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STERNITE MODIFICATION IN MALES OF THE DROSOPHILIDAE (DIPTERA)[1]

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ABSTRACT

Sternites of the dipterous abdomen, as seen in cleared preparations at about 430x magnification, typically possess a pair of minute *sensilla trichodea* along the basal border. By using these as markers of modified or "lost" sternites, it was determined that males (as well as females) of the Drosophilidae possess seven sternites in the preabdomen, and that reduction has occurred in varying degrees among the species examined. Reduction, leading toward ultimate loss, includes loss of macrochaetae, loss of sclerotization, and loss of sensilla; some sternites have become separated into two pieces in this process. Various types of vestigial sternites still present indicate that the sequence of steps leading toward sternite disappearance is not constant. Suggestions are made as to the steps which might have been involved in sternite modification leading to incorporation as genitalial pieces.

The insect abdomen differs from the head and thorax by its relative simplicity of structure, the general lack of segmented appendages, and the tendency toward the reduction or absence of some segments. There is often a tendency toward the reduction of the first abdominal segment, but reduction of the more posterior segments is more extreme, being correlated with the development of the copulatory apparatus.

In males of the acalyptrate Diptera the first five or six segments comprise the preabdomen and show relatively little modification, while the remainder, comprising the postabdomen, have either been lost or have become involved in genital modification. Thus the primitive number of 11 abdominal segments is no longer apparent; but evidence concerning the fate of the "missing" segments in acalyptrate flies is extremely meager, and attempts to establish homologies between abdominal segments and between the genitalial structures in different families of flies have, for the most part, been rather frustrating.

The present study, dealing primarily with the abdominal sternites of males of the Drosophilidae, presents some new evidence concerning two types of sternite modification: reduction and specialization.

In the Drosophilidae the first six tergites of the male belong to the preabdomen, the first (T 1) being somewhat reduced and more or less fused with the second (T 2). Posterior to T 6, and above the genital chamber, is the large genital arch (T 8+9 or 8+9+10) and, still farther posteriorly, is the pair of anal plates (anal cerci of authors).

The abdominal spiracles are located in the membrane below the lower margins of the tergites (fig. 2). In the subfamily Steganinae (*Stegana*, *Leucophenga*, *Amiota*, etc.) there are six spiracles, corresponding to the first six tergites; in the Drosophilinae (*Drosophila*, *Scaptomyza*, *Chymomyza*, etc.) there are seven spiracles, two being located near the lower border of the sixth tergite. In many, but not all, of the species of this subfamily there is a sclerotized plate ("pregenital plate") between T 6 and the genital arch, and which is currently believed to represent the vestigial seventh tergite. In several species, *Chymomyza procnemis* for example, the seventh spiracle is moved dorsad and lies just below the presumed vestigial T 7. The Steganinae have usually been considered to be more primitive than the Drosophilinae; the presence of the seventh spiracle, however, is surely more primitive than its absence, so that for this character at least the Steganinae would seem to be more specialized (or apomorphic, using the terminology of Hennig 1958) and the Drosophilinae more primitive (plesiomorphic).

Modification and reduction in the number of sternites has progressed to varying degrees within the Drosophilidae. Females routinely possess six bristled sternites, the last typically bifurcate and partly enclosing the base of the ovipositor. Males, however, have only four or five bristled sternites. In both sexes (and in all of the species of Diptera so far examined) the first bristled

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sternite invariably shows a secondary division into a narrow, transverse, nonbristled sclerotized bar, usually but not always pigmented, and a larger bristle-bearing apical plate (fig. 1, 2, 8). Since this first sternite lies approximately in line with the second tergite, it has generally been considered as the true second sternite (see, for example, Ferris 1950, for *Drosophila melanogaster*). Some additional evidence that this interpretation is correct is presented below.

STERNAL SENSILLA

When dissected sternites are cleared in phenol, mounted on slides, and examined with the compound microscope at about 430X, one can see a pair of minute sensilla (*sensilla trichodea*) near the basal (anterior) margin of each sternite. A sensillum appears as a microscopic hair set in a rather conspicuous socket (fig. 3, 6). In some species the two sensilla are rather close together near the midline, while in others they are much farther apart. They presumably function as tangoreceptors (Snodgrass 1935), responsive to touch. Due to the telescoping of the abdominal segments, the apical margin of a sternite tends to cover the base of the next one. Thus the basal sensilla of a sternite come to lie in close proximity to the intersegmental membrane attached to the apical margin of the preceding sternite. In this position abdominal movements could easily cause excitation of the sensilla.

Although an occasional abnormal sternite has been found, with a single sensillum or with sensilla in unusual positions, their presence is so nearly constant that they can be used as indicators of sternites even when the latter have become so highly modified that their true nature is not immediately evident. In sternite reduction, furthermore, the sensilla are usually the last vestiges of the sternite to disappear, as is shown in some of the examples described below.

Sensilla of the type described here for the Drosophilidae are not limited to that family, but may well be characteristic of all the Diptera. We have not attempted an extensive survey, but dissections of a few assorted species have shown them to be present in members of the Culicidae, Simuliidae, Coelopidae, Ephydridae, Chloropidae, Lauxaniidae, and Muscidae. *Fucomyia vanduzeei* (Coleopidae) was exceptional in possessing four, rather than two, sensilla on each sternite except the second (figs. 8, 9).

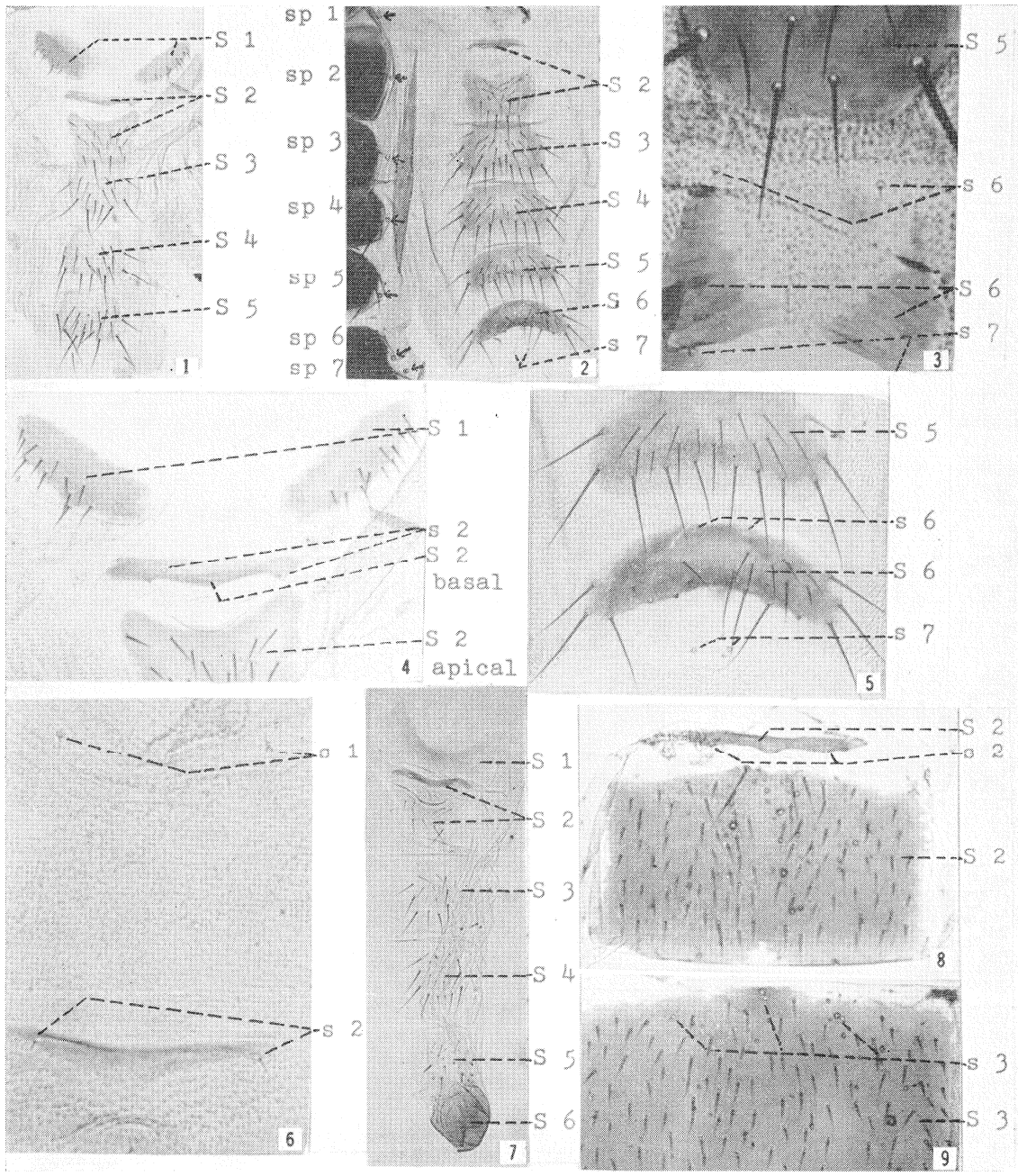
STERNITE NUMBER

Various degrees of reduction of the true first sternite (S 1) have occurred in males of the Drosophilidae, leaving vestigial remnants of several kinds. In species of *Amiota*, *Leucophenga*, and *Stegana* it remains as a crescentic sclerotized plate, without bristles, anterior to the second sternite (fig. 7). In *Drosophila victoria* (figs. 1, 4) the first sternite is represented by a pair of pigmented, bristle-bearing plates; the sensilla of this segment lie in the membrane between these plates and the hind coxae. In the majority of the *Drosophila* species examined, however, no conspicuous vestiges of S 1 remain, although a typical pair of sensilla could usually be found in the membrane behind the last coxae (fig. 6). This is interpreted to mean that all other portions of the first sternite have been lost, leaving only the sternal sensilla as markers of the former existence of the sternite.

The first bristled sternite (S 2), consisting of a basal piece and a larger bristled plate, might possibly be interpreted as representing vestiges of two sternites. It is only the basal transverse piece, however, which bears sensilla, confirming our belief that the two parts belong to the same sternite. The separation of this sternite into two parts is characteristic of all of the species of Diptera so far examined. It seems likely that some important function is served by this arrangement. Dissection in saline shows clearly that a major cluster of muscle fibers is attached to the basal piece while relatively few are attached to the apical portion. The membrane between the two is always modified into a wrinkled, roughly circular area (fig. 6) and in some species of *Drosophila*, at least, this area has a secretory function. The secretory product has not yet been identified.

Since the first bristled sternite of female *Drosophila* is also located in line with the second tergite, females of several species (*melanogaster* and *virilis*, among others) were examined for the presence of the sensilla of the true first sternite; they were present, as we expected, in each of these females. In the female *Drosophila*, therefore, S 1 is represented by sensilla only, and is followed by six bristled plates, making a total of seven preabdominal sternites. Using vestigial sensilla as markers for lost or modified sternites, we have found that the basic number of preabdominal sternites in males also is seven.

In males of the saltans group of *Drosophila* S 6 is a typical bristled sternite (figs. 2, 5); in the membrane just posterior to S 6 is the pair of sensilla representing the vestige of a seventh sternite. In males of *D. melanogaster*, *pseudoobscura*, and others S 6 is a sclerotized plate bearing sensilla but lacking bristles; in these species, also, S 7 is represented by a pair of sensilla in the membrane. In males of *D. virilis*, *repleta*, and many others, possessing only four-bristled sternites (S 2–5), there are two pairs of sensilla in the membrane behind S 5. Thus there is evidence of seven sternites in these species also. In all of the species in which S 6–7 are represented only by sensilla, the last sensilla are moved laterally with respect to those of S 6, the membrane on which they are located forming the lateral boundaries of the genital chamber. Additional vestiges of S 6 are present in *Chymomyza procnemis* (fig. 3). Posterior to the sensilla of S 6 is a pair of pigmented, sclerotized plates, apparently remnants of S 6, followed by the sensilla of S 7.



FIGS. 1–9.—Photomicrographs of sternites and sternal sensilla of some male Diptera. All are ventral views of cleared specimens. Homologous abdominal segments are shown by number. S: sternite; s: sensillum; sp: spiracle. FIGS. 1 and 4.—*Drosophila victoria*. FIGS. 2 and 5.—*Drosophila neocordata*. FIG. 3.—*Chymomyza procnemis*. FIG. 6.—*Drosophila repleta*. FIG. 7.—*Amiota* sp. FIGS. 8 and 9.—*Fucomyia vanduzeei*.

It is nearly universally agreed that the hypandrium of the inner copulatory apparatus represents the ninth sternite (novasternum of authors), and the bridge-like structure connecting the right and left claspers in the Drosophilidae has been called the tenth or decasternum. We have found no evidence in this family of the eighth sternite. This is not surprising, however, since Steyskal (1957) has indicated that only in the genus *Fucomyia* of the Coelopidae is there a sclerite which can be interpreted as the vestigial eighth sternite of an acalyptrate fly.

SEQUENCE OF STERNITE REDUCTION

Judging from the variety of sternal vestiges which have been found in the Drosophilidae, it seems that sternite reduction may follow many different patterns, rather than being limited to any particular sequence of reduction. The major steps in sternite degradation would appear to be: loss of macrochaetae, decrease or loss of sclerotization (with or without separation into two bilateral pieces), and, finally, loss of sensilla.

Six degrees of reduction of the first sternite have been observed in the Drosophilidae. The sternite may remain as a large, non-bristled plate (*Amiota*, etc.), as a pair of small bristled plates (*D. victoria*), as a pair of small nonbristled plates (*D. nannoptera* and others), as sensilla only (many species), as bristles only, or without any vestiges whatever. In *Drosophila hydei* (♂ ♀) the sensilla of S 1 could not be found, but a few bristles were observed instead. The number of bristles varied, as did their position; 9 specimens had no bristles, 16 had a single bristle, 3 had two bristles, and 2 had three bristles. In this species, then, sternal bristles of S 1 seem to be the last vestiges to remain but strict genetic control has apparently been lost. In *D. thoracis*, on the other hand, no vestiges of S 1 of any kind were observed, indicating again that even sensilla may sometimes be lost.

A similar series of stages can be described for the sixth sternite. It occurs in unmodified form (saltans group of *Drosophila*), as a nonbristled sclerotized plate (*D. melanogaster*, etc.), as a pair of reduced sclerotized plates (*C. procnemis*), or as sensilla only (many species). The seventh sternite is represented only by sensilla in all of the species so far examined, with a single exception. In the single male of *D. flavopinicola* which was dissected, the sensilla of S 6 were present as usual, but in the approximate locations where the sensilla of S7 were expected, only a few bristles were seen, one bristle on the right side and two on the left.

STERNITE SPECIALIZATION

Modification of a sternite may result in specialization rather than degradation, and may thus become quite useful in taxonomy. Sabrosky (1959) has recently shown the value of such characters in the genus *Pholeomyia* of the dipterous family Milichiidae. In the Drosophilidae the last bristled sternite is often modified in shape; in *D. parasaltans*, for example, S 6 is partially divided into right and left halves, while in the closely related *subsaltans* no such division is present. In *D. setula* S 5 is enlarged and broadly truncate apically, while in a number of related species this sternite is of normal size and rounded.

More extreme modifications occur in the Steganinae. The sixth sternite of *Sinophthalmus pictus* is an external sclerotized plate situated at nearly a right angle to S 5. In an undescribed species of *Amiota* (subgenus *Phortica*) from Panama S 5 is a V-shaped plate with the point of the V produced inward into the abdomen, and with the arms of the V lying on the surface; in the cleared abdomen one can see the anterior end of the aedeagal apodeme resting in the "pocket" formed by the invaginated portion. In this species S 6 is an enlarged flat plate lying on the surface, without bristles except for its extreme outer corners.

In two unidentified species of *Amiota* (subgenus *Amiota*) S 4 is an enlarged sclerotized plate, of unusual shape and with reduced bristle number. More striking, however, is the modification of S 6 in this subgenus. In dissecting males we have found a dark sclerotized, saclike pouch within the abdomen, just dorsad of S 5, the last bristled sternite (fig. 7). This structure is attached by membrane to the posterior margin of S 5; its free end, however, can be pulled posteriorly and exposed (as in fig. 7). In good preparations one can easily see a pair of sensilla on its basal margin, showing that it is a modified sternite which has turned inward into the abdomen and become folded backward so that it comes to lie just above S 5. In fresh or well preserved specimens this saclike S 6 is visible through the body wall as a dark brown area. In one species of *Amiota* of which there was ample material for repeated dissections, the sensilla of S 7 were found in a membranous mass between the apex of S 5 and the genitalia. We believe that this represents one way in which a sternite may become involved in genitalial structures.

SUMMARY AND DISCUSSION

Judging from the examples which have been observed in the Drosophilidae, the steps in reduction leading to the complete disappearance of a sternite would seem to be: loss of macrochaetae, loss of sclerotized plate, and loss of sternal sensilla. In the process of degradation the sternite may become separated into a pair of bilateral pieces before its ultimate degeneration. Reduction apparently occurs step-wise but the sequence of steps has been quite varied. Thus the last remaining vestige is sometimes the sclerotized plate, sometimes sensilla only, and sometimes bristles only.

Modification of a sternite leading to its in-

corporation as a copulatory structure or auxiliary genitalial structure would probably include: loss of macrochaetae, retention or reinforcement of sclerotization, movement from the surface into the inner abdomen, and, possibly, retention of sensilla. If a sternite should become involved in its entirety, as seems to be occurring in *Amiota* in the case of the sixth sternite, a single, unpaired structure should result. If, however, the process includes some degree of separation into right and left portions, then paired or bilaterally symmetrical structures could result. Since both types of structures do occur in the male copulatory apparatus, it seems quite possible that both types of sternite modification have occurred in the evolution of the genital complex.

It is interesting, although not necessarily significant, that parts of the inner copulatory apparatus in males of the Drosophilidae possess sensilla, usually *sensilla trichodea*. No attempts have ever been made to plot their distribution and frequency, but if it were possible to homologize these with the typical sternal sensilla it would add considerably to the hypothesis that parts of the inner male genitalia have been derived, in part at least, from modified sternites.

Sternal sensilla should be extremely useful in studying problems of sternite homology in different groups of flies. The second sternite, with its conspicuous basal and apical pieces, forms a most conveneint landmark, particularly since the evidence that it truly represents the second sternite is so strong. Some preliminary studies of the complex of sclerites in the asymmetrical genitalia characteristic of some families of Diptera indicate that sensilla can be successfully used as indicators of modified sternites. Further studies along this line are now in progress.

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