* showed clearly that the males could recognize sex at a short distance even in quiescent individuals. It seemed highly probable that the olfactory organs or some chemical receptors of the mouth were making this discrimination. It has been frequently stated that snakes during the breeding season become conspicuous by their odors (Brons, 1882). These odors have been traced to their source in the cloacal glands which are well known to ejaculate their contents when the snakes are roughly handled. Many species, such as the timber rattler (*Crotalus horridus*), copperhead (*Agkistrodon mokasen*), and water moccasin (*Agkistrodon piscivorus*), have a very characteristic odor and differences between the odor of this secretion in foreign species have been frequently described. Wall (1921), who has made a close study of the differences in cloacal gland secretions of various Indian snakes, is not, however, prepared to believe that they serve as the source of sexual attraction. He states: "The glands in both sexes are active at all seasons, and at all ages from the time of hatching, so that I am inclined to question the popular belief fostered by Darwin among others that they are concerned with the sexual functions." On the other hand, Baumann (1929), in studying the courtship of *Vipera aspis*, found that the males would follow the trail of a female during the breeding season and places where the female had opened her cloaca served as regions of great attraction, inducing violent searching movements in the males. In *Storeria* and *Thamnophis*, the female was never observed to open her cloaca when trailed by a male. Moreover, at no stage in the courtship did the males attempt to nose the cloaca of the female. When females were anaesthetized, turned on their backs and some of the secretion forced out on the lips of the cloaca, this ill-smelling fluid never arrested the attention of males

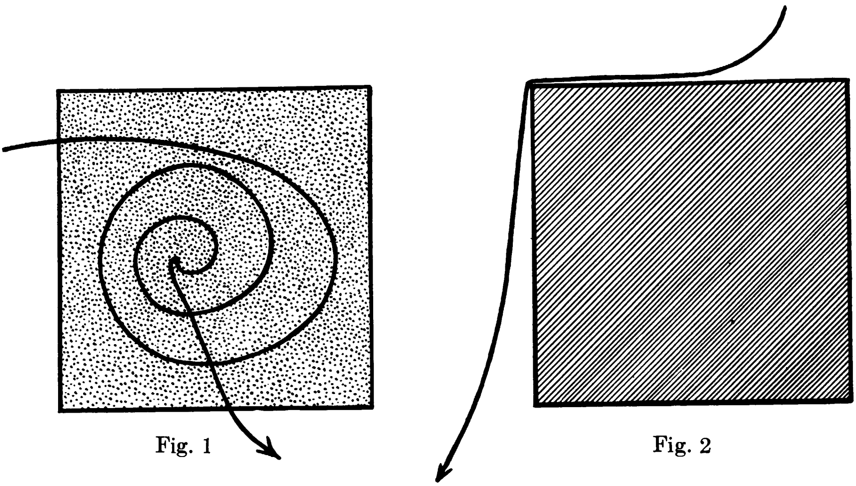

Fig. 1 Fig. 2

Fig. 1. Glass plate, 17 cm. square, rubbed with lateral integument of a female *Thamnophis sirtalis* in oestrum; spiral line, the trail made by a breeding male of the same species.

Fig. 2. The same glass plate rubbed with cloacal gland secretion of the same female *T. sirtalis;* the same male no longer crosses it but follows edge as indicated.

at any stage in their courtship. On the other hand, males intent on courting would respond at once with the chin pressing response to any portion of the female's body they chanced upon in their searching. The integumental covering of the body of snakes is devoid of glands and if kept cleanly is practically devoid of odor. It is, therefore, not surprising that no one has suggested until recently (Noble and Clausen, 1936) that the body skin itself was the chief source of sexual attraction.

In order to test the relative importance of skin versus cloacal gland secretion as a source of attraction a series of clean glass plates were introduced into the cages. Trails were marked on them in various directions by rubbing either the back skin of a female, the cloacal gland secretion of the same, or both of them on different parts of the plate. The male *T. sirtalis* was repeatedly observed to attempt to push his chin through the glass plate which had been rubbed with back skin of a female but he would merely flicker his tongue over the glass rubbed with the cloacal gland secretion of the same female (figure 2). When the back skin of a female was rubbed diagonally across a glass plate,

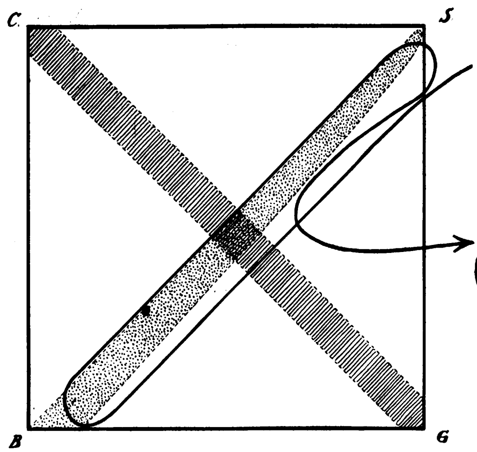

Fig. 3

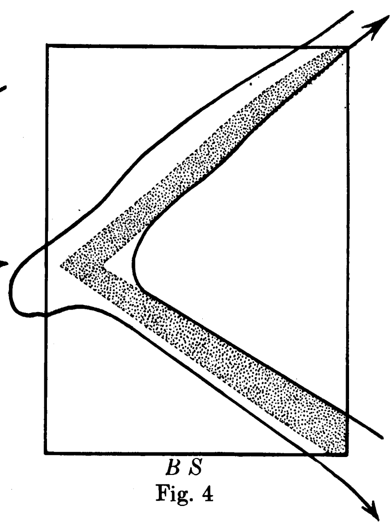

Fig. 4

Fig. 3. Glass plate, 17.5 cm. square, with trails made by rubbing the back skin (B.S.) and the cloacal gland secretion (C.G.) of an oestrous *Thamnophis butleri* diagonally across it. Trail of male of same species indicated by dark line.

Fig. 4. Two trails of a male *Thamnophis sirtalis* which attempted to follow a trail made by rubbing the lateral body integument of an oestrous female on a glass plate, 37 × 28 cm. The sharp angle in the trail usually confused the male.

17.5 cm. square, and the cloacal gland secretion of the same female was rubbed across the same plate in a trail at right angles to the first, one male *T. butleri* made, on May 2, the trail shown in figure 3. The trail on the glass made by the back skin was barely visible while the cloacal secretion trail dried to form a well-marked streak. Nevertheless, the male showed no interest in the latter but doubled back on himself twice to keep to the back skin trail. In another test with a pair of *T. sirtalis*, the male chanced to start across the glass at a point near the cloacal gland secretion. He kept his head high while over the cloacal secretion streak but when he reached the back skin trail he put his chin close to the glass and followed the latter trail.

Trails made by rubbing either the side of the body or the back of the female on the glass plate were equally effective. When the plate was uniformly rubbed with the integument of a female the male in his effort to push through the plate would circle around in the manner

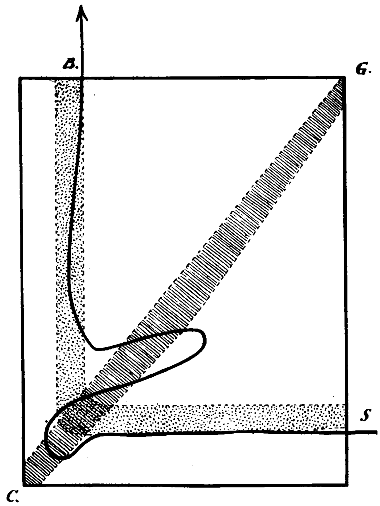

Fig. 5

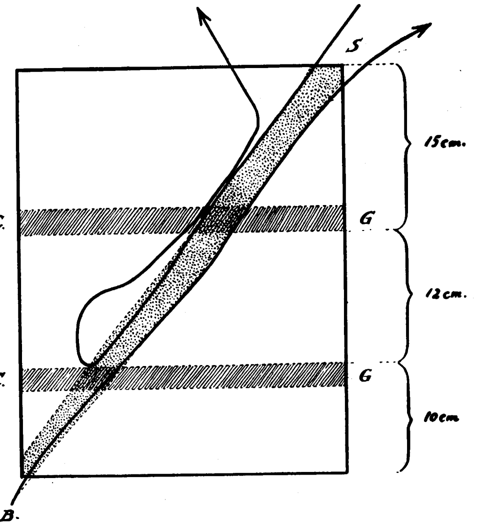

Fig. 6

Fig. 5. Trail made by a male *Thamnophis sirtalis* in attempting to follow the trail of lateral body integument of an oestrous female on a glass plate, 37 × 28 cm. The sharp bend and the presence of cloacal gland secretion (C.G.) at this point confused the male.

Fig. 6. Two trails of a male *Thamnophis sirtalis* which attempted to follow a trail made by rubbing integument of the side of an oestrous female on a glass plate. Two trails of cloacal gland secretion (C.G.) cross the body skin trail (B.S.) and on the second trial one of these turned back the male.

shown in figure 1. A body skin trail made with a sharp angle in it would frequently confuse the male. Thus a trail made as shown in Figure 5 was followed to the right angle bend but then the male moved a short distance along the cloacal secretion trail in two directions before he could locate the remainder of the body skin trail and follow it to the end of the glass. When there was no cloacal gland secretion the male was more apt to negotiate successfully a right angle bend in the body skin trail. When the angle was on the edge of the plate, the male might run off the plate before making the turn. Some males would realize they were coming to a turn and would cut the angle short. Figure 4 shows both kinds of turns made by a male *T. sirtalis*. Since the males frequently passed over the cloacal secretion trail, the odor of this trail

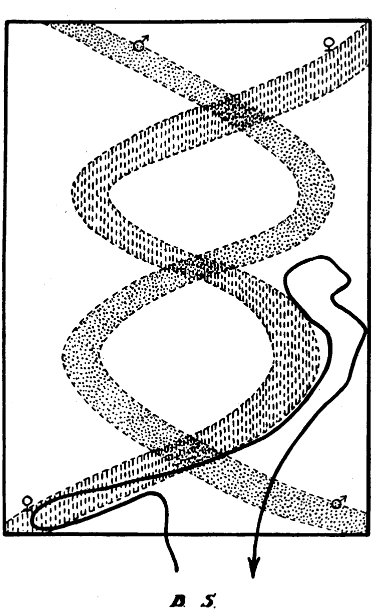

Fig. 7

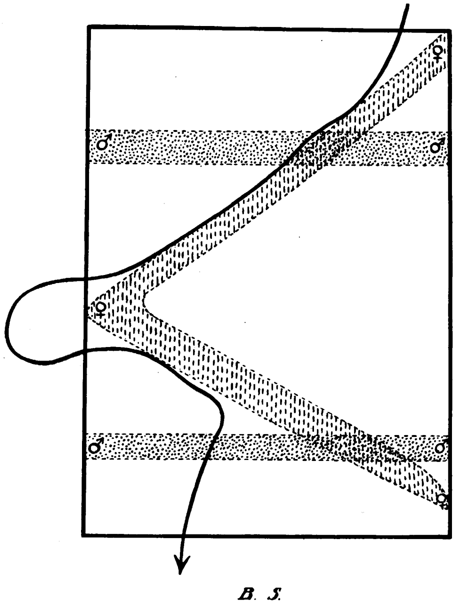

Fig. 8

Fig. 7. Trail of a male *Thamnophis butleri* which attempted to follow the trail of an oestrous female made by rubbing her lateral integument on a glass plate, 11 × 15 cm. The male became confused by the trail of another male which crossed that of the female.

Fig. 8. Trail of a male *T. sirtalis* which attempted to follow that of an oestrous female made by rubbing her lateral integument on a glass plate, 11 × 15 cm. The sharp bend and the presence of trails made by another male's integument eventually confused the trailing male.

was not a deterrent but more likely a distracting factor (figure 5). On one trial a male *T. sirtalis*, for example, ran across two cloacal secretion trails to follow the back skin trail across the plate. But on the next trail he turned back at one crossroad of the two trails. In this case some disturbing factor other than the cloacal gland secretion may have modified the result because he left the skin trail before completing it (figure 6).

One of the most obvious distracting factors is the movement of snakes in adjacent cages. When a series of cages are placed side by side the snakes tend to aggregate along the juxtaposed sides. They also try to push through the glass sides in the direction of their moving companions much more frequently than through the other glass sides. As Noble and Clausen (1936) have shown, vision plays an important rôle in the aggregation of *Storeria* and *Thamnophis*. It is the movement of the nearby companions which attracts.

When numbers of courting snakes are together in a cage the males have no difficulty in distinguishing sex. Two blindfolded rivals attempting to keep their chins on the dorsal surface of a female rarely become confused and court one another. Since blindfolded males put their chins firmly against even the smallest sections of a female's back which may be exposed in a cluster of courting snakes, it is clear that there is some quality in this piece of skin which makes sex discrimination possible.

In order to test the possibility that the discrimination was made on the basis of odor from the body integument, trails were made on clean glass plates as before but with male body skin trails crossing those made from female skin. The results were as clear-cut as in the previous experiments. Males will follow the trails made by the body integument of the female but not, during several minutes of observation, those made by the male. Again, sharp angles tend to throw the snake off the trail and a cross trail of a male may distract the trailing male from following the female trail to the end of the plate. The trail shown in figure 7 was made by a *T. butleri* and that in figure 8 by a *T. sirtalis*. In both cases the glass plate was merely placed in a cage with a male which had been courting some minutes previously. Neither male crossed the plate until, while following the edge of the plate, he came upon the female trail.

These experiments with male and female body skin trails were made on May 7, at what may be considered the height of the breeding season. In the fall of the year, Noble and Clausen (1936) have found that *Storeria* will follow male and female trails indiscriminately. In May, I did not succeed in inducing male *Thamnophis* to follow male trails on glass plate nor females to follow male trails. However, at the end of November, I found that *T. sirtalis*, which had been in the laboratory several weeks would follow for short distances the trail of one of its own species regardless of sex. These observations on trailing at different times of the year have been reported in greater detail elsewhere (Noble and Clausen, 1936). They clearly show that motivation plays a rôle in trailing. In the spring, sex attraction dominates over species attraction. In the fall, when the aggregation drive predominates, sexual attraction cannot be demonstrated. It is, nevertheless, remarkable that the attracting odors emanate from a glandless skin and not from trails made by the pungent cloacal gland secretion.

How far will the odor of the female snake carry? To test this question females of *T. sirtalis* and *T. butleri* which were being actively courted were placed in black cloth bags and returned to the cages with the males. None of the males showed any greater interest in the bags than they did in the moss or similar objects in their cages. The females were then placed in glass finger bowls and covered with finely perforated paper. The dishes were turned in such a way that the females were nearly in contact with the paper. Although these dishes were placed before several males which had been courting a few minutes previously, no male approached the paper and pressed his chin against it. These experiments gave no evidence that the males are able to recognize a living female when she is covered with a perforated screen. The experiments, taken alone, might indicate that a visual stimulus was necessary to initiate the searching response. But since blindfolded males made vigorous efforts to come in contact with uncovered females it seems more probable that the absence of a trail on the outside of the bags or paper covers prevented the males from finding the females. We may conclude that a trail is essential for arresting the attention of the male.

Garter snakes evaporate considerable amounts of water through their skin. It seemed possible that the odorous material might escape with the water from deeper tissues of the snake's body and gradually accumulate by drying on the surface. An attempt was made, therefore, to remove this supposed accumulation by washing. A thorough scrubbing of the female's body with Ivory soap and warm water did not delay the response of the male. Other females which were being courted were washed with 50 per cent or 70 per cent alcohol and others were washed with ether. As soon as the alcohol or ether dried the males began to court these females showing that this treatment had also failed to remove the source of attraction.

Attempts were then made to eliminate the odor by painting the female's back with various chemicals. When the back of a female *T. butleri* was well powdered with quinine sulphate the progress of a male over this area was not seriously delayed even though the powder stuck to his tongue preventing it from flickering normally. Another male

T. butleri crossed a belt of saturated solution of picric acid, 2 cm. wide, on the back of a female. When the belt was extended to cover a much larger part of the back the male thrust his tongue into the acid and drew back. After another test and withdrawal the male moved forward over the acid and began to court normally. A two per cent solution of ammonium hydroxide was no deterrent to a male. Similarly, powdered thymol or sodium bicarbonate when spread widely over the female's back had apparently no effect on delaying courtship.

In striking contrast powdered sodium chloride completely blocked all courtship activities of the male. Similarly vaseline when rubbed across a female's back would prevent the male from progressing forward beyond that point. Females of *T. sirtalis* and *T. butleri* which were being actively courted were rendered entirely unattractive by covering them with a thin layer of white vaseline. This substance has very little taste and in striking contrast to the quinine and picric acid has no effect upon the membranes of the human mouth. Why a male would court a female covered with picric acid or quinine and yet show no interest in one smeared with vaseline, is difficult to understand unless the vaseline, unlike the other substances, covered the odorous source of attraction. Oil of wintergreen was toxic to both the female and the male which thrust his chin into the oil. Concentrated ammonium hydroxide proved highly irritating but not toxic. Balsam St. Roco had a similar effect.

Snakes covered with vaseline do not give any evidence of irritation. Further, they live for long periods following this treatment. This may be considered further evidence that the vaseline functions as a cover and not an irritant in the above experiments. If males are responding to minute quantities of odorous materials it is remarkable that they can detect these substances even when the areas are covered with very sour or very bitter substances.

The recent experiments of Kahmann (1932) have indicated that the tongue of snakes functions during trail finding by picking up minute quantities of odorous substances in the air and carrying them to Jacobson's organ. Kahmann's experiments were concerned with the trailing of prey. When a male *Thamnophis* ready to court comes upon the trail of a female in breeding condition he not only thrusts out his tongue rapidly in the direction of the trail but he lowers his snout over the trail until his chin is frequently in contact with it. It seemed possible that the olfactory organs as well as Jacobson's organ might help in following the trail. Tests were made therefore of the relative importance of these two organs by noting the courtship behavior after the functioning of first one and then the other had been obstructed.

A series of male *Thamnophis sirtalis* and *T. butleri* which were actively courting had their nostrils plugged with adhesive tape covered with vaseline or a stop-cock grease. In no case would one of these snakes return to a female. As soon as the plugs were removed they began courting again. A much larger piece of adhesive tape could be placed across the eyes or anywhere on the upper surface of the head without preventing courtship. Hence, it was not the irritation of the tape itself but the closing of the nasal passages which brought the courting behavior to a halt.

The experiment was repeated with other kinds of nostril plugs. The snakes would rub their snouts vigorously against the ground loosening if not dislodging most of these. A 10 per cent solution of collodion when painted well inside the nostrils seemed to be fairly resistant to the rubbing movements of the snakes. No male *T. butleri* would court after the nostrils had been completely plugged with this material. However, one male *T. sirtalis* which had been received fresh from the field began to court five minutes after the nostrils had been plugged. A check of the nostrils revealed the closure was complete. Since this snake had been given very little opportunity to court in the laboratory its ability to court without the use of its olfactory passages was apparently not due to special training. Two other male *T. sirtalis* with their nostrils merely plugged with cotton soaked in petrolatum trailed and courted females but the completeness of the closure at the moment of trailing could not be determined beyond any doubt. *T. butleri* is more sensitive to bandages placed on its head than is *T. sirtalis*. Hence, the failure to repeat these experiments on the former species is not surprising. It may be concluded that while closing the nostrils of the male *Thamnophis* is a serious obstruction to courtship, the olfactory organs are not indispensable in *T. sirtalis* at least.

Another series of male *Thamnophis* which had been courting in the laboratory had various portions of the tongue removed. This operation usually stopped all courtship behavior. There was usually no return of the courtship although the wounds healed well and the controls continued to court. No *T. butleri* ever courted again whether or not only the forked tip or the entire tongue was removed. On April 17, 1934, I succeeded in inducing two male *T. sirtalis* to court actively a female for over two hours after severing the tongue immediately caudal to the bifurcation. One of these males eventually succeeded in copulating with the female. According to Kahmann (1932), it is the tips of the tongue which are essential to trailing for they carry the odorous substances directly to Jacobson's organ. The operation had presumably prevented all further functioning of that organ. Nevertheless, these two snakes continued to follow the female's trail. It may be concluded that both the olfactory and Jacobson's organs normally enter into the trailing performance but that either one may function alone. Still the complete obstruction of one set of organs is usually sufficiently diverting to prevent courtship from continuing.

Thamnophis, outside of the breeding season, does not trail others of its own species as well as does *Storeria* (Noble and Clausen, 1936). At least a series of *T. sirtalis* when tested in November and December with trails of others of the same sex failed to follow any more than a short distance. The males never held their snouts close to the trail as they moved forward. Hence, during these months the species' odor has little attraction for individuals which have been maintained in cages for a few weeks previously at an approximate temperature of 20° C.

The female odor which is so attractive to males during the breeding season is not produced in equal amounts by all adult females. Particular females become sexually attractive during short periods during which they and not other mature females in the cages are sought by the males. Females which were being courted by males were marked and placed in cool cages with several other adult females and males. At intervals during several days the cages were exposed to sufficient warmth to induce courtship. In these cases it was always the marked females which attracted the males. Hence, it may be assumed that female snakes experience an oestrum during which particles rubbed from their skin are particularly attractive to males which are in a breeding condition. The males do not follow actively any adult female during the breeding season but only those that are in this oestrum. Davis (1936) has recorded a *T. radix* as passing by one female in the field to court another indicating that the same condition prevails there. Since the oestrum has no definite relation to the molt, it seems highly probable that as the female comes into oestrum, fluids attractive to the male are exuded through her skin. There is no visible indication of these fluids on the outside of the skin but since the experiments discussed above have shown that the skin is attractive even to a blindfolded snake something must be in the skin during oestrum to render it attractive to males.

The odorous substance in the skin of an oestrous female is highly specific. On many occasions an attempt was made to replace a female

T. butleri which was being courted with a female *T. sirtalis* in oestrum. After flickering the tongue over the skin of the new female the male would turn away. The converse experiment substituting a female *T. butleri* for a *T. sirtalis* gave similar results.

THE RÔLE OF MOVEMENT IN COURTSHIP

It was frequently noted throughout the work on large numbers of courting *Thamnophis* that movement of the female excited the males to greater activity. Vigorous caudocephalic waves could be elicited in a courting male, which had quieted down, merely by pinching the tail of the female, thus inducing her to move forward. Male *T. butleri* and *T. sirtalis* which had been actively courting particular females soon lost interest in these individuals when they were etherized. Pithed or decapitated females of both species lost their attractions for the same males which had been courting them a few minutes previously. When the dead female was placed in contact with the male or near him he frequently would court for a short time. Usually this was a matter of seconds. But two decapitated *T. butleri* were courted five minutes and one for 11 minutes. In one case a male which had not been courting previously that day went to a decapitated female *T. butleri* placed in his cage and courted her for 8 minutes 45 seconds. This was the record for courtship of a dead female by a new male. No male *T. sirtalis* courted freshly killed females for so long a period.

On the other hand if etherized or freshly killed females were moved, the males usually showed an immediate interest. One record will illustrate this response.

May 4. A female *T. butleri*, which was being actively courted, was killed by ether and then thoroughly washed with soap and water. An hour later the dead snake was placed in the cage with the male which had been courting her. The day was overcast and by this time no other *T. butleri* were courting. Two pairs of *T. sirtalis* were courting in the same room but their movements were very slow. The head of the dead female was held in the fingers and the body pulled slowly about the cage. This excited the male to violent courtship. After running the length of her body he pressed his chin against her neck and gave vigorous caudocephalic undulations of his body. He continued to court from 1:05 to 1:57 P.M. A second male began to court at 2 P.M. and continued to 2:07. At 2:07 the first male began again and was joined by the second at 2:09. The latter quit at 2:11 but the first persisted until 2:39.

In the above experiment the dead but slowly moved female induced a male *T. butleri* to court for 52 minutes and later for 32 minutes at a stretch. A second male was also attracted to the body but was displaced by his rival. Such persistence was never found when the freshly killed female of either *T. butleri* or *T. sirtalis* was left immobile in the cage.

The slow forward movement of the female which usually accompanies a normal courtship is an aid to orientation. If a courting male comes in contact with a quiescent female he frequently runs his chin caudally along her body instead of cephalically. Only when the tail is reached does the male turn to assume the normal position. When etherized females were placed near courting males the latter frequently started wrong and in two instances with *T. sirtalis* continued to court with the chin over the tail base of the female. When a male has started in the wrong direction a forward movement of the female will frequently orient him correctly. Apparently in the normal courtship of *Thamnophis* the slow forward movement of the female is a definite aid to the orientation of the male.

It seemed remarkable that although a large series of experiments was performed with anaesthetized and freshly killed females no courtship with this material ended in copulation. A possible explanation for this failure to complete the act was suggested by observations on normal material. Copulation was observed many times in *T. sirtalis* and *T. butleri* and when conditions for observation were good it could be observed that the female actually opened her cloaca before the male everted his hemipenis. The best record was made April 17, 1934, when a female was seen to hold her cloaca slightly open for 45 seconds before the male finally inserted his hemipenis. Since the cloaca is never opened at any other time except for defecation the open cloaca seemed to be a necessary feature to permit copulation.

A long series of experiments with anaesthetized females were performed. Their cloacas were held open to various degrees with cotton, cork plugs or different types of stitches. Although the male frequently brought his cloaca in contact with the gaping cloaca of the female, in no case was his hemipenis inserted. When the females recovered from the anaesthetic many would appear to progress normally about the cage but males never succeeded in copulating with them. It was clear from these experiments that some essential factor was missing.

In order to secure further evidence as to the cause for this failure to mate, experiments were conducted on females with transected cords, The break was made from five to ten vertebrae anterior to the cloaca. Females lived well after this operation although the body posterior to the level of injury did not take part in any of the movements of locomotion. Such females were actively courted but no males succeeded in bringing their cloacas in close juxtaposition to those of these females. Apparently this was due to the lack of resistance in the cloacal and tail regions of the experimental females. Courtship would continue because the movement and odor of the anterior part of the experimentals attracted the males but the paralyzed posterior parts of these snakes lacked certain qualities essential for the males to secure the normal mating grip with their tails. These experiments suggest that an anaesthetized female with gaping cloaca also lacks certain qualities of resistance or possibly reciprocal movement which prevent the insertion of the hemipenis.

THE RÔLE OF TACTILE ORGANS IN COURTSHIP

The above experiment with partly paralyzed snakes seemed to indicate that the tactile sense must aid the males during courtship. It has been previously noted that a small male when courting a large female may slide too far forward along her body but before the caudocephalic undulations have well begun the male moves back until his cloaca is not far from that of the female. Obviously vision does not aid the males in determining their position because blindfolded males make the adjustment as quickly as do the controls. A chemical sense would not appear to enter into the problem because the exact position of the male's head on the back of a female varies with the size of the female. Hence, by a matter of elimination, it seemed probable that the male depended chiefly on his tactile sense to secure the proper position on the body of the female.

Apparent confirmation of this view was secured by binding the cloacal region of the male *Thamnophis* with one or more thicknesses of adhesive tape. Such treatment did not prevent the male from actively pursuing the female nor practicing his caudocephalic undulations but even when the tape did not extend more than a centimeter or two on the tail base the male was unable to assume the proper position for mating. When a much heavier wrapping of adhesive tape was made around the middle section of the tail of a male *T. butleri* leaving the cloacal region and tail tip free, the snake succeeded in assuming the normal pose. A band of adhesive tape only two centimeters wide wrapped three times around the cloaca of a female *T. butleri* prevented a male from encircling the female's tail in the normal manner. His caudocephalic undulations continued for ten minutes. On a second test the male came voluntarily to the female and continued the body undulations for three minutes without encircling the female's tail although the latter was entirely free from tape except for its base. These experiments showed that encircling the cloacal region of either the male or the female with tape prevented the male from securing his normal position with cloaca near that of the female. Apparently the body integument of the cloacal region of the male is sufficiently sensitive to determine accurately the position of the male's body with relation to the female's cloaca.

It was noted at the beginning of this work that the male *Thamnophis* when courting the female attempts to rub his chin along her back. He continues in his efforts even when blindfolded with blackened adhesive tape. It was interesting to find that a single piece of adhesive tape stuck over the chin of either *T. butleri* or *T. sirtalis* completely disrupts the courtship of even the most ardent males. A thin layer of collodion on the chin may not prevent courtship entirely but the male frequently pushes with such vigor into the back of the female that the head is carried forward in a series of jerks. Covering the chin with tape or collodion has, therefore, a very different effect on courtship than has covering the cloacal region. All males with taped chins gave up the courtship within a few seconds, while males with taped cloacas not only continued their old courtships but began new ones. One male *T. butleri*, with his cloacal region so firmly wrapped that the tail was held at an angle of 45° to the axis of his body, continued his courtship for 45 minutes. A male *T. sirtalis* with his tail wrapped so tightly that it could not be bent, courted a female for 48 minutes. Whether or not the male's rubbing with his chin serves to stimulate the female, these same movements have a stimulating effect on the male for without them courtship will not continue. The cessation of courtship after taping the chin cannot be due to irritation. In several instances the male *T. sirtalis* after taping went back to the moving female but after a few thrusts with the chin turned away again.

The tactile organs in the chin of the male *Thamnophis* may have other functions during courtship besides those of autoeroticism. It has been pointed out that a blindfolded male may start in the wrong direction on the body of a quiet female but when he reaches her tail base he usually turns quickly about and makes his way to the neck region. The most distinctive feature of the upper surface of the tail base is the slight narrowing of the scale rows in correlation with the tapering of the tail. Whether or not this slight difference gives a clue to the male as to his position is impossible to say. Small obstructions on the dorsal surface of a female are usually passed over. But a piece of tape 13 × 80 mm. when firmly stuck to the back of the female *T. butleri* prevented courtship. The male ran his chin back and forth from tail base to tape but would not come to rest with his chin over the tape. It is possible that tape seriously decreased the odor of this dorsal region but the speed with which the male turned at the edge of the tape suggests that mechanical factors, namely, the edge of the tape, entered into the problem.

Although male *Thamnophis* with cloacal region taped may come to rest too far forward on the body of the female they do not as a rule move forward over the head. This was particularly well shown in a blindfolded *T. sirtalis* which had his tail taped in a fixed position at 45° to his body axis. In a series of tests this male invariably stopped his forward progress along the female's body in the anterior part of the neck where the scale rows, like those on the tail base, are slightly narrowed.

There is, therefore, some evidence that the character of the scale rows may have some influence on directing the movements of a courting male. Attempts to induce the male to court rubber tubes of approximately the same diameter as the female's body were not successful. When such a tube was moved near a male which had been courting previously he would follow it with head well raised above it. When the same tube was vigorously rubbed with the integument from the side of a female's body and then moved about the cage the male would not only follow but keep his chin pressed tightly against it. But in no case would the male attempt to encircle the tube with his tail, nor were any caudocephalic undulations of his body induced. As soon as the movements of the tube were stopped the male turned his head away and showed no further interest. While it is possible that not a sufficient amount of odorous substances was removed from the body of the female to permit a more extensive courtship with the rubber tube, it seems equally likely that the smooth tube, like smooth adhesive tape, is not sufficiently stimulating to the male to permit his courtship to continue.

HOMOSEXUALITY

The males throughout the course of the series of experiments reported above frequently came in contact with one another but in no case did male *T. butleri* court one another. It is, therefore, of interest to record two cases where male *T. sirtalis* persistently courted other males. On May 3, 1933, a large male collected at Pelham Bay, N. Y., was placed in a cage with a series of smaller males from Olean, N. Y. Two of these smaller males immediately began to rub their chins along the larger male and exhibit well-marked caudocephalic undulations. The courtship continued for half an hour when a large female from Olean which was being courted in another cage was placed in the cage with the homosexual males. For nearly five minutes the small males continued to court the larger one. Then one deserted the large male for the female. The other continued his homosexual courtship for 35 minutes. On May 4, the pair was left in an icebox at 10° C. On May 5, and again on May 9, the same male began to court the large male again. Both males were tested with sexually attractive females without result. On May 10, the small homosexual male was tested again with a sexually attractive female and immediately began to court her. A trail was made on a glass plate by rubbing the back of this female in a circuitous course at an angle to a trail made with the back skin of the large male. The male which had previously displayed only homosexual interest followed the female trail across that of the large male.

The large snake which had proved attractive to two different males exhibited well-developed supracloacal tubercles. His sex was confirmed by everting the hemipenes. On dissection no ovarian tissue was discovered. The right testis measured 18 × 4 mm. and the left 17 × 4 mm. The kidneys were less yellow than in typical breeding males and this, together with the late date, would indicate that the breeding season of this particular male had passed. It seems highly unlikely that the attractiveness of this male could have been due to female secretion being rubbed over him because he was handled in the same manner as all the other snakes. Possibly male *T. sirtalis* from Pelham Bay have evolved odors sufficiently like the females from Olean as to confuse the males from that locality. It is also possible that the homosexual courtship was due to conditioning on the part of the Olean males. In this connection it may be noted that both males eventually deserted the large male for a female. It is also significant that the only other case of homosexual courtships among the several hundred snakes which have courted in the laboratory during the past four years was produced by mixing males from distant localities. A male *T. sirtalis* from Baltimore, Md., introduced into a cage of courting pairs from Flushing, Long Island, settled down to persistently court another male. Four days later, on April 21, this same male divided his attentions equally between a male and a female pushing his chin along the back of both and attempting to encircle first one and then the other. Later the same day the same male responded only to the female. Hence, in neither case of homosexuality witnessed in the laboratory was the attraction of one male for another persistent throughout the whole breeding season.

Although snakes have frequently been observed to mate both in the laboratory and in the field, there is apparently only one other record of homosexuality in this group. This was a case of two male *Agkistrodon piscivorus* which had lived together for three years previous to the mating. The copulation was reported as lasting seven and a half hours (Lederer, 1931). The sex of the moccasin which functioned as a female was determined by dissection. Apparently the dominant male never had access to a female during the three years in captivity. This single case of homosexual mating might be attributed to conditioning induced by the long confinement with another male snake.

THE OESTROUS CYCLE

It has been pointed out above that garter snakes appear to experience an oestrous cycle in that courting males return on successive days to the same female while ignoring the females which seem identical in size and color to the selected one. I have dissected five females of *T. butleri* which were being actively courted and have found no eggs in the oviducts. The largest in the ovaries were 5 × 3 mm. in four of the specimens. In the fifth specimen the largest ovarian eggs were 7.5 mm. in greatest diameter. The trailing experiments reported above clearly indicated that these females had present in their general body integument an odorous substance which was attractive to males of their own species.

The brief season of sexual attractiveness of snakes is comparable with that of mammals in that the female of both leaves an odorous trail which is followed by the males. In mammals the relation of the ovary to the elaboration and release of these odorous substances is well known. Snakes appear to differ from most mammals in that oestrum may occur during pregnancy. At least Wall (1906/1907) has recorded two apparent cases of courtship during pregnancy in *Ptyas mucosus* and one in *Natrix piscator*. He has also reported (1921) a case in the cobra and another (1910) in *Elaphe radiata*. Bishop and Alexander (1927) dissected a female *Storeria occipitomaculata* which they found mating July 9, and found that her body contained well-developed embryos. Similarly, Wood (1933) has found that *Crotalus viridis* may copulate during pregnancy. Hence, it may be concluded that copulation during pregnancy is possibly a normal occurrence in many snakes.

Although most snakes living in the north temperate regions breed in the spring, a second oestrum apparently normally occurs in the fall in the case of many species. September matings have been recorded in *Natrix natrix* (Bolam, 1922; Hecht, 1930), *N. tessellata* (Hecht, 1930) as well as in *Thamnophis radix* (Coues and Yarrow, 1878). In our laboratory in the American Museum a male *Thamnophis sirtalis* began to court a female of the same species on October 9 and continued for several days the caudocephalic body undulations without securing a copulation. Dymond and Fry (1932) observed *Liopeltis vernalis* copulating on August 18 and 22. The copperhead, *Agkistrodon mokasen*, has been observed mating as late as August 28 (Hay, 1893). The European *Vipera berus* has been found pregnant in March (Vainio, 1932), giving evidence of a fall mating for this species.

It may be assumed that if the fall breeding season began very early some males might copulate with pregnant females. It is nevertheless surprising that a female snake while carrying well-advanced young should enter a definite oestrum, that is, become sexually attractive to males. This raises the question of the nature and strength of the odorous substances which attract the males of snakes in general.

In this connection Amaral (1932) has reported a male *Bothrops jararaca* copulating with a dead female *Crotalus durissus terrificus*. Since Amaral did not witness the beginning of the mating it is possible the female was still alive when copulation began. Mole (1924) has recorded a case of *Spilotes pullatus* copulating with *Phrynonax poecilonotus polylepis* in captivity and Klinge (1925) has described a cross-mating between *Natrix viperina* and *Natrix tessellata*. Bonnenberger (1909) has reported a hybrid between *Thamnophis elegans* and *Natrix fasciatus* after the parents had been kept together for a long period. Davis (1936) has described a mating between *Crotalus molossus* and *C. atrox* in captivity. I was able to induce an actively courting *T. sirtalis* to continue his caudocephalic undulations for some minutes after he was transferred to the body of a *Natrix sipedon*. In no case, however, have courtships between two different species occurred in our laboratory even though actively courting pairs of *T. sirtalis* and *T. butleri* were frequently mixed. In other laboratories where many species of snakes have been mixed, as for example in the Snake Park at Port Elizabeth, South Africa, mating between different species is so rare that Fitzsimons (1932) denies its occurrence. This rarity of courtship between two different species of snakes stands in striking contrast to the behavior of lizards. In these, vision is the dominant receptor during courtship and there are many records of one species attempting to mate with another (Noble and Bradley, 1933). In snakes, where the chemical senses dominate, this mistake is rarely made. Nevertheless, a few authentic cases of cross-mating are on record and these, like the instances of homosexuality reported above, must be attributed to a failure of the mechanism of discrimination which, as shown above, lies primarily in the chemical receptors.

COMPARISON BETWEEN THE FEEDING AND COURTING RESPONSES

It has been shown elsewhere that Dekay's snake when following a food trail makes use of its olfactory as well as its Jacobson's organs (Noble and Clausen, 1936). Snakes in general exhibit a wide range of feeding responses and the question arises as to how closely the evolution of courting behavior parallels the evolution of feeding behavior.

There is little evidence that snakes can "test the wind," that is, react to odors carried to them from a distance. Baumann (1929) found that *Vipera aspis*, a species which depends primarily on its chemical senses to secure food, did not respond to odors from prey which were at a greater distance than 10 cm. Several experiments with garter snakes behind perforated screens showed that in the absence of a trail these snakes will not push through a cover concealing individuals of the opposite sex.

Motion is of great importance for food seeking or mate hunting. Plaster casts of frogs will not call forth the seizing response of water snakes (Wiedemann, 1931) nor anaesthetized females hold the attention of garter snakes of the opposite sex. Large objects near at hand cause flight while small moving objects evoke an approach response. Visual discrimination is apparently poor in many snakes. Wiedemann (1931) describes *Natrix natrix* as striking toward large objects which were at a distance and apparently seemed small. Since snakes are greatly attracted by motion during the breeding season, this may account for the frequent report of snakes attacking people at that time. Apparently they, like the viper recently reported by Lotherington (1934), come toward a large moving object because it appears small at a distance. Outside of the breeding season the moving object would arrest the attention but not attract a viper. Snakes, such as *Storeria dekayi*, which are more social would be attracted at all seasons (Noble and Clausen, 1936).

Once the attention is arrested the chemical senses are used for identification of the object. Many strange objects are seized and swallowed by snakes when smeared with secretion from a prey animal (Wiedemann, 1931). For courtship to continue, the object must have a certain form and, apparently, texture of skin. Moreover, it must respond with movement of body and later of the cloacal region. Hence, an object to be courted successfully must have a much greater number of qualities than an object accepted as prey. The tactile sense may be of great service to water snakes which seize their prey under the surface of muddy water. Although the tactile sense may, therefore, function in food finding, it is not essential for this process while it is a *sine qua non* of courtship.

Visual images, and often not very clear ones, release the seizing reflexes of many snakes. The swallowing reflexes follow if the object has certain taste qualities. Olfaction and Jacobson's organ sense (which is essentially olfaction) may facilitate or even replace vision in bringing about the seizing reflexes. The labial and facial pits of snakes release the strike toward warm-blooded prey even when this is not seen (Noble and Schmidt, 1937). In courtship, olfaction or Jacobson's organ sense plays an indispensable rôle. Further, tactile sense which is least important in the feeding responses assumes a primary part in courtship.

THE RELATION OF COURTSHIP PATTERN TO THE SENSE ORGANS

It was pointed out in one of the earlier sections of this paper that the courtship pattern of snakes has undergone some evolution within the group. In correlation with this change some receptors would tend to have more significance and others less with the change in the pattern of behavior. For example, in *Thamnophis*, where the base of the male's tail has important tactile functions in sensing the position of the female's cloaca, section of the cord anterior to the tail in either sex prevents copulation from occurring. On the other hand in *Lampropeltis*, where the tails are not entwined, a case has been reported above of a male successfully mating with a female having a broken back.

When more is known of the courtship of *Heterodon contortrix* some explanation may be found for the observation of Medsger (1927), who reported two males simultaneously copulating with a female which, although nearly cut in half, may have been alive when mating began. The female was dead when picked up by Medsger, who shook the body before determining that each male had a hemipenis inserted into the cloaca. In *Thamnophis*, killing or even etherizing the female very soon causes the male to lose interest in her. It may be that in *Heterodon*, as well as in *Bothrops*, as reported by Amaral (1932), movement in the female is not an essential factor in stimulating the male to proceed with the mating.

Similarly, the male *Thamnophis* is in no way attracted by secretions of the female's cloaca but in *Vipera aspis*, Baumann (1929) found that places where the female had opened her cloaca were centers of great attraction for the male. Unfortunately, a series of *V. aspis* are not at hand to test the relative strength of trails left by body integument with those made by cloacal secretions.

When the courtship patterns of more species are known some explanation may be found for the variation in body proportions found in the different groups. In most snakes the tail of the male is longer and this is correlated with the fact that he has need for speed in following the female and that he requires an efficient gripping mechanism once he has caught her. This greater length of the male's tail is not due to a mere shifting forward of the vent as Boulenger (1913) was inclined to believe. In some snakes the number of ventral scales is higher in the male (Pope, 1935).

There is one feature in the courtship of *Thamnophis* and *Storeria* which seems to be due to the environment rather than to the pattern of behavior. It is frequently said that snakes gather together in balls during the breeding season. This, however, seems to be true only of northern species which have hibernated near together in especially favorable areas. In the New York area not only *Storeria* and *Thamnophis* aggregate for hibernation but also *Crotalus* and *Agkistrodon.* In southern parts of the United States, where rattlers do not hibernate in large groups, there is no aggregation formed during courtship. At least isolated pairs of *C. cerastes* have been found mating in April (Van Denburgh, 1922). This is in agreement with the earlier observation of Merriam (Stejneger, 1895). An isolated pair of *C. mitchellii stephensi* has also been taken in April, apparently courting (Stejneger, 1895). Linsdale (1932) has observed an isolated pair of *C. ruber* courting during April. As the pair moved off they remained pressed one against the other. Mating pairs of this species have been recorded as late as July 2 (Stejneger, 1895) but no reference is made to larger aggregations which are apparently not formed during the breeding season.

In the tropics, where with very few exceptions snakes do not hibernate in masses, the snake "balls" characteristic of many northern species do not occur. At least only single pairs of many species have been found courting or mating. The list of isolated unions or attempts at union includes *Helicops schistosus* (Wall, 1921), *Enhydris enhydris* (Wall, 1925), *Rhamphiophis oxyrhynchus* (Loveridge, 1923) and *Naja hannah* (Wall, 1925). We may assume from the experiments with *Thamnophis* that males follow the trails of individual females during the breeding season. Fitzsimons (1932) graphically describes the case of a male Mamba following the trail of a female. In the tropics and subtropics, where environmental conditions do not cause the females to draw together for hibernation, the mass courtships which have been reported in northern latitudes do not occur. Most male snakes do not fight their rivals during courtship and hence an occasional supernumerary male, such as Wright and Bishop (1915) reported in Georgia, may be found with a mated pair. There is no evidence that these supernumerary males ever mate with the female. Although Brennan (1924) reported a case of two male *Thamnophis* mating with a female at the same time, it appears from his description that he was actually witnessing merely a double courtship. As pointed out above, it is this absence of rivalry in the male and his failure to defend a particular territory which makes it unnecessary that he should be conspicuously colored or strikingly different in form from the female. The few snakes which exhibit rivalry are differently colored in the two sexes.

THE HYPERTROPHY OF TACTILE ORGANS IN MALE SNAKES

As pointed out previously (Noble, 1934), the tactile organs in the cloacal and chin regions of male *Thamnophis* differ considerably in structure. The hypertrophy of supracloacal tubercles in the natricine snakes is correlated with the rôle of tactile sense in making it possible for the male to locate his position relative to the female. The tactile organs of the chin, although found in both sexes, are equally indispensable to the male during courtship. A period of self-stimulation must precede the release of the male's caudocephalic undulations. It is in that group of natricine snakes which practice head nodding that the chin tubercles are most developed. Although the different functions of these mental and supracloacal tactile organs have been pointed out previously (Noble, 1934), a detailed comparison between these structures and other tactile organs in reptiles has not been published.

The tactile organs on the heads of snakes have been known since 1868 when Leydig described them on the snout of *Coronella austriaca.* In 1872 he described similar structures from the snout of *Natrix natrix* but in emphasizing their dermal nature failed to realize their homology to the tactile organs of *Coronella* which he assumed to be epidermal. Todaro (1878) considered the same structures in *Coluber viridiflavus* as epidermal and published two figures which seem to support his contention. The investigators who followed Todaro usually considered the tactile organs on the heads of snakes to be formed by a cluster of tactile cells which have been pushed from the dermis into the overlying epidermis. Schmidt (1918) has shown, however, that the question cannot be settled from a study of adult material alone for it is possible that various changes take place during ontogeny which make an interpretation of adult conditions difficult.

Neither Schmidt nor the authors who preceded him succeeded in following the nerves to their terminations. This desideratum was supplied as recently as 1927 by Jaburek, who gave a full account of the tactile organs on the lower jaw scales of *Natrix natrix.* Schmidt (1918) pointed out that although these structures were usually called tactile organs we had no proof of their function. Further, the presence of free nerve terminations in the epithelium of the head shields makes any experimental proof difficult.

The so-called tactile organs are found on the anterior labials, the mentals and submentals of snakes. They are absent from the throat scales of *Thamnophis, Storeria* and *Coluber.* They are equally numerous in both sexes of *Coluber* but are slightly more numerous and extend more caudally in the males of *Thamnophis sirtalis* and *T. butleri*. The fact that the organs are equally well developed in both sexes of snakes shows that their primary function is not sexual. That their function is primarily tactile is indicated by two facts. First, the region where these organs occur has important tactile functions while regions of free nerve terminations lack these particular tactile functions. Second, these organs become involved in the formation of tubercles which seem to have important tactile functions during courtship.

Several species of Asiatic snakes of the genera *Natrix* and *Opisthotropis* have tubercles on the chin of the male (Pope, 1935). None of these have been available in living condition which would permit adequate histological studies. Hence, my observations on the innervation and detailed structure of these organs has been restricted to the American *Natrix rhombifera*. However, I have checked my conclusions with sections of the tubercles of the male *Natrix aequifasciata* preserved in formalin. It is clear that in both this species and *N. rhombifera* dermal papillae force up the overlying epidermis to form the tubercles. These dermal papillae are not sensory, for nerve fibers may be traced through them to the finger-like sense organs in the overlying epidermis (Pl. IX, fig. *D*). Sections stained with a modification of the Gros silver nitrate technique previously described (Noble and Schmidt, 1937) show nerve fibers penetrating the epidermal cells, after losing their connective tissue sheaths. Under oil immersion the relation of the nerve terminals to the epidermal cells may be readily seen. Several tactile organs may overlie a single dermal papilla, but others may be adjacent to it (Pl. IX, fig. *C*). Hence, not all the tactile organs have had their efficiency increased by the elaboration of a papilla of connective tissue in the underlying dermis.

Each tactile organ seems to be formed by a column of dermal cells which are thrust like a finger into the epidermis. Although these cells may be slightly flattened, as Jaburek figures them, they may also show some irregularity. What appears to be an incipient stage in the formation of one of these tactile organs is found at irregular intervals on the chins of some *Thamnophis* (Pl. X, fig. *A*). In these the dermal origin of the core of the tactile organ is more apparent.

The nerve endings of the tactile organs are button-like and often very superficial in the epidermis directly under a thinned portion of the horny layer (Pl. IX, fig. *A*). In the male *Coluber constrictor* the endings form a very regular crown on the surface of the tactile organ (Pl. IX, fig. *B*). The endings in this crown are more numerous and arranged more regularly than those lying on the outer margin of the tactile organ of the garter snake (Pl. IX, fig. *A*).

The supracloacal tubercles of *Thamnophis* and *Natrix* differ radically from the chin tubercles of some *Natrix* in that there are no extensions of the dermis into the epidermis (Pl. X, fig. *B*). Further nerve fibers ramify between the cells of the dermal papilla without extending into the overlying epidermis. The epidermis covering the dermal papilla to form a tubercle is slightly thinned and not thickened as one would expect if the tubercle were a rubbing organ as previous observers have assumed. The dermal papilla is formed of polygonal or elongate cells irregularly scattered through a capsule of collagenous fibers. The nerve fibers which ramify through the capsule end in small knob-like enlargements in contact with the elongate cells. These may be considered tactile cells although they are not discoidal or hyaline as the tactile cells of some other vertebrates.

Although *Storeria* has no clear cut development of supracloacal tubercles in the male, sections of the integument prepared with Mallory's connective tissue stain reveal incipient tactile organs in the same position as in *Thamnophis* but not pushing up the overlying epidermis in the form of tubercles. These organs are formed by an accumulation of tactile cells bound together by a sheath of collagenous fibers. Pigment cells are lacking from the capsule but are often numerous directly beneath it. Mallory preparations of the same region of the female *Storeria dekayi* fail to show similar structures. Hence, there is a sexual difference in the supracloacal scales of *Storeria*. The male possesses tactile cells in its supracloacal scales but the capsule of cells fails to lift up the overlying epidermis.

Tubercles on the tail or cloacal region of snakes may have other functions than those of these Natricinae. Those on the tail scales of *Rhinophis* are undoubtedly sensory (Burmeister, 1908) but probably correlated with fossorial life. The enlarged scales of many male sea snakes apparently act as holding organs for I have failed to find any accumulation of tactile cells on the tips of the scales of male *Lapemis hardwickii*. On the other hand, the epidermis overlying a tactile organ may be extended into hair-like structures which presumably have general tactile functions. These are found in the acrochordine snakes (Schmidt, 1918) and in many gekkonids, agamids and iguanids (Preiss, 1922). In brief, reptiles exhibit a wide variety of tactile organs but only in the case of the organs described above has a correlation between the hypertrophy of an organ and the elaboration of a particular habit been pointed out.

SUMMARY

1.—The courtship and mating behavior of *Storeria dekayi* agrees with that of *Thamnophis* in its main features. *Thamnophis* lacks the lateral head movements of male *Storeria* and most of the writhing. The caudocephalic waves resemble those of *Thamnophis* but vary in tempo with the species, being greater in the *Storeria* and *T. butleri* than in *T. sirtalis*.

2.—In both *Storeria* and *Thamnophis* a loop of the male's body is thrown across the female's body to lift up her cloacal region from the substratum. The cloacal orifice of the female gapes before copulation occurs. In both genera a copulating male releases his grip and is dragged by the female, his position being held chiefly by the hemipenal spines which become firmly fixed to the lining of the female's cloaca.

3.—In *Coluber constrictor constrictor* a series of rushes precede the courtship and serve to stimulate the breeding group. The remainder of the courtship agrees closely with that of the natricine snakes but there is less entwining of tails in the courting pair. Further, a close adjustment of the cloacas does not precede copulation.

4.—In *Elaphe obsoleta obsoleta* the female stimulates the male by body twitching. The caudocephalic undulations are reduced.

5.—The courtship of *Crotalus viridis viridis* has been evolved from the natricine pattern. The caudocephalic undulations have been reduced to spasmodic forward thrusts and the tail entwining modified to a sharp bend of the male's cloacal region.

6.—The courtship of the natricine snakes is primitive and from it the courtships of other crotalids, also viperids, and elapids may have been derived. The courtship of *Lampropeltis* and *Coronella* represents a highly divergent pattern of behavior from which no other types have been evolved. The pythonid-boid pattern approaches most closely that of lizards and from it that of the natricine snakes developed.

7.—Sex dichromatism is very rare in snakes and is correlated with the development of rivalry among the males of certain species. Artificially coloring *Thamnophis*, which exhibits no male rivalry, has no effect on courtship.

8.—Moving objects attract snakes during the breeding season and in this way vision aids courtship. Sex recognition is accomplished chiefly by chemical sense, both olfactory and Jacobson's organs playing a part. Males distinguish the skins of their companions by their odor, both species and sex differences being recognized. The cloacal glands play no rôle in sex attraction or identification in *Thamnophis*.

9.—There is a definite oestrous period during which the skin of a particular female is attractive. Since snakes may copulate during pregnancy the oestrous period may occur during this period.

10.—Movement plays an important rôle during courtship. An etherized or freshly killed female *Thamnophis* is not sexually attractive. When moved artificially, copulation does not follow, apparently because of the lack of movement or tonus in the cloacal region.

11.—The texture of the skin may aid males in orienting themselves in relation to the female but the forward movement of the female assists in the process.

12.—Tactile sense is essential to courtship. Males with covered chins fail to court and males with covered cloacal regions cannot adjust themselves to the female's body.

13.—The hypertrophy of tactile organs in natricine snakes is correlated with the important rôle of tactile sense during courtship, those organs on the chin of the male facilitating self-stimulation, those above the cloaca aiding adjustment of the cloacas relative to the opposite sex. Snakes which lack these structures usually have other patterns of courtship, but in some with the same pattern, as *Storeria*, the tactile organs may be present above the cloaca but not indicated externally by tubercles.

14.—The tubercles on the chin of *Natrix rhombifera* are formed by dermal papillae underlying tactile organs in the epidermis. The supracloacal tubercles lack tactile organs in the epidermis and represent a purely dermal accumulation of tactile cells.

15.—Homosexuality is rare in snakes but may occur between male *Thamnophis* from different geographical areas.

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Plate VIII

Fig. *A*. Tails of a courting pair of *Thamnophis sirtalis*. The male's cloaca (slightly above center) is approaching that of the female and his left hemipenis is forming a slight protuberance.

Fig. *B*. A female *Thamnophis sirtalis* (center) being courted by two males. The male in the foreground is blindfolded but has adjusted himself to the proper position by the aid of his numerous tactile organs lying in the integument above the cloaca.

A

B

Plate IX

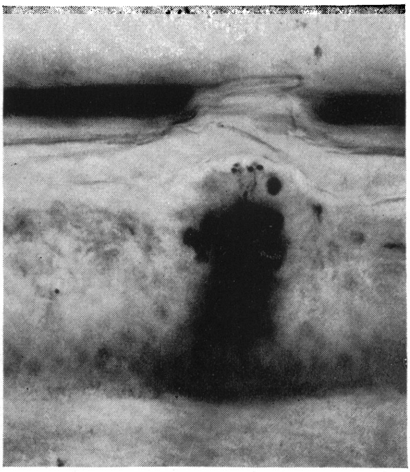
Fig. *A*. Section of the integument of the chin of a male *Thamnophis sirtalis*. The nerve fibers penetrate the epidermis to end in small knob-like enlargements between the cells of the tactile organs. Nuclei poorly indicated, but two nerve endings visible near the outer part of the tactile organ. Modified Gros silver nitrate technique. × 760.

Fig. *B*. Similar section through the integument of the chin of a male *Coluber constrictor*. A cluster of nerve endings form a rosette near the outer margin of the tactile organ. Modified Gros silver nitrate technique. × 475.

Fig. *C*. Section of the integument from the chin of a male *Natrix rhombifera* including one of the tubercles and an isolated tactile organ (below). The cuticle is barely visible on the left. Mallory triple connective tissue stain. × 200.

Fig. *D*. Section similar to figure C but stained by a modification of the Gros silver nitrate technique. Nerve fibers cross the dermal capsule of the tubercle and end in a tactile organ in the overlying epidermis. The tactile organ at the top of the section is not involved in a tubercle formation. The cuticle, darkly stained on the left, has lifted away from the epidermis. × 110.

A



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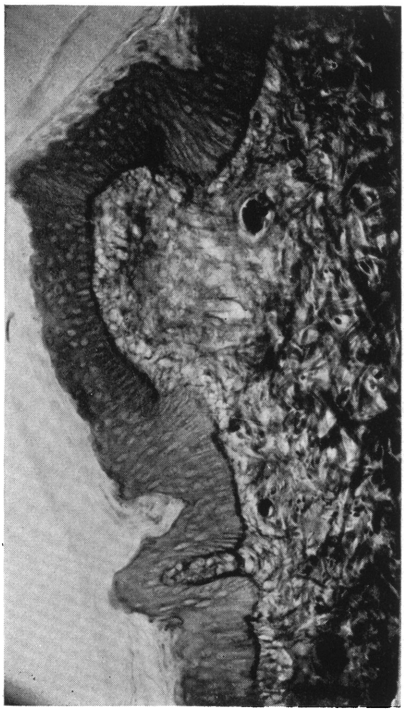
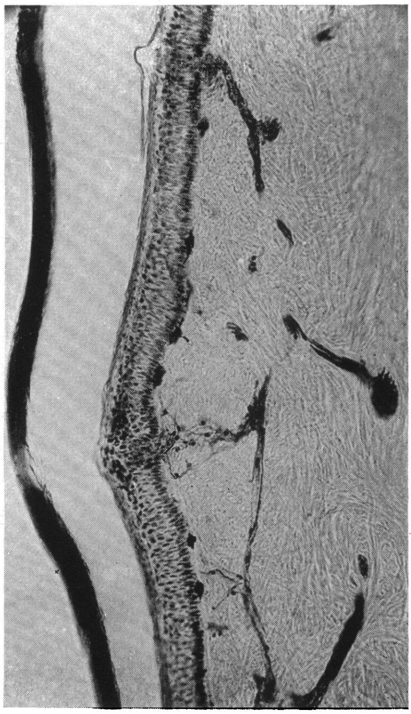


C

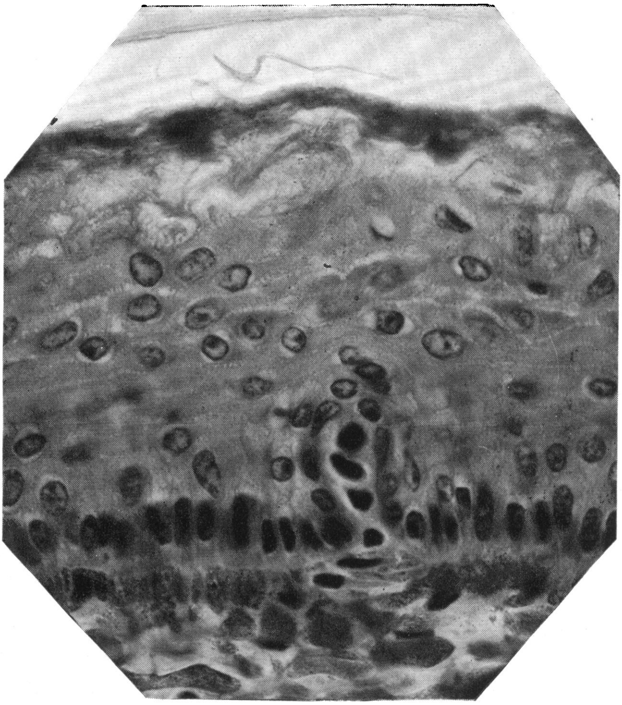


D

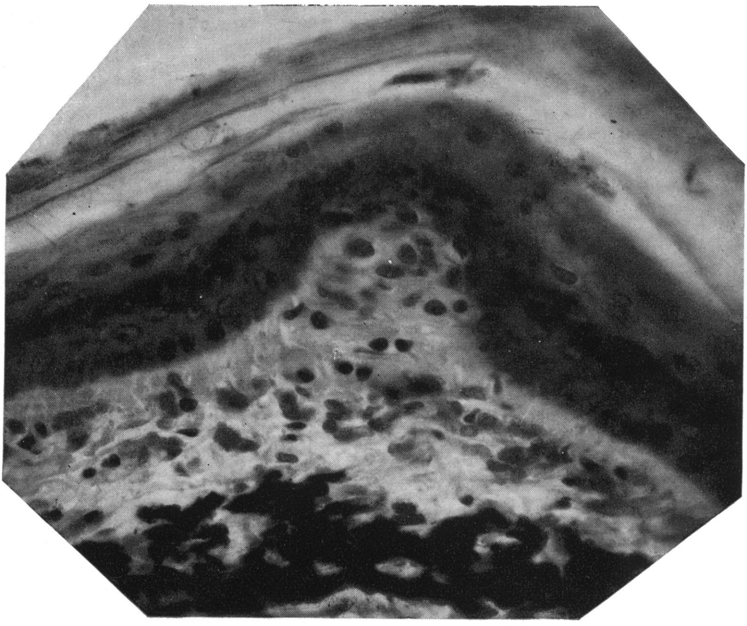
Plate X

Fig. *A*. Rudimentary tactile organ on the chin of a male *Thamnophis sirtalis*, section vertical to the surface. The narrow core of dermal cells is apparently penetrating the epidermis. Delafield haematoxylin and eosin. × 760.

Fig. *B*. Section of supracloacal tubercle of male *Thamnophis sirtalis*. A large capsule of tactile cells forces up the overlying epidermis to form a tubercle. There are no tactile organs within the epidermis. Delafield haematoxylin and eosin. × 475.



A



B