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COPULATORY ADJUSTMENT IN SNAKES

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The reproductive habits of snakes, though long neglected, are at last receiving considerable attention from a variety of angles. Sex recognition, courtship patterns, and viability of the sperm have been investigated recently with surprising results.

The literature is, however, silent on one aspect of reproduction, namely, the actual position of the hemipenis in the cloaca during copulation. Just how is the seminal fluid conducted to the oviducts? The older literature, Boulenger's "Snakes of Europe" (1913), for example, states that one hemipenis is pressed against the other so that the two sulci form a canal through which the semen is conducted "into the oviduct." Such a statement is obviously erroneous, since recent observations, as cited in two excellent summaries of snake courtship (Davis, 1936; Noble, 1937), prove that only one hemipenis is used at a time. Therefore, the sulcus of one organ must alone convey the semen.

This separate use of the hemipenes is fully confirmed by a pair of colubrid snakes (*Liophis poecilogyrus* Wied, F.M.N.H. Nos. 35697-8 from Bolivia) killed while copulating and preserved without dislodging the hemipenis. Dissection shows that each branch of the sulcus ends in a lip surrounded by a ridge which is firmly pressed against an area of the cloaca, in the center of which an oviduct opens. Thus each sulcus makes a direct connection with an oviduct, as shown in the accompanying figure. Moreover, the numerous hemipenial spines grip the cloacal walls so firmly that no shifting is possible. The turgid male organ greatly distends the cloaca, as also noted by Noble (op. cit., p. 677) and others in various species of snakes during copulation.

Hans Beuchelt's study of penial erection in the aquatic European colubrid snake, *Natrix natrix*, led him to conclude that the organ is inserted in a half-tumescent condition and that full and complete evagination is accomplished only after the basal spines have become

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anchored. Obviously, then, these spines serve a dual purpose: they keep the hemipenis from being pulled out and they hold the basal part firmly in place as a support for the distal section, which in turn can, quite independently of the male's movements, attain its ultimate position. The independent adjustment and firm grip must be of considerable advantage, since the male often loses his position and is dragged along by the female (Noble, op. cit., p. 678, etc.).

One unfamiliar with snake genitalia might conclude that this observation on *Liophis poecilogyrus* virtually closes the problem of hemipenial adjustment, whereas actually the problem is barely opened, for the hemipenes in snakes vary greatly in structure. They may be simple, with either a divided or an undivided sulcus; or shallowly bifid, as in *L. poecilogyrus*; or deeply bifid, as in the king cobra (*Hamadryas hannah*). The bifid section in this cobra is seven times as long as the simple one. Many other types are known and each one must have its own special adjustment.

There is, moreover, close correlation between penial and cloacal structure. Cope (1900, p. 700) states that the vaginal part of the cloaca may be deeply bilobate. Apparently, he did not connect this condition with bifid hemipenes, since he wrote: "It [the hemipenis] enters the vagina of the female and its extremity occupies the corresponding anterior lobe of the latter." In the few species that I have dissected, the cloaca is bilobed and the hemipenis bifid to about the same extent. It is reasonable to conclude that each branch of the male organ fits into a lobe of the cloaca. *Liophis poecilogyrus* illustrates an intermediate condition in which the hemipenis is only slightly bifid and the cloaca shallowly bilobate. Distortion by the turgid hemipenis has obscured the latter condition in the female figured.

Cope (loc. cit.) also noted that when the hemipenis is spiny the cloacal walls are thick, but when the male organ is unarmed the cloaca is thin-walled. I have been able to confirm this point nicely in two species of Asiatic pit-vipers, *Trimeresurus albolabris* Gray and *T. stejnegeri* Schmidt, known to be astonishingly alike in color and all other external characters. They were, in fact, long considered identical and the females cannot yet be distinguished by external characters alone. In 1933 my wife and I demonstrated that the two species could be recognized by their strikingly different hemipenes, that of the former being long, slender, devoid of spines and deeply bifid, whereas that of the latter is shorter, thicker, not as deeply forked, and spinous. Dissection of a female of the former

(F.M.N.H. No. 6711) shows that the cloaca is long, deeply bilobed, and thin-walled. In contrast to this a specimen of the latter (F.M.N.H. No. 25201) has a shorter cloaca with shorter lobes and thick walls. The correlation is obvious enough.

The question at once arises whether such a marked difference in penial structure is an efficient isolating mechanism making cross-breeding of these two strikingly similar species physically impossible.

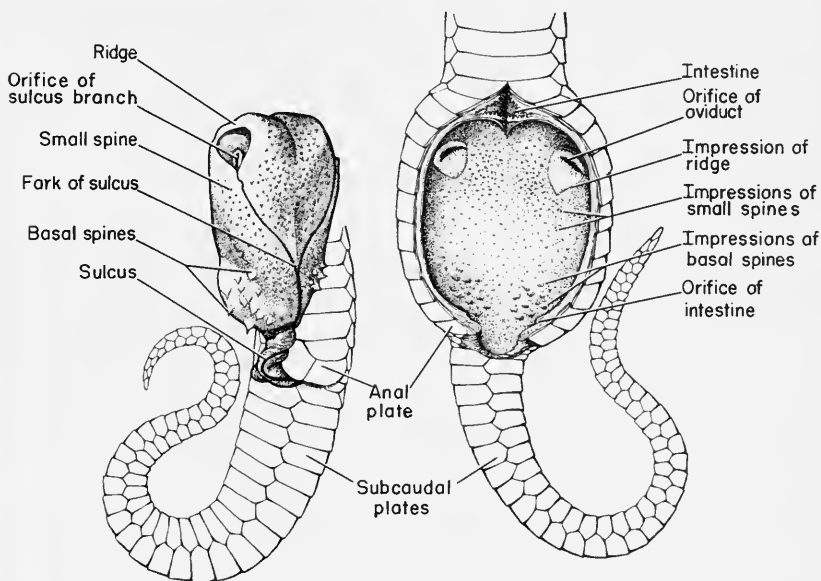


FIG. 23. Anal region of a male (left) and of a female of the colubrid snake *Liophis poecilogyrus* seen from below. The ventral body wall of the female has been bisected and its halves spread apart to expose the interior of the cloaca, from which the turgid hemipenis was removed. The exposed side of the latter lay against the dorsal wall of the cloaca so that each sulcus spermaticus opened at the orifice of an oviduct. $\times 3$. Drawing by H. Elizabeth Story.

The long spines of *T. stejnegeri* would probably do considerable damage to the delicate walls of the *T. albolabris* cloaca. Moreover, the differences in form and proportion of the two organs would present other difficulties. Noble (op. cit.) has summarized the few authentic cases of cross-mating in snakes, but too few details are known about them to permit the drawing of conclusions as to the frequency of their occurrence in nature or its results under any conditions. Very careful experiments would have to be devised to investigate this matter, since evidence that sperm remain viable

in females for months if not years is rapidly accumulating (see Rahn, 1940, and Haines, 1940, and their bibliographies).

SUMMARY

During copulation the raised terminal lip of each branch of the bifid sulcus spermaticus in a colubrid snake, *Liophis poecilogyrus*, fits snugly against the orifice of an oviduct. It is reasonable to conclude that a similar adjustment occurs in other snakes with divided sulci.

Close correlation between penial and cloacal structure occurs in two Asiatic pit-vipers and a South American colubrid snake. Such a correlation is probably of common occurrence among snakes.

It is suggested that penial structure may be an important isolating mechanism in certain snakes. Therefore, penial adjustment is a subject worthy of further investigation because of its bearing on the important problem of speciation.

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