STUDIES OF THE SEX-ORGANS OF MATING POLYGYRID LANDSNAILS

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This paper is the sequel of earlier studies (Webb, in press, *Naut.*). Aside from describing and figuring the functional form of the sex-organs in mating-anatomies[1] and discussing the mating-behavior, some of the evolutionary and taxonomic implications of the data are mentioned. Also the relationships of the *Euchemotrema* (Archer 1939 a, b) to the typical *Stenotrema* species are somewhat strikingly indicated by the present data, although conclusive results will require the study of many more species.

Supplementary more-detailed data on the methods used in obtaining the observations, matings, and the mating-anatomies, will be found in the Amer. Nat. (Webb, 1947). In regard to the choice of species to be studied, opportunity has been determinative. It has just so happened that specimens of these species have been available for study and sufficient data have accumulated to permit publication. Thus the particular interspecies comparisons which have been occasioned are not as satisfactory as could be desired had specimens of a larger array of *Stenotrema* been available. The much enlarged sketch-figures were drawn from the freshly-obtained anatomies; the other figures were from projection-tracings (inversion uncorrected) of unstained toto-mounts preserved in canada balsam (the scale-lines represent 2 mm.)

[1] Definition: the anatomies of snails exhibiting the sex-organs in the extruded, functional condition.

STENOTREMA HUBRICHTI PILSBRY 1940

The material was collected August 23, 1945, about .5-1 mile south of the type locality near Aldridge, Union County, Illinois. About 27 specimens were obtained, half being juveniles; most of the specimens were taken actively crawling about because of rain. Under the over-hanging portions of the cliff-habitat of the species, flat spider-webs yielded several living, aestivating, specimens of this and other snails. The species thrives and breeds readily in captivity, and in the laboratory at least one generation has matured from eggs deposited by the adults. The species was considered a Pleistocene form until its discoverer found some living specimens (Hubricht 1943). All of the available information would seem to indicate that this is either a relict or a suddenly, newly arisen, species.

MATING

A pair of specimens was first noted October 9, 1945 head-on (in the courtship-position) each with dilated genital pore but mating was not noted to occur until the 11th when 4 pairs of specimens previously held in isolation from others of their species were placed together at 4:30 P.M. At 8:05 P.M. a pair was noted in the head-on position; these soon separated. Later, another or the same pair was noted in a head-on

position clinging to the cover-glass; the genital pore of each animal was prominent and dilated, and from one a papilliform body was outthrust intermittently about 1 mm. A few seconds later, the snails shifted their bodies slightly and the sex-organs everted-protruded,[2] simultaneously entwining. The organs were separated and retracted within about a minute. The glimpse of the organs indicated a vermiform penis, but this is not exactly the case.

Courtships continued to be noted, but no more matings were witnessed until the 24th when 6 specimens were placed together experimentally for observations. One of these snails was noted to have a swollen, slightly-protruding genital pore. After a short interval, one specimen was noted crawling suspended from the cover-glass in such direction that it would probably contact a resting animal head-on. Such contact occured. The inactive animal "awakened," protruded-everted the tentacles, and for a short period the two animals remained head-on with the but moderately extended tentacles separated by only a slight distance. A period of head-swaying then ensued in which each animal's superior tentacle is held nearly immobile, but is caused by head movements to oscillate through a short arc opposite the corresponding tentacle of the mate-animal. Seldom is the movement so great as to cause the left tentacle of one snail to move past the right tentacle of the other; instead, the two left tentacles oscillate in apposition, and the two right tentacles oscillate in apposition. The homologous tentacles of each snail thus oscillate from side to side in apposition but seem almost never to brush together or to collide although the intervening space is much less than 1 mm. The inferior tentacles move similarly but less strikingly. During this head-swaying, tentacle-oscillation period, the genital pore of the ex-resting animal became tumid, dilated, and an irregular body became slightly extended therefrom. The crawling snail had progressively shortened its tentacles coincident with a decelerating closer approach; and during the ensuing period of vigorous tentacle-oscillation, its tentacles "arced" in a shorter condition than in the previous period. The genital pore of each animal had by now been completely dilated and both exhibited therefrom a slightly extrudent, irregular, fleshy body. The snails then moved so that the genital pores became nearly contiguous, and the sex-organs were vigorously everted-protruded, entwisting simultaneously. Mating - anatomies were secured by plunging the couple into boiling water. The resultant anatomies, however, were found to be disfigured from the effects of being drawn against the aperture during the fixation process.

The additional matings observed do not differ essentially from that described above. The shifting of the animals' foreparts to bring the genital pores into proximity is sometimes very swiftly accomplished, and possibly may be correlated with the detection by the inferior tentacles of some odor accompanying the dilation of the mate-animal's genital pore.

[2] Since the sub-terminal parts of the penis evert and cause the protrusion of the apical pilaster which forms the penis-capsule and adjacent parts, the organ is both everted and protruded. This is indicated by the compounded term. Only in *S. hirsutum* is the penis solely everted.

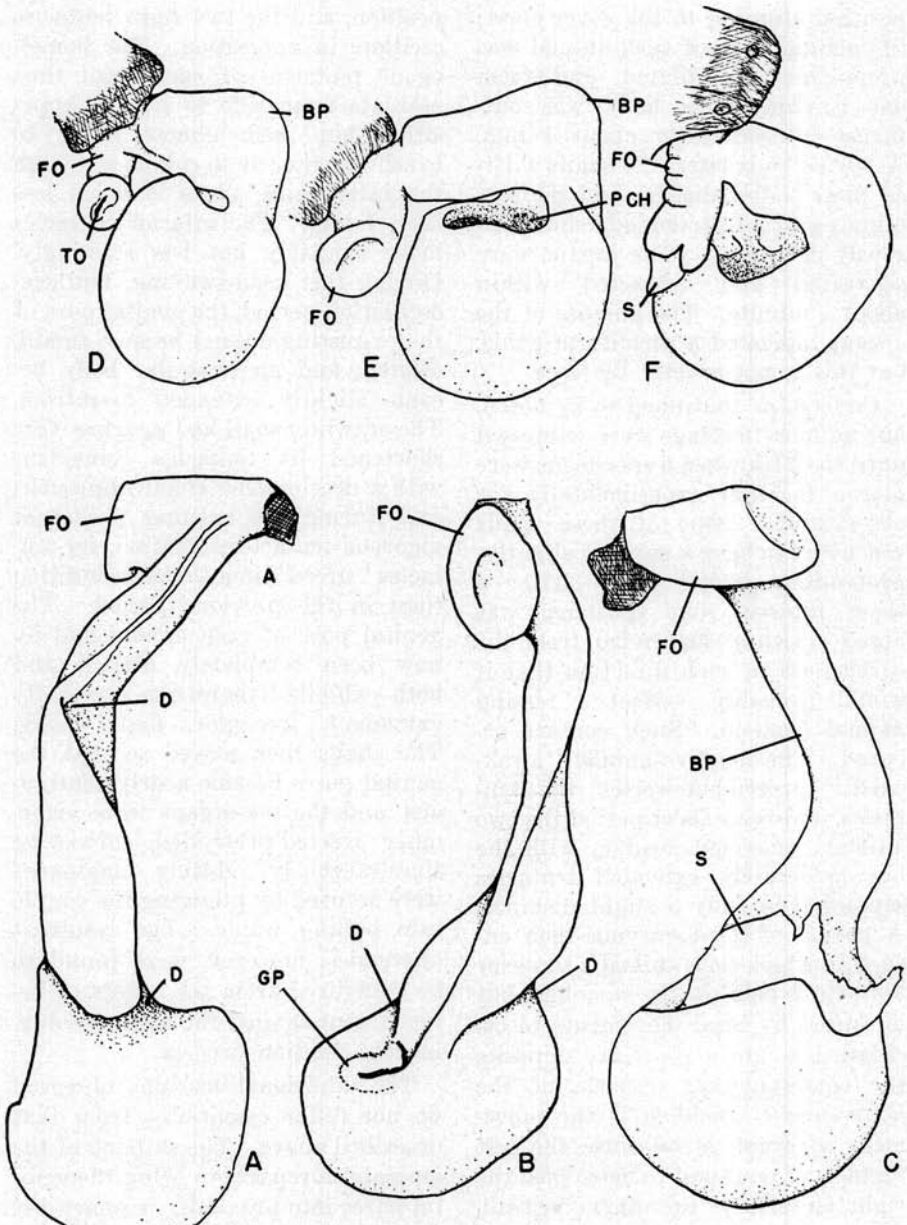

FIG. 1.—*Stenotrema hubrichti* Pilsbry, Aldridge, Illinois. A, B, and C are successive views of a deformed mating-anatomy; D and E are seemingly normal mating-anatomies; F is another specimen. Explanation of symbols: A—atrium BP—basal penis, D—deformation, FO—female-organ, GP—granular patch, PCh—penis chalice, S—semen, TO—terminal orifice of female-organ.

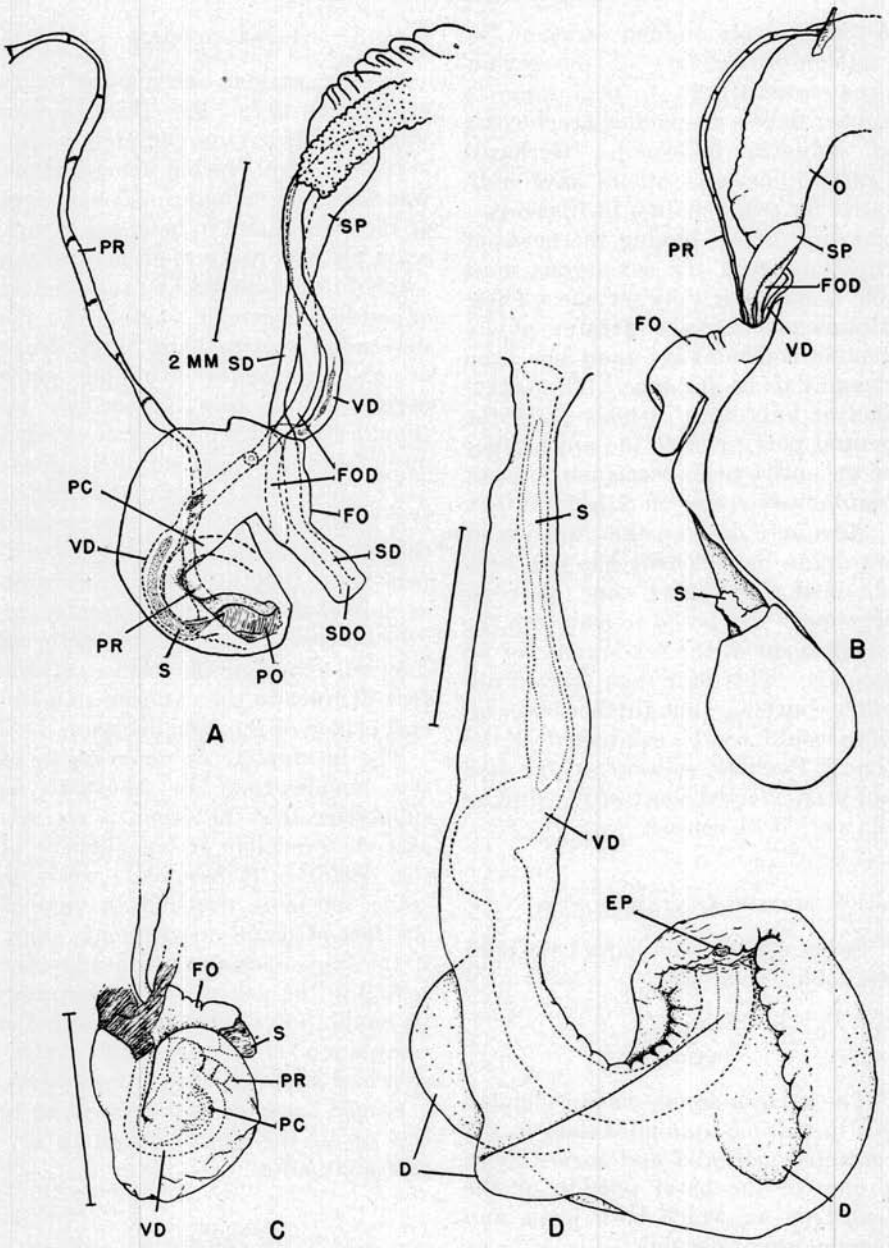

FIG. 2.—A—*Stenotrema monodon* (Rackett) Brown's Lake, Michigan, mating-anatomy; B—*S. hubrichti*, a deformed mating-anatomy showing non-everted parts of the sex-organs; C—normal mating-anatomy; D—*S. hirsutum* (Say) Indiana, mating-anatomy. Explanation of symbols: EP—ejaculatory pore; D—deformation; FO—female-organ; FOD—free oviduct; O—oviduct; PC—penis-capsule; PO—pocket of penis; PR—penis retractor; S—semen; SD—spermathecal duct; SDO—spermathecal duct orifice; SP—spermathecum; VD—vas deferens.

An explosively sudden eversion (or eversion-protrusion) of the sex-organs entwistingly is beginning to appear to be a common characteristic of polygrin landsnails; Gerhardt (1933, 1939) and others have indicated its commonality in limacids—the snail group having the mode of functioning of the sex-organs most like that of our Polygyrinae. These groups may have a greater phylogenetic commonality than has been thought to be the case. The extrusion or bulging of a body from the genital pore prior to the appearance of the entire penis seems not to be of regular occurrence in *S. hubrichti.*

Adequate data on the duration of sex-organ engagement has not been obtained. However, one pair of specimens was noted to maintain the engagement of the sex-organs for 15 seconds. This pair then started another courtship, but further observations could not be conducted at the time. Possibly sperm-transfer had not been effected successfully during the period of contact.

MATING-ANATOMY DATA

Seven mating-anatomies have been available for study.

ATRIUM

The atrium seems more conspicuous in mating-anatomies than in the retracted genitalia and forms about 1 mm. of the basal portion of the sex-organ on which both penis and female-organ[3] depend.

[3] Because of the disconformity in nomenclature and function among the various organs composing the female parts of the sex-organs (the vagina, basal spermathecal duct, and the oviduct may form a single functional organ), the term "female-organ" has been adopted for the female parts of the extruded sex-organs collectively.

FEMALE-ORGAN

In the various mating-anatomies examined, twice the female-organ was found nearly or completely noneverted. The everted female-organ was found to extend .5-1.5 mm. free of the atrium and to be about .5 mm. wide. Structurally the female-organ seems formed entirely by the slightly expanded, evertable vagina and the descended spermathecal duct. None of the anatomies available show other than a terminal orifice, although the orifice of the free oviduct and of the spermathecal duct appear as two pits in this terminal orifice of the female-organ. In this regard the female-organ of this species differs from that of either *fraternum* or *monodon* in which the greater degree of eversion of the spermathecal duct also brings the orifice of the free oviduct to the exterior as a lateral orifice of the female-organ.

The incomplete or noneversion of the female-organ in *hubrichti* is suggestive that the organ is retractable or evertable independently of the penis. Subsequent eversion seems the more probable in view of the fact of penis-entwistment; since, if the female-organ is to occupy the cavity in the penis-tip, this seemingly could not occur until after the completion of the eversion-protrusion and entwistment of the penises.

Semen has been found adhering to the tip of the female-organ in several anatomies.[4]

PENIS

Early in the studies, the frequent deformation of the penis in mating-

[4] No attempts to observe sperm have been made; the material has been identified as seminal because of its similarity to matter in the vas deferens.

anatomies caused some misconception of its true form; however, seemingly undeformed penises (fig. 1 D, E, F, and fig. 2 C) have been obtained by precrushing the shell before plunging the mating specimens into the boiling water. In freshly fixed material, the greatest length of the deformed penis was found to be 10 mm., and the greatest width (which is at the tip) about 2.5 mm. (fig. 2B). Straightening, basal constriction and shell-lip and denticle impressions are some of the penis-deformations noted (fig. 1, A, B, C).

In apparently normal mating-anatomies, the penis is cylindrical with a low, spiral twist of nearly 360 degrees. The penis-tip is rounded and slightly more inflated than the basal penis and bears subterminally a small chalice which is formed by a thickened capsule-like body as in *fraternum* and *monodon*. In *hubrichti* this penis-capsule seems least developed and is about one-fourth the volume of the entire penis. I have not been able to discern clearly an ejaculatory furrow, but such may be present. A part of the rim of the penis-chalice is noticeably more opaque and granular than the surrounding tissues in the fresh material, but this does not show so clearly in the toto-mounts. I have not happened to note a similar opaque-granular area in *monodon* or *fraternum* but perhaps the careful observation of fresh material would reveal it.

Stenotrema monodon (Rackett)

For most of the material, I am indebted to the late Dr. Phil L. Marsh. The material was labeled "N. Shore of Brown's Lake, Jackson Co., Michigan, 10-12-1941." Some observations on matings have also been obtained from specimens collected in the fall of 1945 about Muskelunge Lake, near Warsaw, Kosciusko County, Indiana.

MATING

The Michigan material was received October 16, 1941, and specimens were observed mating on the 17th. In courtship the animals are head-on with the extreme anterior end protruded in a peculiar fashion, as in courting specimens of *fraternum*. This constricted appearance of the extreme anterior parts seems due partly to a tumefaction of the body parts above and posterior to the genital pore. Eventually a dilation of the genital pore occurs and the rest of the courtship and mating resembles that of *fraternum*, with the animals mouthing or gnawing at or about a lobular body protruded from the mate-animal's genital pore. Sperm transfer is accomplished when the penises are suddenly everted-protruded and the female-organ comes to be enveloped by the penis-capsule. (The exact procedure is obscure. It appears more probable that the female-organ is everted into the penis-capsule, than that the capsule engulfs the female-organ.) The disengagement of the organs seems to follow sooner in this species than in *fraternum*. One pair was noted of which one animal pivoted before mating ended the courtship. The mating anatomies of this pair revealed the female-organ of each to be engaged reciprocally in the mate's penis-chalice.

In contrast to *fraternum*, gnawing, biting, and pivoting acts have been observed to occur much more rarely,

but too few observations are at hand to justify the conclusion that a difference in behavior exists.

MATING-ANATOMY DATA

Only two pairs of mating-anatomies have been available for study, although the extruded organs of several additional pairs have been momentarily glimpsed in life (fig. 2A.).

ATRIUM

This is not a sharply differentiated part of the extruded sex-organs, but presumably forms the parts adjacent to the genital pore area.

FEMALE-ORGAN

This appears slimmer and without the low annulations exhibited in *fraternum* and does not project from beneath a low fold as in that species; both a terminal orifice (spermathecal duct) and a lateral orifice are present.

PENIS

This is similar in general form to that of *fraternum* but differs in the following details: it is more ellipsoid and less globular in shape, bears a smaller penis-capsule forming a smaller penis-chalice, and lacks the slight ridge overhanging the female-organ and basal penis. The internal structure of the penis-chalice in *monodon* also differs in having a wide, shelf-like pocket instead of a sinuous, ejaculatory fissure. The orifice of the penis-chalice is triangular or elongate in *monodon* whereas it is rounded in *fraternum*.

STENOTREMA HIRSUTUM (SAY)

Most of the material was collected in Indiana in 1939 or 1940, presumably near Indianapolis. While the shells of some of the specimens seem identical with the material from Indianapolis which Pilsbry (1940, p. 658, fig. 409a) designates as *S. stenotrema* (Pfeiffer), I am not convinced that a central Indiana population exists which is specifically separable from the local *hirsutum*. Some will prefer to regard the material studied, however, as a mixture of *hirsutum* and *stenotrema*. One mating and a pair of mating-anatomies were obtained from material collected on the hillsides of Big Bureau Creek, within 2 miles upstream of the route 26 bridge near Princeton, Illinois.

MATING

The first complete observations on mating were made November 27, 1940, when specimens were noted crawling about suspended from the cage cover-glass. The specimens formed courting couples which separated and reformed with new or old partners. The specimens crawled actively, waving the tentacles, and frequently pivoting. Prior to mating, two specimens were noted head-on with the genital pore dilated and forming a curved swelling. When the edge of the swelling of one snail touched that of the other, the penises were reciprocally everted entwiningly.

In the pair of Bureau County specimens observed October 22, 1945 (uncontroversially *hirsutum*), the courtship started with a circling movement of one animal following the tail of the other. After being in a head-on position, pivoting ensued and the animals discontinued activi-

ties. Shortly thereafter, another or the same pair were noted in courtship. In these a reciprocal spiraliform movement occurred clockwise (the animals were suspended from the cage cover-glass) such that the head of one animal was opposite the non-genital pore side of the other, and the bodies were bent nearly at a right angle. Pivoting by both animals followed. The snails failed to rejoin head-on but resumed the spiraliform, reciprocal circling as before. One animal pivoted (possibly because of a mild gnawing by the other against the side of the foot or body) and the genital pore was seen to be slightly prominent as a pimple-like swelling. The specimens continued these maneuvers until they happened to rejoin head-on, each with the genital-pore bulging convexly. As soon as the animals were close enough together to contact with the fore parts of the genital swelling of the mate-animal, the penises everted entwiningly; the animals were still suspended from the cover-glass by the foot as before. Exclusive of the first, interrupted courtship, the courtship is estimated to have lasted about half-an-hour. Biting was not noted, but a gentle rasping on the side of the foot may have occurred. These specimens had been kept in isolation from others of the species until they were placed together for possible matings.

MATING-ANATOMY DATA

None of the four mating-anatomies obtained probably have been free of the deformations which result from the wedgement of the extruded sex-organs against the aperture during fixation (fig. 2D).

ATRIUM

This is continuous with the basal part of the penis and is not discernable from it.

FEMALE-ORGAN

An everted female-organ has not been found in any mating-anatomy. Other evidence of the nonevertability of this organ is the absence of a thickened vaginal duct, basal spermathecal duct, and free oviduct; in *monodon, fraternum,* and *hubrichti* these ducts are noticeably thickened and muscular in the retracted organs. Some other Polygyrinae are known to have nonevertable female-organs, as *Mesodon thyroidus* and *M. elevatus.*

PENIS

Despite more or less disfigurement, the essential form of the penis seems to be that of a tapering, somewhat flatsided sac bearing the ejaculatory pore distally. The pore opens to the exterior centrally on the tip of the penis. A strand of seminal matter protrudes from the pore in one anatomy. No capsule, chalice, or comparable structures are present. The entire penis has a curved or spiraliform twist. Were the recurved penis-tip to become fused with the midportion, a condition somewhat analogous to that in *hubrichti* would result, except that a penis-capsule and a female-organ would yet be lacking.

Conclusions

In the *Euchemotrema* (subgenus) studied, all have a similar type of mating-behavior. Pivoting is not a frequent and prominent part of the

mating-actions; this probably is due to the infrequency of biting or other extremely stimulative actions, and to the slow head-on approach utilized which prevents the attainment of positions unfavorable to mating. *S. hubrichti* seems to have the most quiet type of mating-behavior with seemingly the complete absence of biting or gnawing actions, and is characterized by the elaborateness of the head-arcing process in courtship.

In the *Stenotrema* (subgenus) studied, *hirsutum* and/or *stenotrema,* the behavior differs from the preceding group in the greater activity of the animals with the greater part of the courtship period being occupied with rotations, spiraliform-movements, and pivoting, rather than a very slow, head-on approach.

From the standpoint of sex-organ anatomy, *fraternum, monodon,* and *hubrichti* seem to exhibit modifications of a common basic type. The slight specific differences between *monodon* and *fraternum* anatomically may be useful in varietal and species diagnosis, although some of the many varieties of these two species may be found to exhibit transitional types. Phylogenetically *hubrichti* would seem to be the most divergent of the three species. The apical, globular pilaster noted by Archer as characterizing the *Euchemotrema* is the seeming homologue of the penis-capsule, and would seem to be a more important criterion than penis-length. In the lack of female-organ and penis-capsule, *hirsutum* (subgenus *Stenotrema*) would seem to be rather divergent from the preceding.

The sex-organ structure of these species seems to illustrate possible sex-organ barriers to panmixy. Thus *monodon* and *fraternum* might be expected to cross-mate, but *hubrichti,* because of entwistment, would seem apomixic to these other two species. In regard to *hirsutum, hubrichti* might be panmixic anatomically since an entwistment of penises between these two species conceivably might accomplish sperm-transfer; however, the differences in mating-behavior would probably prevent the courtship from arriving at the entwistment stage. The present data strongly suggest the presence of sex-organ barriers and mating-behavior barriers to panmixy to varying degrees within the polygrin genus *Stenotrema.* Such barriers in all likelihood have influenced and continue to influence the evolution and speciation of these snails.

Summary

1. The form of the sex-organs in the extended, functional condition, the mating behavior, and the evolutionary significance of the data are given for *Stenotrema hirsutum* (Say), *S. hubrichti* Pilsbry, and *S. monodon* (Rackett) in comparison to *S. fraternum* (Say).

2. The form of the sex-organs of *monodon* appear essentially as in *fraternum,* but the penis is more eliptical, the penis-capsule smaller, and the female-organ slimmer and less ornate. *Stenotrema hubrichti* differs from *monodon* and *fraternum* in having a stalked penis, a more-reduced penis-capsule, and lateral-poreless, much smaller female-organ. The sex-organ of *hirsutum* differs markedly from that of the preceding species in lacking a female-organ, and in having a simpler, tubular-

spiraliform penis which has a terminal ejaculatory pore, but no capsule or chalice.

3. The mating-behavior of *monodon* is essentially like that of *fraternum*, but *hubrichti* differs slightly in the exaggeration given the arcing process of the head-and-tentacles, and in the absence of biting during mating. Almost constant maneuvering with fleeting periods of the head-on position characterizes the mating-behavior of *hirsutum*.

4. Sperm-transfer in *monodon* and *fraternum* is accomplished by the sudden eversion-protrusion of the penis and deposition of seminal material on the everted female-organ which occupies the penis-chalice. In *hubrichti* an entwistment of the everting-protruding penises occurs, but it appears probable that otherwise sperm-tranfer is accomplished similarly. In *hirsutum* the lack of a female-organ modifies sperm-transfer in necessitating the use of the penis also in securing the exchanged or shared semen.

5. Evolutionarily, *fraternum* and *monodon* seem least likely of the species studied to have an effective sex-organ difference barrier to panmixy; *hubrichti* does seem to have a sex-organ difference barrier to panmixy with the preceding, and also possibly with *hirsutum*. While seemingly apomixic to *monodon* and *fraternum*, possibly *hirsutum* has only a behavior barrier to panmixy with *hubrichti*.

6. The present data indicate that sex-organ differences affecting panmixy probably exist among the species of the polygyrin genus *Stenotrema*, and in all likelihood have influenced the evolution and speciation of these snails.

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