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THE MORPHOLOGY AND HISTOLOGY OF NEW SEX PHEROMONE GLANDS IN MALE SCORPIONFLIES, *PANORPA* AND *BRACHYPANORPA* (MECOPTERA: PANORPIDAE AND PANORPODIDAE)[1]

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ABSTRACT

The morphology and histology of a previously undescribed sex pheromone gland in male scorpionflies of the genus *Panorpa* (Mecoptera: Panorpidae) and a morphologically similar gland in *Brachypanorpa* (Mecoptera: Panorpodidae) are described and discussed. The gland and the associated pheromone dispersing structure consist of an eversible pouch that lies in the ventral part of the male genital bulb at the point where the basistyles diverge. The glandular layer of epithelium is composed of three types of cells that vary in size between species of *Panorpa* and between *Panorpa* and *Brachypanorpa*. It is suggested that the gland may have evolved from a structure that is everted by the male during copulation and used to push the female's terminal abdominal segments out of the way and/or open the female genital aperture.

INTRODUCTION

The extant scorpionflies, or insects of the order Mecoptera, are a minor order of insects containing only a few hundred described species and are relics of a once larger and more widespread order. The fossil record indicates that the Mecoptera were most abundant during the last Paleozoic and Mesozoic Eras. In some Permian deposits in Russia and parts of North American, the Mecoptera comprise a large component of the total insect fauna. One fossil mecopteran dates back to the Upper Carboniferous Period and is thus the oldest known fossil of an insect having complete metamorphosis. Their antiquity and generally primitive state makes them of great importance in the understanding of the evolutionary history of insects, and many insect evolutionists believe that a mecopteran ancestor probably gave rise to what is referred to as the Panorpoid complex of insect orders, i.e., the Neuroptera, Mecoptera, Lepidoptera, Trichoptera, Diptera and Siphonaptera.

Despite their phylogenetic significance, the insects of the order Mecoptera have been studied very little relative to most orders of insects. Most of the literature on the mecopterous insects is taxonomic or morphological in nature. However, a few authors, including Caron (1966), Cooper (1940), Newkirk (1957), Brownson (1964), and Bornemissza (1964, 1966a, 1966b) have discussed certain aspects of the behavior and ecology of these insects. Two year ago I initiated a study of the comparative behavior and comparative ecology of the eastern North American Mecoptera in hopes of filling in some of the gaps in our understanding of this interesting order of insects. Future papers will stress: 1) the behavioral strategies of the Mecoptera surrounding pair formation, courtship and copulation and the origin and evolution of these strategies particularly in the selective contents of sexual selection and sperm competition; 2) inter- and intraspecific ecological competition in the genus *Panorpa* as selective contexts leading to the evolution of adult seasonal emergence patterns. This paper is a first report on the reproductive behavior of eastern North American Mecoptera and includes information on the morphology and histology of a previously undescribed sex pheromone gland in male scorpionflies of the genus *Panorpa* (Panorpidae) and a morphologically similar gland in *Brachypanorpa* (Panorpodidae) of unknown but probably similar function.

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Felt (1895) was the first worker to mention the possibility of chemical communication in *Panorpa.* He observed females palpating the dorsum of the third and fourth abdominal segments of males during courtship, and later noticed a "peculiar organ" at this location. He concluded that this structure probably secretes a volatile oil that attracts the female to the male. However, that structure has no associated glandular tissue and Mickoleit (1971) recently reported on the significance of this organ: it forms a clamp-like structure that holds the costa of the wing of the female during copulation. True olfactory sex pheromones have been reported in the Mecoptera. Bornemissza (1964, 1966a, 1966b), in studies of four species of *Harpobittacus* (Mecoptera: Bittacidae) in Australia, found that apparently species-specific sex pheromones are secreted by the males from two eversible intertergal vesicles between abdominal segments 6-7 and 7-8. The pheromones in this case were detectable by the human nose and had an odor similar to butyric acid. Crossley and Waterhouse (1969) studied the ultrastructure of the pheromone secreting gland in *Harpobittacus* and found that the pheromone is secreted directly on the intertergal membrane and dispersed when the intertergal membranes are everted. These authors felt that the eversion of the glands is probably under the control of hemostatic pressure and inversion under the control of retractor muscles.

Eversible abdominal sacs were described by Setty (1940), Newkirk (1957) and Brownson (1964) in the males of various North American species of *Bittacus* and these authors suggested that these structures might be the source of a sex pheromone. During my study of the eastern Mecoptera, I have investigated chemical communication in detail in three species of *Bittacus* and found that olfactory sex pheromones that are apparently species-specific are produced by males in glands homologous with those in *Harpobittacus.* However, the pheromones in the North American bittacids are not detectable by the human nose. The results of the pheromone studies in *Bittacus* will be published at a later date.

Pheromone glands have not been reported in *Panorpa* or *Brachypanorpa.* However, Grell (1942) in a detailed study of the morphology of the male genital bulb of *P. communis* L., a European species, observed a layer of glandular epithelium surrounding the genital pouch in the genital bulb and the results of my investigation show that this is undoubtedly the source of the sex pheromone in these insects.

MATERIALS AND METHODS

The species referred to in this paper were collected at the following localities:

Panorpa banksi Hine–Washtenaw Co., Michigan, near Ann Arbor, June and July, 1972.

Panorpa flexa Carpenter–Swain Co., North Carolina, along road from Newfound Gap to Clingman's Dome, elev. 5100 ft., June 9, 1972.

Brachypanorpa carolinensis (Banks)–Mitchell Co., North Carolina, Crabtree Meadows Campground, elev. 3700 ft., June 4 and 5, 1972.

The genital bulbs of males preserved in 80% ethyl alcohol were removed and placed in dioxane for 24 hours for dehydration and then embedded in a 1:1 Paraplast^{R} dioxane mixture for 2 hours and finally embedded in pure Paraplast (m.p. 56°) for 2 hours. Serial sections cut at 5-10 μ were stained with Delafield's hematoxylin-eosin for observation.

RESULTS AND DISCUSSION

Morphology and Histology of the Pheromone Gland in Males of the Genus Panorpa– Early in my investigation of the behavior of the Panorpidae, I noticed that a portion of the exoskeleton between the basistyles on the venter of the male genital bulb[2,3] was

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[2] The genital bulb is the bulbous genital apparatus of male scorpionflies, consisting of the 9th, 10th and 11th abdominal segments.

[3] See the excellent paper by Grell (1942) for morphological details of structures other than the pheromone gland in the male genital bulb of *Panorpa.*

everted in the form of a sac or vesicle during courtship. Chemical assays were not conducted to confirm that this structure produces a pheromone. However, tests involving observations of the responses of receptive females to courting males before and after the glands were covered with beeswax or Testor's Pla airplane dope showed conclusively that the everted vesicle is the source of a pheromone. Further studies, which will be described in a subsequent paper, revealed that this is the site of production of an apparently species-specific olfactory pheromone which serves to attract receptive females from distances up to 25 feet. Fig. 1 shows a courting male of *P. banksi* with his pheromone gland (P) everted. The figure also shows a coil of solidified saliva (S) projecting from the male's mouth. The solidified saliva is presented to an attracted female just prior to copulation.

The sex pheromone gland of *Panorpa* males is not homologous with those of the Bittacidae *(vide supra)*. In *Panorpa*, the gland is a) a single eversible pouch, b) lined ventrally with glandular epithelium, c) located in the ventral part of the genital bulb, and d) projecting anteriorly into the genital bulb at the point where the basistyles diverge (GP, Figs. 2, 4, 5, 7, 8). The hypovalvae, i.e., the bifurcate portion of abdominal sternum

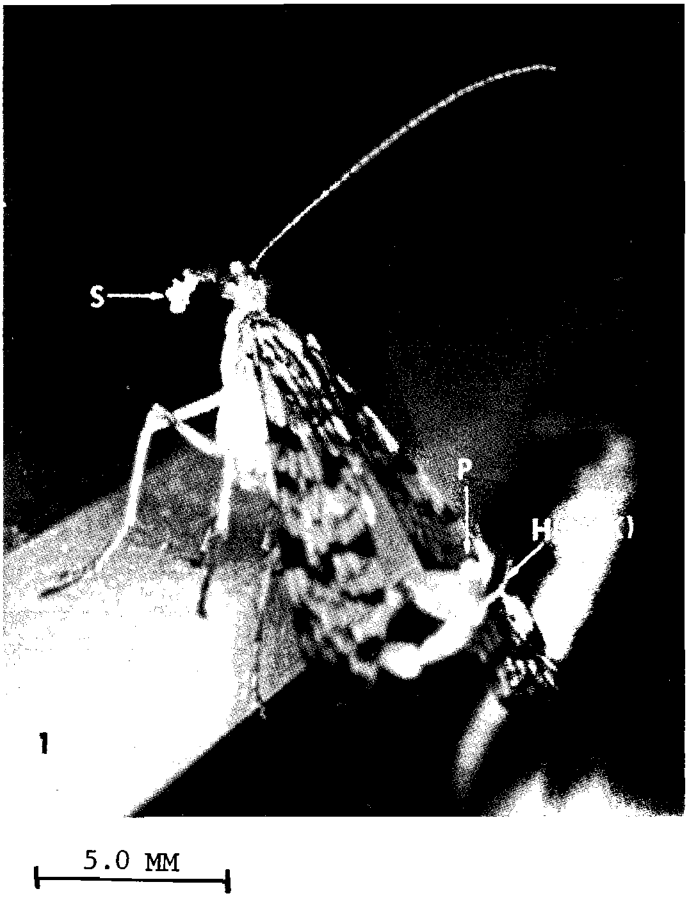
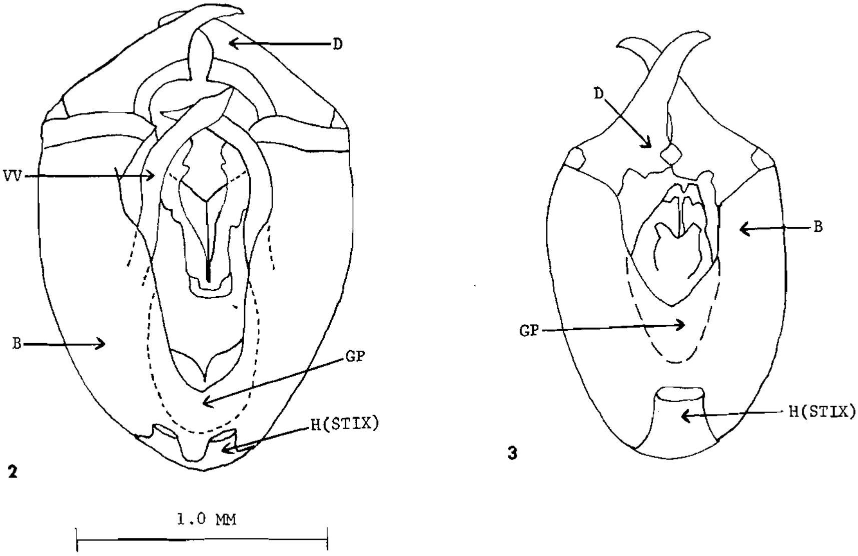


Fig. 1. Male of *Panorpa banksi* with genital pouch everted and dispersing sex pheromone. The structure projecting from the male's mouth is a solidified coil of salivary secretion which is presented to an attracted female as a nuptial offering.

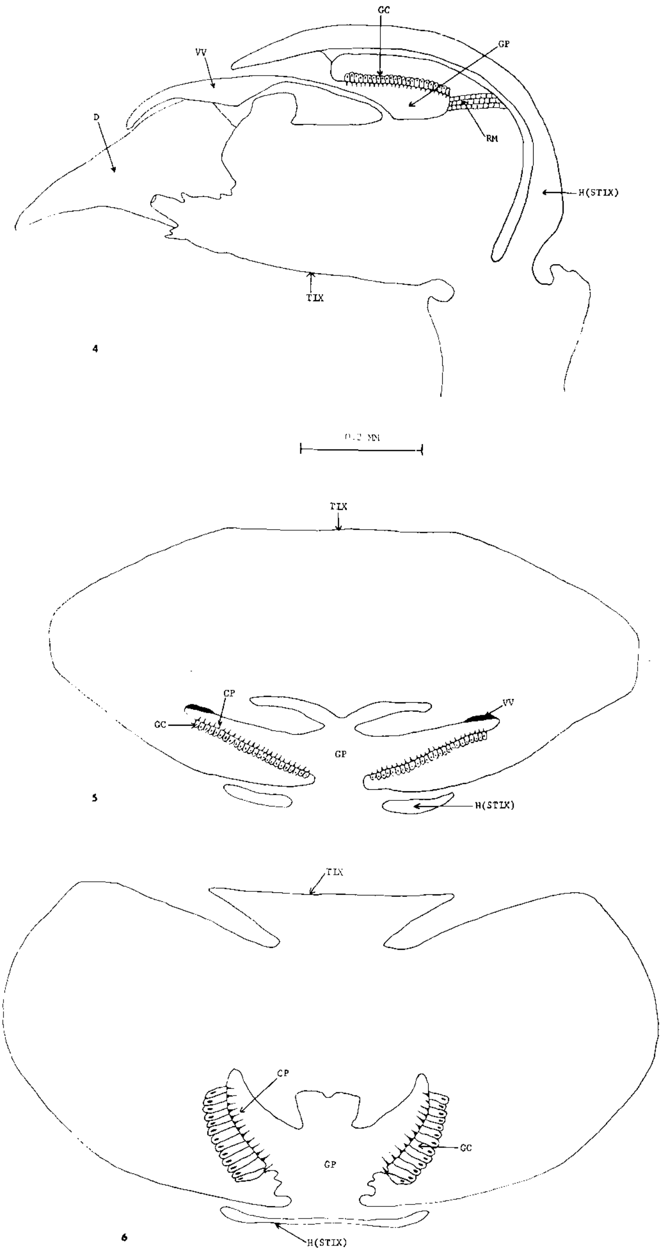
IX, have been partially removed in Fig. 2 to show the location of the genital pouch which varies in size slightly between species of *Panorpa* and which is very large in some species of *Neopanorpa* (Byers, personal communication), an Asian genus of panorpid. The genital pouch is probably everted by hemostatic pressure and is inverted by 2 sets of retractor muscles (RM, Fig. 4).

At the base of the layer of glandular epithelium lining the ventral wall of the genital chamber the cuticle forms filamentous processes projecting into the chamber (CP, Figs. 5, 11, 12). The processes vary in length from 15 μ to 17.5 μ and are about 2 μ wide at their bases in *P. flexa.* In *P. banksi* the processes are about 35 μ in length (CP, Fig. 12). The cuticular lining of the genital pouch also forms vesicles which invaginate into the glandular layer (V, Fig. 11). Grell (1942) noticed a variation in the size of these vesicles in *P. communis* in Europe, and felt that the large vesicles were probably associated only with sexually mature males. I could not see any marked variation in the size of the vesicles between individuals or between species of *Panorpa* even though some individuals sectioned were teneral and some definitely sexually mature, i.e., individuals that were seen exposing their pheromone gland in courtship prior to their preservation in ethyl alcohol. No differences were observed in the structure of the glandular layer of epithelium of individuals of *P. flexa* ranging from very teneral (less than one day old) up to 49 days of age when preserved and sectioned. On the other hand, the height of the glandular layer of cells does vary between species and this variation is discussed below. Courtship and mating in most species of *Panorpa* occur primarily at dawn, at dusk and at night. Courtship and the simultaneous release of a pheromone begins in males at an age of two to four days and continues in a circadian manner until the death of the male. Although this general pattern is probably typical of most of our panorpid fauna, Byers (1963) reported that *P. nuptialis* Gerstaecker probably mates during the day and is inactive at night.

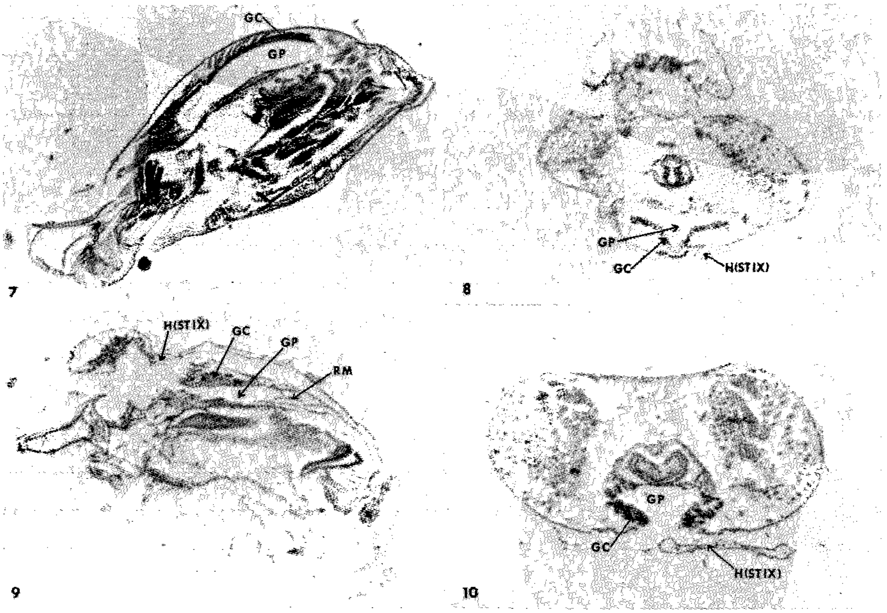
The epithelial components making up the pheromone gland of *Panorpa* are of three types of usually closely packed cells. These three cell types were described by Grell (1942) and I will employ his terminology. A layer of flat matrix epithelial cells (MCN,



Figs. 2 and 3. Ventral views of the genital bulbs of male scorpionflies, hypovalves (sternum IX) partially removed. Both same scale. Fig. 2. *Panorpa flexa.* Fig. 3. *Brachypanorpa carolinensis.*



Figs. 4, 5, and 6. Diagrams of the genital bulbs of male scorpionflies. All same scale. Accessory and matrix cells omitted. Fig. 4. *Panorpa flexa;* sagittal section. Fig. 5. *Panorpa flexa;* cross section. Fig. 6. *Brachypanorpa carolinensis;* cross section.



Figs. 7, 8, 9, and 10. Photomicrographs of the genital bulbs of male scorpionflies. 35X. Fig. 7. *Panorpa flexa;* sagittal section made lateral to the hypovalves (sternum IX). Fig. 8. *Panorpa flexa;* cross section. Fig. 9. *Brachypanorpa carolinensis;* sagittal section. Fig. 10. *Brachypanorpa carolinensis;* cross section.

Figs. 11 and 12) lies just below the cuticular lining of the genital pouch. The boundaries of these cells in the region of the gland cannot be determined with light microscopy. However, the subelongate or elongate nuclei are conspicuous, and in *P. banksi* range in length from 5μ to 8μ (1.5μ to 2.5μ in P. flexa). The vacuolated columnar glandular cells (GC, Figs. 11, 12) located below the matrix layer of cells, range in height from 37μ to 71μ (17.5μ to 28.5μ in *P. flexa*) and from 7μ to 31μ in width (4μ to 9.5μ in *P. flexa*). The shapes of the nuclei of these columnar cells range from oval to elongate and from 11μ to 17μ in length (3.5μ to 5μ in *P. flexa*). Accessory cells (AC, Fig. 11, 12) usually with indistinct boundaries, can be seen between the glandular cells. The nuclei of the accessory cells show approximately the same range in shape and size as the nuclei of the matrix cells.

The secretory mechanism of the glandular cells is unknown, but the morphological evidence presented above suggests that the vacuoles containing droplets of the pheromone move through the glandular cells to the vesicle and through the cuticle of the vesicle to the genital chamber. The pheromone is then dispersed when the genital chamber is everted by hemostatic pressure.

Morphology and Histology of a Similar Gland in Brachypanorpa carolinensis (Banks)–The male genital pouch of *B. carolinensis* (GP, Figs. 3, 6, 9, 10) is about the same size as in *Panorpa*. The epithelial components of the glandular structure are made up of the same three cell types (GC, AC, MCN; Fig. 13) as in *Panorpa*; however the glandular cells are larger than in *P. flexa* but about the size of those in *P. banksi,* ranging in height from 17.5μ to 87.5μ and in width from 3.5μ to 7μ. The processes (CP, Fig. 13) of the cuticular lining of the genital chamber vary from 5.25 to 8.75 in length, and the vesicles formed by invaginations of the cuticle into the glandular cells are small and indistinct and very difficult to discern with the light microscope unlike those in *Panorpa.* As in

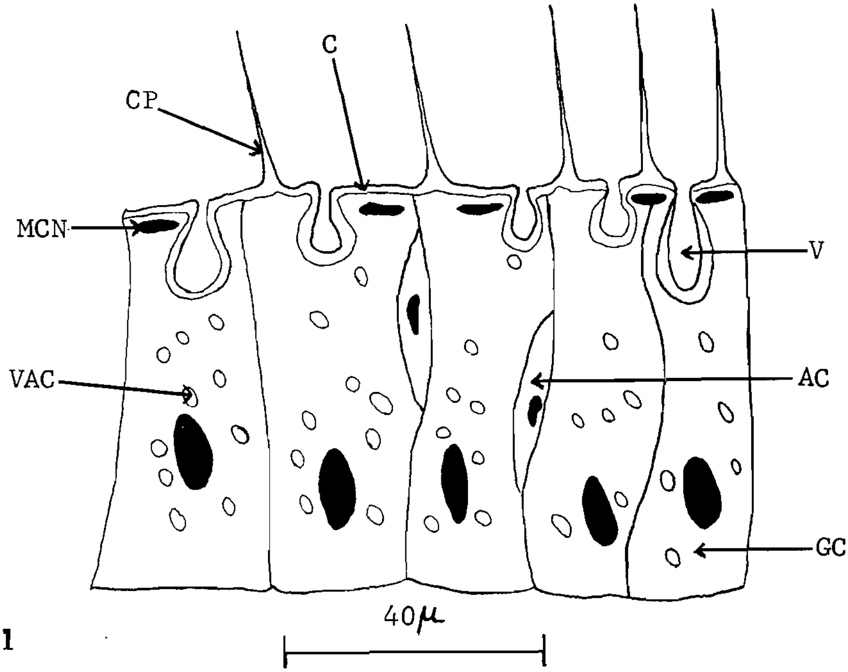


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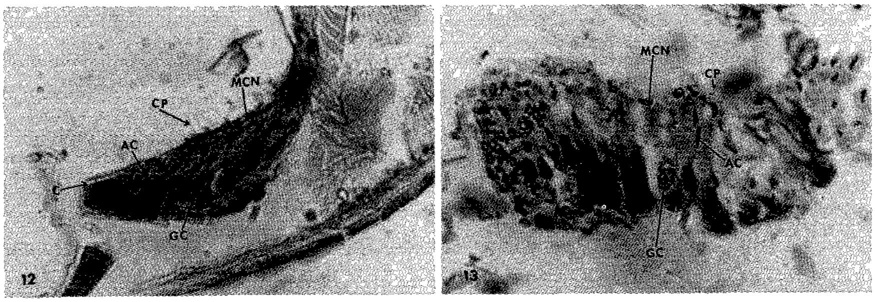
Fig. 11. Diagram of the epithelial components of the glandular layer of the sex pheromone gland of *Panorpa banksi.*



Figs. 12 and 13. Photomicrographs of the epithelial components of the glandular layer of the sex pheromone gland of male scorpionflies. 400X. Fig. 12. *Panorpa banksi.* Fig. 13. *Brachypanorpa carolinensis.*

Panorpa, retractor muscles (RM, Fig. 9) connect the anterior part of the genital pouch to the wall of genital bulb and probably control the inversion of the genital pouch.

During two weeks of field observations on *B. carolinensis* in the southern Appalachian Mountains last summer, I did not observe a single male everting his genital pouch in a courtship situation, nor did I observe mating in this species. However, the morphology of the chamber suggests a function similar to that in *Panorpa*. Further field and perhaps laboratory observations must be conducted in order to elucidate the function of this gland in *Brachypanorpa carolinensis* and the importance of chemical communication during pair formation in this species.

CONCLUDING REMARKS

Miyake (1913, Fig. 4, p. 287) in a study of the Mecoptera of Japan mentioned that males of *P. klugi* M'Lachlan evert a vesicle from the venter of the genital bulb during copulation and that the everted vesicle protrudes posteriorly and presses the terminal abdominal segments (9th–11th) of the copulating female nearly at a right angle to the rest of the abdomen. He goes on to say that *Panorpodes* (Panorpodidae) has a structure in the genital bulb which may correspond to the eversible vesicle of *Panorpa.* The literature on the genitalia of the Mecoptera indicates that the genital bulb of *Panorpa* was very difficult to interpret and prior to Miyake morphologists had thought the eversible vesicle to be the penis (see Stitz, 1906:538). Miyake's observation clearly demonstrated that the vesicle was not inserted into the female during copulation.

Without question the eversible vesicle of Miyake is the same structure referred to as the genital pouch in the present paper. I have seen several hundred pairs of panorpas copulating and recorded numerous copulations on TV tape and 16 mm film. From these data it is apparent that the genital pouch is not always everted during an entire copulation, but is occasionally inverted and then immediately everted at irregular intervals. The female's terminal abdominal segments may fall to a plane with the other abdominal segments when the pouch is inverted and are raised to angles from 55° to 85° from the horizontal axis of the body when the pouch is everted. Therefore, Miyake's observation is correct, that is, the eversion of the pouch does lift the terminal segments of the female's abdomen during copulation. The question remaining is whether the everted genital pouch, in addition to its function as a pheromone dispersing structure, serves to allow the entry of the aedeagus into the female genital aperture; or alternatively, are the terminal abdominal segments of the female merely pushed up incidentally when the male everts his genital pouch to attract additional females. (Receptive females and occasionally males are attracted to copulating pairs.) This can be tested by covering the genital pouch of *Panorpa* males with beeswax and allowing them to mate with receptive virgin females. If sperm are not transferred by these males but are by untreated males this will indicate that the genital pouch does serve to move the terminal portion of the female's abdomen out of the way and/or open the genital aperture of the female so the aedeagus is properly received. If it is found that the eversible pouch, besides functioning as a pheromone gland, is also important as a mechanical aid in copulation, a reasonable context for the origin of the pheromone structure will have been provided, that is, originally functioning only as a device to help open the genital aperture of the female with its later cellular modification into a pheromone secreting structure. This would also explain the presence of the pheromone gland in the male sex of *Panorpa,* rather than in the female.

Insight into the question of the origin of the pheromone gland in *Panorpa* could probably also be obtained by a morphological, coupled with a behavioral investigation of copulation in other panorpid genera such as *Leptopanorpa* and *Neopanorpa,* both of which are Asian in distribution. In addition it might be fruitful to investigate copulation in families of Mecoptera other than Panorpidae and Panorpodidae: the Apteropanorpidae, Choristidae, Nannochoristidae, Notiothaumidae all of which are extra-Nearctic in distribution and the Meropeidae, which occurs in North America and Australia. The literature on the comparative morphology of the genitalia of the Mecoptera is inadequate to determine whether the males in these families possess a structure similar to the genital pouch in the Panorpidae and Panorpodidae. On the other hand, the genitalia in the mecopterous family Boreidae has been described in some detail by Stitz (1908), Crampton (1923), Potter (1938), and Cooper (1940). These studies reveal no indication of an eversible genital pouch in *Boreus* and after observing copulating pairs of *Bittacus* and histological studies of their genitalia, I am convinced that males of this genus do not have a genital pouch either.

ABBREVIATIONS USED IN FIGURES

AC	accessory cell	MCN	matrix cell nucleus
B	basistyle	P	pheromone gland
C	cuticle	RM	retractor muscle
CP	cuticular process	S	salivary secretion
D	dististyle	VAC	vacuole
GC	glandular cell	V	vesicle
GP	genital pouch	VV	ventral valve (paramere)
H (STIX)	hypovalve (sternum IX)		

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