SPERMATOPHORES AND THELYCA OF THE AMERICAN WHITE SHRIMPS, GENUS *PENAEUS*, SUBGENUS *LITOPENAEUS*

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The spermatophores of the five species of the American subgenus *Litopenaeus* of the genus *Penaeus*, three in the Pacific–*P.* (*L.*) *occidentalis*, *P.* (*L.*) *stylirostris*, and *P.* (*L.*) *vannamei*–and two in the Atlantic–*P.* (*L.*) *schmitti* and *P.* (*L.*) *setiferus*–are described in detail and illustrated. The spermatophore of *P. vannamei* uniquely lacks a wing and a lateral blade. That of *P. stylirostris* possesses a sac with overlapping walls, the free lateral margin not being attached to the underlying wall throughout most of its length; this spermatophore also exhibits the broadest wing, consisting of a rigid anterior region and a posterior membranous one. The spermatophore of *P. occidentalis* is the only one armed with an anterior lobe, a transverse anterior lamina, and a sclerotized flap. The spermatophores of the Atlantic species are very similar, both possessing moderately broad wings, large caudolateral flanges, and a lateral blade; however, in *P. schmitti* the blade is broad anteriorly, whereas in *P. setiferus* it is very narrow. During copulation, as the males deposit paired spermatophores on the females, the sperm masses are released through anterodorsal ruptures of the sperm sacs and become lodged on the thelycum, protected ventrally by the anterior part of the sacs. The open-type thelycum (sperm receptacle lacking), characteristic of the members of *Litopenaeus*, is unique within the genus *Penaeus*. The thelyca are described in order to facilitate understanding how the compound spermatophores are held in place. The thelycum of each species exhibits at least one obvious typical feature by which it may be easily recognized: that of *P. vannamei* is provided with an inverted troughlike median protuberance on sternite XIII; in *P. occidentalis* it possesses densely set setae over most of sternite XIV; in *P. stylirostris* it is armed with a strong, subpyramidal median protuberance on sternite XIV; in *P. schmitti*, on the other hand, it exhibits paired subparallel anterolateral ridges; and in *P. setiferus* paired crescentic anterolateral ridges are present which, although convergent, do not meet on the midline. In all but one species, thelycal concavities of sternite XIII serve to lodge the sperm masses which protrude from attached spermatophores; however, in *P. occidentalis* spoonlike coxal plates of the third pereopods receive the sperm masses.

The five species of *Penaeus*, subgenus *Litopenaeus*, commonly known as white shrimps, support some of the most intensive and valuable fisheries in American waters. Three species are limited to the eastern Pacific, *Penaeus occidentalis*, *P. stylirostris*, and *P. vannamei*, and two occur in the western Atlantic, *P. schmitti* and *P. setiferus*. Mass rearing experiments to discover methods for artificial cultivation on a commercial scale are being conducted on all five species, and spermatophore-bearing or "impregnated" females are needed for this undertaking. Despite these efforts, and the considerable interest of biologists in the reproduction of these species (including mating, spawning, and fertilization), descriptions of the spermatophores of only two of them and brief notes on a third are available. General features of the spermatophore of *P. setiferus* were presented by both Burkenroad (1934) and King (1948), and an account of that of *P. stylirostris* was given by Cárdenas Figueroa (1952). Subsequently, Ewald (1965) and Pérez Farfante (1969) recorded a few observations on the spermatophore of *P. schmitti*. The spermatophores of the remaining two species, *P. occidentalis* and *P. vannamei*, have not been mentioned previously.

Lack of information on spermatophores of the subgenus *Litopenaeus* is due, at least in part, to the fact that impregnated females are not readily found (Weymouth et al. 1933; Burkenroad 1939; Heegaard 1953). In this exclusively American group, the females possess an open-type thelycum (Burkenroad 1934; Pérez Farfante 1969), lacking a seminal receptacle and consisting, instead, of protuberances, ridges, concavities, or grooves and, occasionally, lamellae on sternites XII to XIV to which the spermatophore is attached. The latter is thus exposed to the surrounding water and might be dislodged during capture, as suggested by Burkenroad (1939), or retained for only a short period after copulation. In the females of all other

[1]Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, DC 20560.

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subgenera of *Penaeus*, the thelycum exhibits a seminal receptacle where the spermatophores, deposited by the male, remain well protected until the time of spawning or until the succeeding molt.

Among the extensive collections of the subgenus *Litopenaeus* that I have examined, no females of either *P. occidentalis* of *P. vannamei* carrying spermatophores were found. Four impregnated females of *P. stylirostris* and two of *P. schmitti* in the National Museum of Natural History, Smithsonian Institution, constituted the only material at my disposal when this study was initiated. After several unfruitful attempts to collect spermatophore-bearing females in various localities throughout the range of the Pacific species, I obtained such specimens of the three in the Gulf of Panama in March 1973. I caught an additional one of *P. occidentalis* in the same month off Buenaventura, Colombia. In the fall of 1974, Billy R. Drummond sent me three impregnated females of *P. stylirostris* which had been collected off Costa Rica, and recently Harold H. Webber brought me eight spermatophore-bearing females of *P. stylirostris* and five of *P. vannamei* from the same area. The study of the spermatophore of the Atlantic *P. setiferus* was based largely on one female carrying a complete spermatophore and three additional ones in which paired masses of sperm embraced by winglike processes were present on sternite XIII; these specimens had been caught in the waters of North Carolina, and were made available to me by Austin B. Williams. Recently, further observations were made on four impregnated females, two from Apalachicola Bay, Fla., and two from off Texas, given to me by William H. Clark, Jr. and Kenneth N. Baxter.

The spermatophores of the various species are similar (herein described as when in position on the female), each consisting basically of a roughly semicylindrical hardened sperm sac enclosing a columnar sperm mass (spermatozoa within a viscous fluid) surrounded by a thick "sheath" (King 1948) of gelatinous substance (Figure 1A, B). The sac usually bears an anterolateral aliform process, the wing, and is produced caudally or caudolaterally, in a flange. A lateral flap, variable in width and consistency, extends both along the sac and the flange, or only along the latter, usually attached to a firm, elongate blade, and a hardened but plastic dorsal plate is present on the posterodorsal surface of the spermatophore. Finally, a glutinous material always lies against the flange, adhering to the mesial side of the flap. These various accessories associated with the sperm sac presumably help to anchor the spermatophores to the female.

The wall of the sperm sac consists of three somewhat distinct longitudinal regions: a thick, opaque ventral wall, a mostly thin and translucent lateral wall, and an entirely translucent dorsomesial wall. The heavy ventral wall is produced in a longitudinal mesial lapel, clearly delimited by a line along which the ventral and dorsomesial walls meet. The above terminology is consistently employed in the descriptions that follow.

During copulation, two closely attached spermatophores, which are here referred as the compound spermatophore, are transferred to the female (Figure 1C). Immediately after expulsion from the paired terminal ampullae of the male, each spermatophore joins its mate firmly along the dorsomesial walls of the sacs, thus forcing the mesial lapels to project ventrally from the contiguous ventral walls (Figure 1D). These walls, becoming strongly convex when the compound spermatophore is anchored to the thelycum, are responsible for the podlike appearance of the conjoined paired sacs, which constitute a median double structure referred to below as the geminate body.

If the posterior part of the thorax of live mature males is compressed, the spermatophores are readily expelled through the gonopores situated mesially on the coxae of the fifth pereopods. It then may be observed that the spermatophores leave the ampullae with the anterior end foremost, the surface facing the sternum of the male being the same as that which, through a rotation, comes to lie against the thelycum. Consequently, as Kishinouye (1900) first indicated, the right and left spermatophores on the female originate in the corresponding right and left terminal ampullae of the male. Observations by Hudinaga (1942) on *Penaeus* (*Marsupenaeus*) *japonicus* Bate 1888, demonstrated that copulation takes place in a head to head position, the sternum of the male pressing against that of the female. Previously, Burkenroad (1934) and later King (1948) presented hypotheses concerning the transfer of the spermatophores to the thelycum, taking into account the probable utilization of the petasma—apparently so well fitted to lodge the compound spermatophore—and the pereopods. No satisfactory explanation, however, has been advanced as to how a rotation of the spermatophore through 180° around its longitudinal axis, is accomplished.

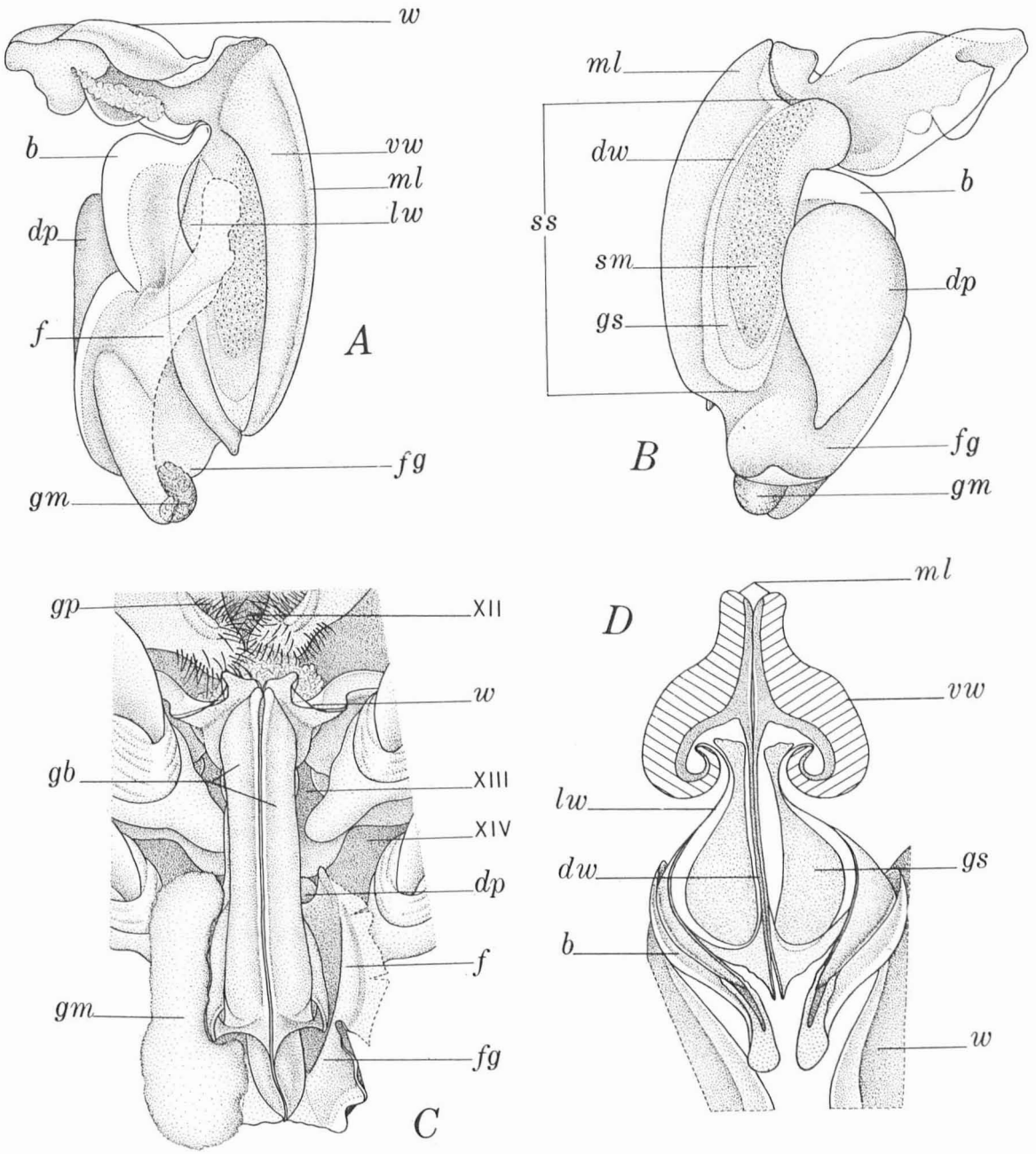

FIGURE 1.—The spermatophores of *Penaeus* (*Litopenaeus*) *schmitti* and *P.* (*L.*) *setiferus* illustrating terms used in the descriptive accounts. *A*, Ventrolateral view of *P.* (*L.*) *schmitti*. *B*, Dorsomesial view of same. *C*, Ventral view of a compound spermatophore of *P.* (*L.*) *setiferus* attached to female. *D*, Cross section of the geminate body of same, immediately posterior to the wings (in preparation of the section the blades together with the torn contiguous portion of the lateral walls have become displaced laterally). *b*, blade; *dp*, dorsal plate; *dw*, dorsomesial wall; *f*, flap; *fg*, flange; *gb*, geminate body; *gm*, glutinous material; *gp*, gonopore; *gs*, gelatinous substance; *lw*, lateral wall; *ml*, mesial lapel; *sm*, sperm mass; *ss*, sperm sac; *vw*, ventral wall; *w*, wing; XII, XIII, and XIV, sternites.

The intent of this paper is to present detailed descriptions of the spermatophores of the five species of *Litopenaeus*. Except for the close resemblance of the spermatophores of *P. schmitti* and *P. setiferus*, all of them, although structurally similar, are quite different in appearance; therefore I have emphasized apparent homologies. An effort has been made to explain the manner in which the spermatozoa egress from the spermatophores to fertilize the eggs. The association of the components of attached spermatophores with the corresponding thelycum in each species is indicated. Finally, the role played by the coxal plates of the third through the fifth pairs of pereopods of the females in keeping the compound spermatophore attached to the thelycum is briefly discussed.

The material examined is indicated in the treatment of each species. The following abbreviations are used for repositories of the specimens: ANSP - Academy of Natural Sciences of Philadelphia; INIBP - Instituto Nacional de Investigaciones Biológico-Pesqueras, México; UNC-IMS - Institute of Marine Sciences, University of North Carolina; USNM - National Museum of Natural History, Smithsonian Institution; and YPM - Peabody Museum of Natural History, Yale University. The carapace length (cl) is the linear distance between the orbital margin and the mid-posterior margin of the carapace. The illustrations have been made from preserved specimens; the accompanying scales are in millimeters.

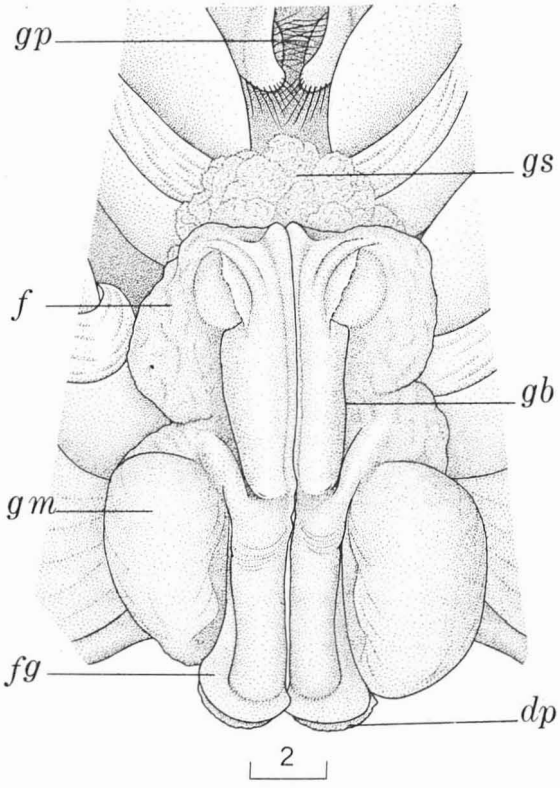

FIGURE 2.—*Penaeus* (*Litopenaeus*) *vannamei* Boone. Compound spermatophore attached to female, ♀ 43 mm cl, off Panamá Province, Panamá. Abbreviations as in Figure 1.

DESCRIPTIONS OF SPERMATOPHORES AND THELYCA

The descriptive accounts of the Pacific species are ordered according to the relative complexity of the respective spermatophores (*P. vannamei, P. occidentalis,* and *P. stylirostris*), and are followed by those of the Atlantic species (*P. schmitti* and *P. setiferus*), the spermatophores of which are markedly similar. The spermatophores of each species are described both as attached to the females, where they invariably occur in pairs, and as they appear when removed from the terminal ampullae of males. Next, detailed accounts of the thelyca are presented, which emphasize the main features for the support of the component parts of the spermatophores. A list of the material examined is given, including the numbers of impregnated females. Finally, the geographic range of each species is indicated.

Penaeus (*Litopenaeus*) *vannamei* Boone 1931
Figures 2-4

Spermatophore

The compound spermatophore (Figure 2) consists of a slender geminate body lacking wings and blades, and bearing thick, broad, lateral flaps, and a pair of long, caudal flanges.

Ventrally, each spermatophore (Figure 3A) exhibits a lateral furrow that roughly delimits a subovate anterior portion, bulging laterally, from an elongate, smoothly convex portion that extends to the flange; the thick, opaque ventral wall merges indistinctly with the lateral wall, which is mostly opaque and to which is loosely attached a conspicuous internal lamina; posteriorly, just before joining the flange, these walls turn strongly dorsad along an oblique line forming the fundus of the sac. The broad, mantlelike flap projecting from the lateral wall is thick, fleshy ventrally, and

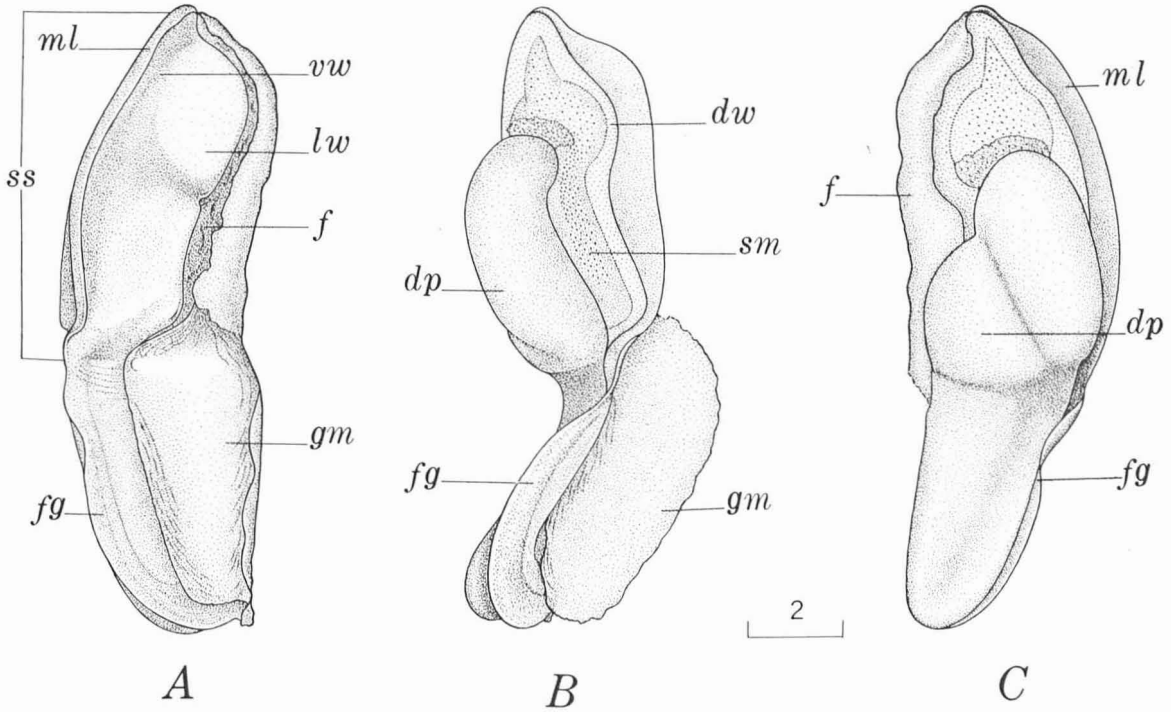

FIGURE 3.—*Penaeus* (*Litopenaeus*) *vannamei*. Left spermatophore dissected from terminal ampulla, ♂ off Juan Díaz, Panamá. *A*, Ventrolateral view. *B*, Mesial view. *C*, Dorsolateral view (glutinous material removed). Abbreviations as in Figure 1.

narrows anteromesially along the border of the sac; posteriorly along the flange, it continues as a flexible, but rather tough, narrow band. The flange is long, directed caudally, with the anterior portion marked by transverse wrinkles; a convex ridge runs parallel and contiguous to the free mesial margin along most of the entire length of the flange, and its lateral margin bears the narrow band from which a voluminous glutinous material is suspended. The thin but rigid dorsomesial wall (Figure 3B) is very broad basally and tapers anteriorly where it is produced in a subconical hood.

The dorsal plate is long (Figure 3C), the longest in the spermatophores of the five species, and at the base of the flange is bent strongly dorsally, the concavity thus formed delimiting two distinct parts. The anterior part, firmly attached to the dorsomesial wall, is nearly triangular in outline and elevated in a blunt mesial ridge which terminates anteriorly in a convex border at about the level of the lateral furrow; the posterior part is mostly flattened, and extends over the flange reaching, or almost reaching, its posterior margin.

The sperm mass, together with the gelatinous substance, is concentrated anteriorly in a large subspherical protuberance filling the lateral bulge and extends as a column in the posterior portion of the sac.

Thelycum (Figure 4A, B)

Sternite XIV bears a pair of setose, sigmoid, obliquely oriented anterolateral ridges, the lateral portions of which are low and rounded and the posteromesial portions high and sharp; the latter are continuous caudally with short elevations flanking a shallow central depression; sculpture is lacking on the posterior part of the sternite. Extending ventrally from the platelike posterior part of sternite XIII is a large, inverted, troughlike median protuberance which forms the anterior wall of a concavity bounded posteriorly by ridges of sternite XIV; the posterior part of the sternite XIII is also provided with a pair of small teeth, subjacent to the base of the median protuberance, and a pair of hornlike marginal projections lateral to the protuberance. The anterior part of sternite XIII bears two small setose lateral prominences, located close to the margin which is overhung

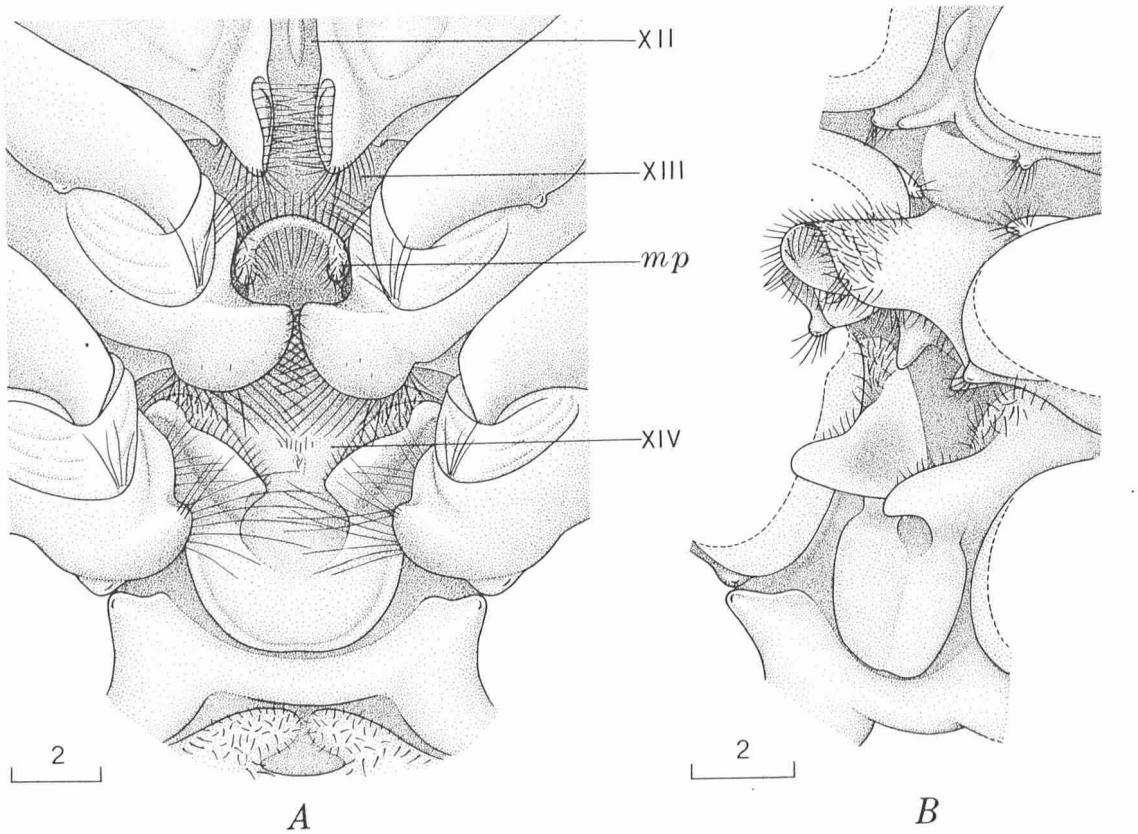

FIGURE 4.—*Penaeus* (*Litopenaeus*) *vannamei*. *A*, Thelycum, ♀51 mm cl, NW Península de Azuero, Panamá. B, Ventrolateral view of thelycum, ♀48 mm cl, same locality, *mp*, median protuberance; XII, XIII, and XIV, sternites.

ventrally by the short posteromesial extensions (protecting the gonopores) of the coxae of the third pereopods.

Disposition of the Compound Spermatophore on the Thelycum

When attached to the female, the compound spermatophore forms a distinct arc, the fundus of the sperm sacs being elevated (ventrally) well above the sternum. The sacs are thus directed anterodorsally with the anteriormost portions of their ventral walls resting on the border of the median protuberance of sternite XIII, and the contiguous lateral flaps extending over the coxae of the fourth pereopods; these flaps seem to serve as stabilizers for the rather compressed, vertically extended sacs. Anteriorly, the bulges of the sacs become very conspicuous, and the practically fused dorsomesial walls lie almost perpendicular to the horizontal coxal plates of the fourth pereopods. The sperm is released at the level of the median protuberance of the female, thus not as close to the gonopores as in the remaining species of the group. In opposition to the paired sacs, the flanges are directed posterodorsally reaching the first pleonic sternite; they cover the dorsal plates ventrally, embrace them mesially, and are flanked laterally by the glutinous material suspended from their narrow flaps. The anterior parts of the dorsal plates, which seem to be the principal elements of attachment of the spermatophores in this species, become fused along their mesial ridges, and are basally affixed to sternite XIV (pressing against the thelycal ridges) as well as to the coxae of the fifth pereopods. The posterior parts of the dorsal plates, in turn, lie on the transverse setose patch of the first pleonic sternite. Finally, the gelatinous substance, protruding through the anterodorsal extremity of the spermatophore, spreads over and beyond the thelycal protuberance of sternite XIII, while the paired

masses of glutinous material somewhat support the flanges.

Material

MEXICO. 6 ♂ 3♀, USNM, 6 km S of Bahía de Guaymas, Sonora, 23 November 1939, M. J. Lindner.- 10♂9♀, USNM, off San Simón, Chiapas, 24 m, I. Edén-Reyna.- 8♂3♀, INIBP, off Barra de Soconusco, Chiapas, 11 June 1960, F. Aguilar.

NICARAGUA. 2♂ 2♀, USNM, ex. Galveston Laboratory, National Marine Fisheries Service.

COSTA RICA. 1♀ [impregnated], USNM, off Parrita, 11 m, 8 March 1975, B. R. Drummond.- 4♀ [impregnated], USNM, off Dominical, 27 m, 8 March 1975, B. R. Drummond.

PANAMA. 18 ♂ 8♀, YPM, off Bella Vista, 8 February 1934, Bingham Oceanogr. Exped.- 2♂8♀, USNM, off Juan Díaz, 12 m, 16 February 1973, *Patricia*.- 2♂1♀,off Juan Díaz, 4 February 1969, L. G. Abele.- 4♂, USNM, off Juan Díaz, 8 m, 5 March 1973.- 4♀ [impregnated], USNM, off Panamá Prov., *Patricia*, 6 March 1973.- 1♀ [impregnated], Golfo de Panamá, ex. Instituto Nacional de Pesca de Panamá.- 3♀, USNM, NW Península de Azuero, 18 m, 14 December 1963, *Pelican* stn. 1614.

ECUADOR. 2♂ 1♀, USNM, Puerto Bolívar, 2 January 1964, Ortiz.

PERU. 2♀, USNM, Caleta Cruz, January 1969, E. M. del Solar.

Species Range

Gulf of California to Tumbes, Perú.

Penaeus (*Litopenaeus*) *occidentalis* Streets 1871
Figures 5-7

Spermatophore

The compound spermatophore is rather bizarre in appearance (Figure 5A, B), its geminate body bearing a pair of small anterolateral wings and a

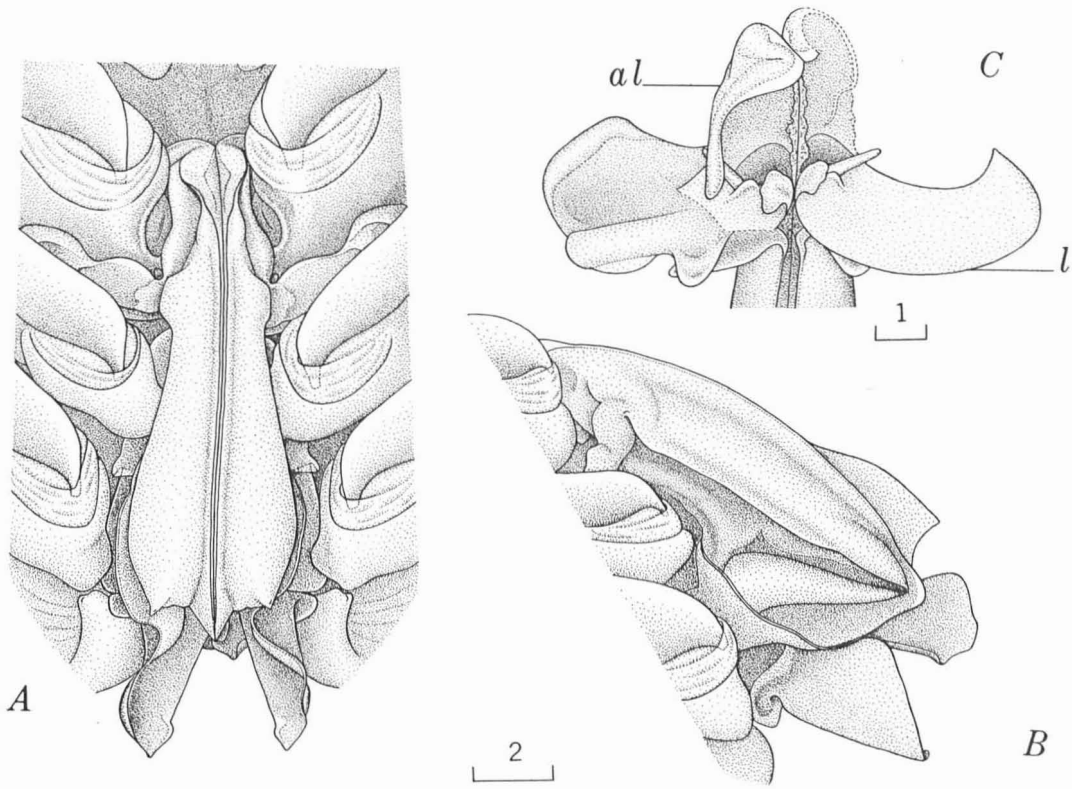

FIGURE 5.—***Penaeus* (*Litopenaeus*) *occidentalis*** Streets. ***A***, Compound spermatophore attached to female, ♀ 35.5 mm cl, off Panamá Province, Panamá. ***B***, Lateral view of same specimen. ***C***, Dorsal view of anterior part of compound spermatophore removed from female, ♀ 40 mm cl, same locality. *al*, anterior lobe; *l*, lamina.

pair of long, broad lateral blades; the posterior parts of the blades are continuous with rigid ventromesial extensions or flaps flanking the posterolateral portions of the geminate body, and terminate in large caudal lobes. The flanges, extremely short and extending caudolaterally, are hidden by the ventromesial extensions.

The thick ventral wall of each spermatophore broadens at the level of the wing and from there tapers anteriorly continuing as a bridge (marked by a dorsal concavity) joining a firm, fanlike anterior lobe (Figure 6A). This lobe is bordered anteromesially by a rib that is produced laterally in a small projection, and its lateral margin bears a shallow emargination which demarks two lateral convexities, the posterior one is hollow. The ventral wall and the thick caudal portion of the lateral wall join in an acute angle, and continue in a short, heavily sclerotized, caudal flange. A dorsolateral rib marks the junction of the mostly thin and translucent lateral wall with the dorsomesial wall, and serves as the base of the blade. The blade exhibits two lateral constrictions that mark three sections: the anterior one is broad, roughly subelliptical, and delimited posteriorly by a transverse rib; the median section, also broad, is subtrapezoidal, and the posterior one narrow and bends around the apex of the caudal lobe, finally turning mesially to join the posterior border of the flange. The caudal lobe is the rather flexible extremity of the rigid ventromesial extension projecting from the line along which the flange and corresponding blade meet. A narrow, iridescent membrane runs along the margin of the ventromesial extension, which sustains a glutinous material on its inner surface (the membrane is not represented in Figure 6A, D for the sake of clarity). The rigid and translucent dorsomesial wall (Figure 6B) completes the sperm sac, which terminates and opens anteriorly at the base of the anterior lobe, mesial to the base of the wing.

The small wing (Figure 6C) is roughly subelliptical in ventral view, but bears a proximodorsal lobular process and is produced distally and posteriorly in a ventrally turned fold continuous with a small shelf at the base of the process (Figure 5C). A rigid but fragile lamina (Figures 5C, 6A, B) lies at the base of, and perpendicular to the anterior lobe; it extends from the mesial part of the sperm sac laterally almost to the tip of the wing. This peculiar lamina bears on its mesial border two conspicuous projections with a small ridge between them; one of the projections is dorsally located, flattened and strongly curved

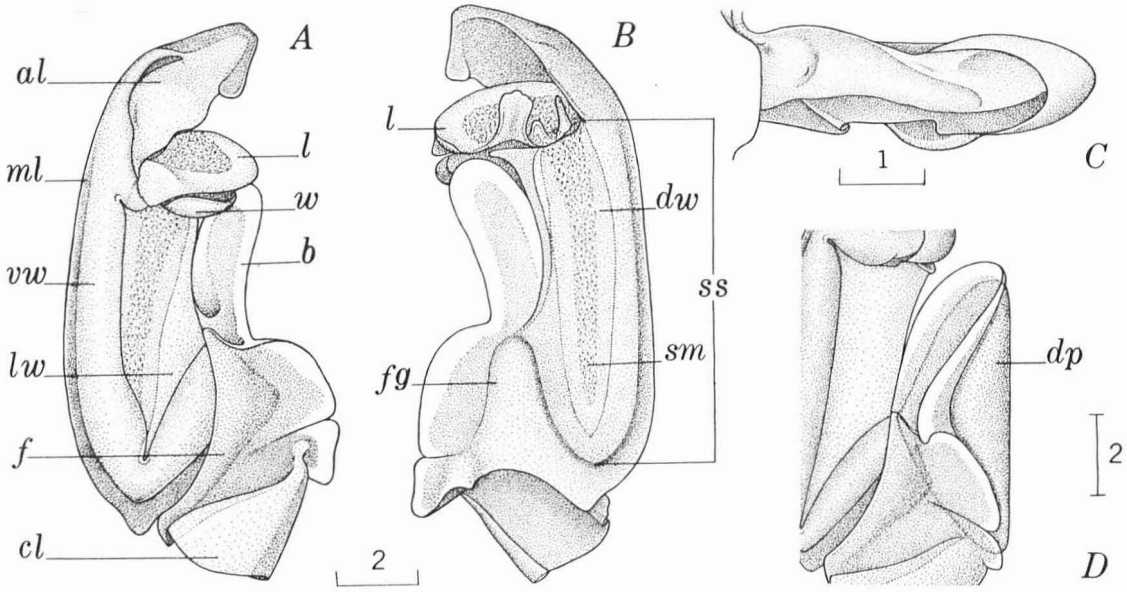

FIGURE 6.—*Penaeus (Litopenaeus) occidentalis*. *A*, Ventrolateral view of left spermatophore (dorsal plate removed) dissected from terminal ampulla, ♂ off Bella Vista, Panamá. *B*, Dorsomesial view of same specimen. *C*, Ventral view of wing as attached to female, ♀ 35.5 mm cl, off Panamá Province, Panamá. *D*, Lateral view of dorsal plate, ♂ off Punta Soldado, Buenaventura, Colombia. *al*, anterior lobe; *cl*, caudal lobe; *l*, lámina. Other abbreviations as in Figure 1.

laterally, whereas the other is spiniform—the tip of the latter projection shows in Figure 5A at the vertex of the emargination between anterior lobe and the base of wing.

The dorsal plate (Figure 6D) is almost as long as, and lies against the dorsal surface of the blade; it is produced in a central prominence that fits into the concavity on the posterior extremity of the anterior section of the blade.

Thelycum (Figure 7)

Sternite XIV is densely covered with setae except over a pair of posterolateral crescentic elevations separated by a short, sharp posteromedian ridge; this ridge is hidden in the adult by the bulging surrounding area. The posterior portions of the elevations are parallel to the thoracic ridge which typically bears a pair of lateral prominences provided with a brush of setae. Sternite XIII is heavily sclerotized posteriorly forming a plate with a broadly concave posteromedian margin not overlapping sternite XIV, but with lateral extremities produced into hornlike projections freely overhanging sternite XIV. The central region of the plate bears a strong rounded to subconical knob and the posterior margin occasionally is armed with a small median tooth. The anterior part of sternite XIII is provided with a pair of transverse folds, the mesial portions of which are produced into sharply pointed conical projections covered by minute setae. The strong posterior ridge of sternite XII is divided by a median depression, and its lateral extremities are produced caudally in a pair of convexities hidden by the scooplike coxal plates of the third pereopods. These uniquely shaped coxal plates support the sperm sacs anteriorly and seem to retain, at least briefly, the sperm masses immediately after their release. It should be remembered that the coxal plates are covered ventrally by the bases of the anterior lobes of the spermatophores.

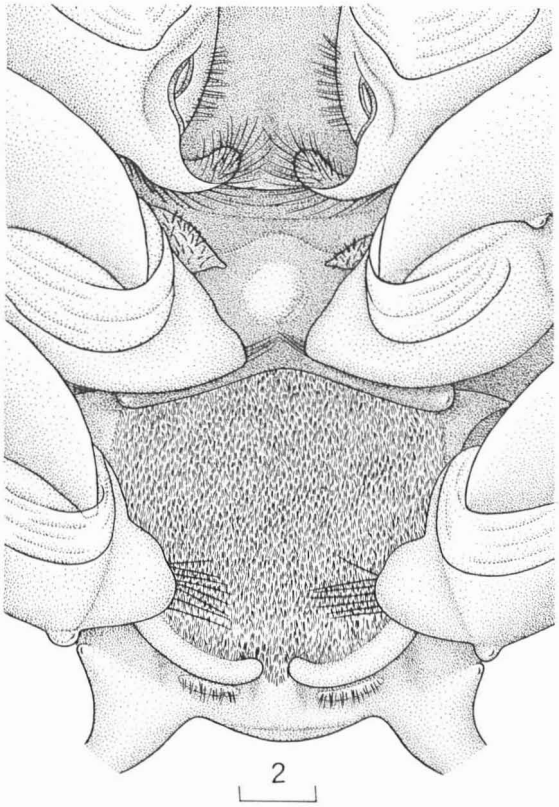

FIGURE 7.—*Penaeus* (*Litopenaeus*) *occidentalis*. Thelycum, ♀53.5 mm, cl, Golfo de Panamá, Panamá.

Disposition of the Compound Spermatophore on the Thelycum

When the compound spermatophore is in position on the female, the fanlike anterior lobes become affixed to sternite XII with the lateral portions lying beneath the coxae of the third pereopods while their basal portions extend over (ventrally) the coxal plates. The angular junctions between the anterior lobes and the wings embrace the posterior extremity of the corresponding female gonopore. The mesial borders of the laminae, in turn, form supporting rims along the lateral borders of the apertures of the respective sperm sacs, and the flattened projections of the laminae meet in the sagittal plane, while the spiniform projections lie contiguous to the posterior convexities of the anterior lobes (Figure 5C). The laminae extend laterally, adhering to the posteroventral surface of the coxae of the third pereopods, and the wings rest ventrally over and against the laminae, both processes helping to anchor the spermatophores to the thelycum. The position assumed by the anterior part of the spermatophore on the female brings the apertures of the sperm sacs to the coxal plates of the third pereopods and thus close to the gonopores; consequently, it seems that the sperm might well accumulate on these spoonlike coxal plates. Whether or not the opening of each sac is permanent, or results from a rupture, has not been ascertained.

Posterior to the wings, the lateral blades press

against the subjacent dorsal plates which come together, meeting mesially, and adhere to sternites XIII and XIV. The narrow posterior portions of the blades meet on the midline, forcing the geminate body ventrally and causing the caudal lobes to project posteroventrally, resembling paired rudders.

Material

MEXICO. 1♀, USNM, between Monte Alto and San José, Chiapas, 25 m, 8 August 1970, D. Palacios.

PANAMA. 6 ♂ 2♀, syntypes, ANSP No. 73, "Isthmus of Panama," J. A. McNeil.- 6♂ 12♀, YPM, off Bella Vista, 9 February 1934, Bingham Oceanogr. Exped.- 7♂, USNM, off Juan Díaz, 4.5-7 m, 26 February 1973, *Patricia*.-2♀ [impregnated], USNM, off Panamá Prov., 6 March 1973, *Patricia*.- 1♂ 1♀, USNM, E of Panamá City, 7 m, 5 November 1971, D. E. Sweat.

COLOMBIA. 12♂ 12♀ [1♀ impregnated], USNM, off Punta Soldado, Buenaventura, 4.5 m, 1 March 1973, *Santanderino*.- 6 ♂ 13 ♀, USNM, Tortugas Grounds, Buenaventura, 9 m, 19 September 1969, *Cacique* stn. 69-24.

ECUADOR. 6 ♂ 3♀, USNM, off Playas, 1963, commercial catches.

PERU. 1♀, USNM, Caleta Cruz, Tumbes, 18 m, January 1969, E. M. del Solar.

Species Range

Chiapas, México, to Tumbes, Perú, and Islas Galápagos.

Penaeus (*Litopenaeus*) *stylirostris* Stimpson 1871 Figures 8-12

Spermatophore

The compound spermatophore consists of a slender, geminate body produced into large anterolateral wings, broad posterolateral flanges, and bearing paired elongate blades (Figure 8).

The ventral wall of each spermatophore is truncate anteriorly; posteriorly it continues indistinctly with the thick posterior portion of the lateral wall, both walls then turning abruptly dorsad forming the fundus of the sac just before joining the flange (Figure 9A). The lateral wall, mostly thin, is bounded by a very fine dorsolateral rib. This rib serves as the base of a long, moderately broad blade, which extends from the base of the wing (there fused to its posterior ridge) to the anterior extremity of the flange, and continues along the entire border of the latter. The blade is somewhat arched over its attachment to the rib, which delimits two longitudinal parts. One part is directed dorsomesially to the base of the flange, where it twists laterally, the other part projects ventromesially throughout its entire length, and bears anteriorly an iridescent, rather membranous broad flap to which adheres (dorsally) a mass of viscous material; along the flange the ventromesially projecting part becomes flexible and sustains a narrow extension of the flap, supporting a mass of glutinous material on its mesial surface. The flange is somewhat broadly ovate, and is covered by a large dorsal plate which occupies its entire surface and extends beyond the flange

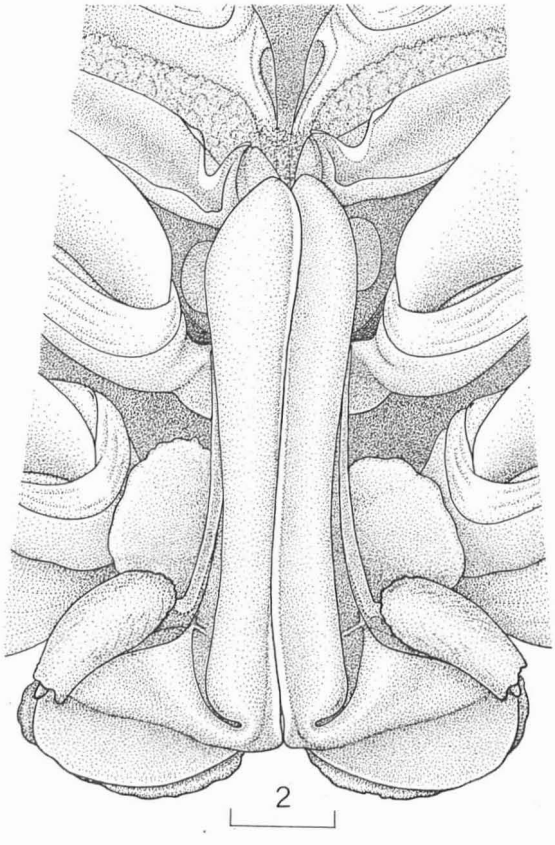

FIGURE 8.—*Penaeus* (*Litopenaeus*) *stylirostris* Stimpson. Compound spermatophore attached to female (geminate body slightly displaced posteriorly to show bases of wings),♀38 mm cl, off Panamá Province, Panamá.

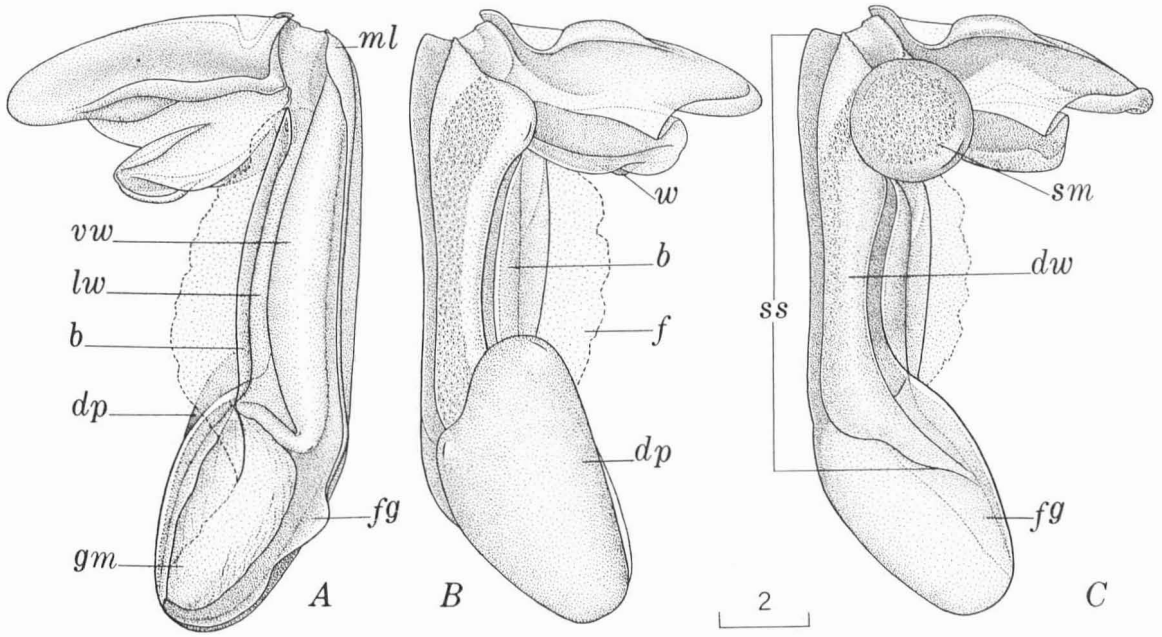

FIGURE 9.—*Penaeus* (*Litopenaeus*) *stylirostris*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂ off Juan Díaz, Panamá. *B*, Dorsomesial view of same specimen. *C*, Dorsomesial view of right spermatophore forcefully expelled from terminal ampulla, ♂ off Panamá Province, Panamá. (For the purpose of illustration the anterior ventromesially directed part of the blade has been turned laterally and the viscous material removed.) Abbreviations as in Figure 1.

anteriorly in a rounded portion affixed to the dorsomesial wall.

In this spermatophore, the dorsomesial wall (Figure 9B, C) is turned upon itself and attached to the mesial lapel of the ventral wall, but not joining the lateral wall—except posteriorly, where they become fused. Consequently, the lateral wall and part of the ventral wall overlap the sac (largely formed by the dorsomesial wall) as a protecting shield. The sac is subconical anteriorly; it expands in a conspicuous rounded bulge at the base of the wing, and continues into the elongate posterior portion affixed to the base of the flange and firmly attached to the dorsal plate.

The wing (Figure 10A, B) consists of a transversely elongate, mostly sclerotized anterior region, and a subrectangular, membranous posterior region. The anterior region bears a long, sharp, ventral ridge, joining a short, pointed, basal rib at almost a 90° angle; the area laterally contiguous to the basal rib is membranous, whereas that mesial to it is thick, but soft, and meets the ventral wall of the sac. Dorsally, the wing is produced in a broad, rounded lobe, situated close to its anteroproximal margin. The membranous region of the wing bears a posterior rib that ends

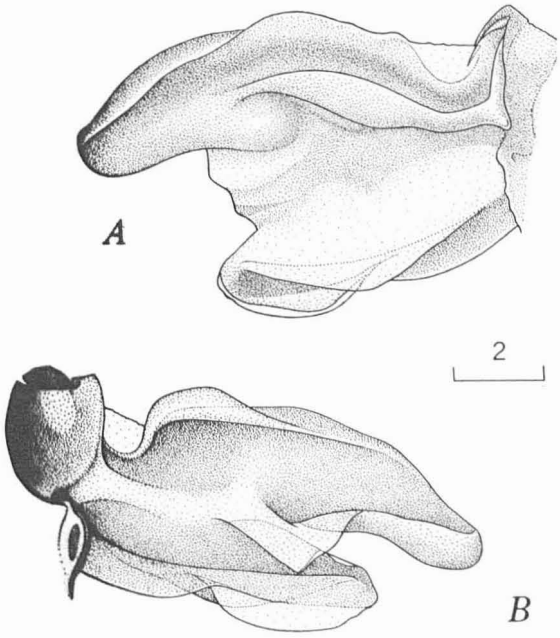

FIGURE 10.—*Penaeus* (*Litopenaeus*) *stylirostris*. Wing severed from geminate body of right spermatophore, ♂ off Playas, Ecuador. *A*, Ventral view, posterior membranous region extended. *B*, Dorsal view of same specimen.

premarginally. The posterolateral membranous extension is reflexed and attached to the rib dorsally, thus forming a shallow pocket. After the compound spermatophore is deposited on the thelycum, the pockets of the paired wings come to lie posteromesially and are quite conspicuous on those impregnated females in which the geminate body has been lost.

Thelycum (Figure 11)

Sternite XIV bears a large median subpyramidal prominence with a subtriangular base (broad anteriorly, tapering posteriorly), its sharp midlongitudinal carina armed with a row of very minute setae. The highly sclerotized posterior part of sternite XIII is produced into a rigid, subvertical shelf overhanging sternite XIV; this shelf constitutes the posterior wall of a pair of concavities which are separated by a sharp median ridge and are delimited anteriorly and laterally by strong angular paired ridges, the posterior bases of which extend laterally and bear toothlike projections. The anterolateral part of sternite XIII bears paired transverse rigid elevations covered by long setae. Heavily sclerotized sternite XII is nearly straight along its posteromedian margin, and produced caudally in a pair of lateral projections armed with tufts of setae. The conspicuous concavities of sternite XIII serve to lodge the sperm masses which emerge from the ruptured anterodorsal bulges of the compound spermatophore.

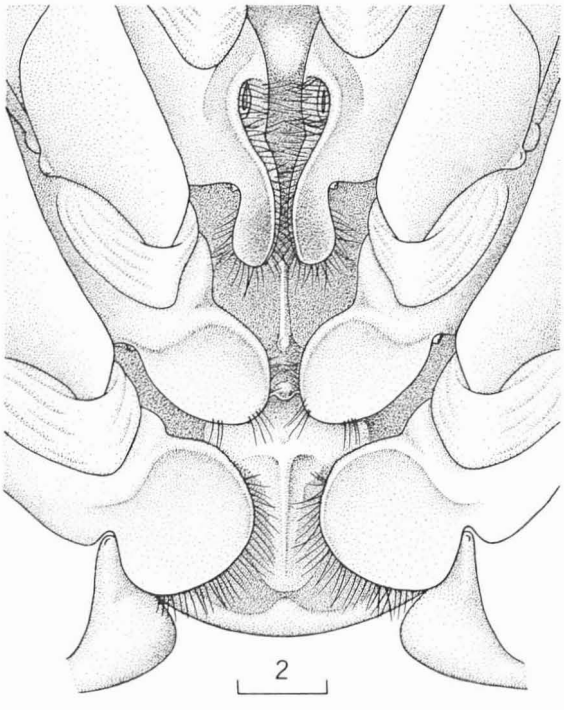

FIGURE 11.—*Penaeus* (*Litopenaeus*) *stylirostris*. Thelycum, ♀46 mm cl, off Bella Vista, Panamá.

Disposition of the Compound Spermatophore on the Thelycum

When the compound spermatophore is in position on the female, the anterior extremity of the geminate body lies on the ventrally turned mesial borders of the coxal plates of the third pereopods, with the sperm masses (projecting through the anterodorsal bulges) lodged in paired thelycal concavities of sternite XIII, near the gonopores (Figure 12). The wings contribute to anchoring the spermatophore: their anterior regions are attached to the posteroventral surfaces of the coxae of the third pereopods, the mesial portions following the contour of the strongly curved coxal plates; lobes borne on the dorsal side of the anterior regions certainly function as adhesive elements. The posterior region of each wing is extended

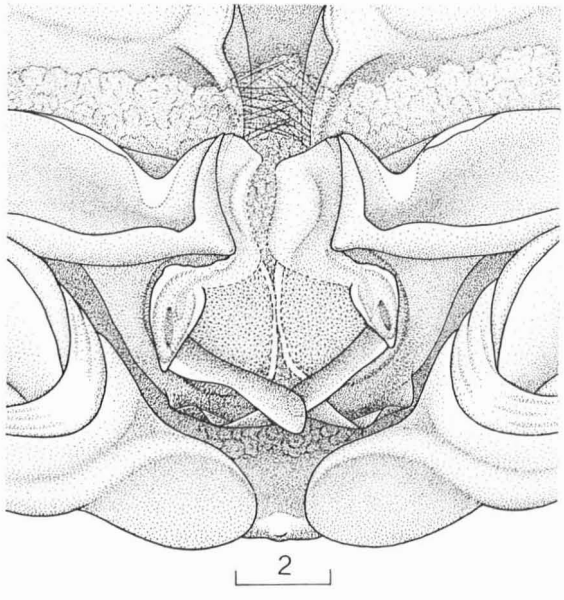

FIGURE 12.—*Penaeus* (*Litopenaeus*) *stylirostris*. Sternites XII and XIII bearing paired masses of sperm and wings of a compound spermatophore, the geminate body of which has been lost (see explanation in text), ♀48 mm cl, off Guaymas, México.

mesially, each with its marginal rib embracing the sperm mass protruding through the corresponding sac; the adjacent membranous portions cover each mass laterally and from there extend tightly attached to sternite XIII.

From the bases of the wings posteriorly, the lateral portions of the ventral walls together with the lateral walls are turned mesially in a spiral thus reducing the lumen of the sacs; at the same time, each blade comes to occupy a position deep within a fold so that the dorsomesial part of the blade abuts against the respective sac, and the other part, together with its flap, projects somewhat laterally. Caudally, the geminate body reaches the first pleonic sternite, and the thick portions of the lateral walls are turned sharply anterolaterad resulting in the elevation of paired ridges. These are continuous with the flanges which posteriorly extend laterally from the geminate body and either embrace or enfold the dorsal plates. These plates are attached in such a way that their smaller anterior parts rest against the coxal plates of the fifth pereopods, and their broad posterior parts (extending across the corresponding flange) lie almost entirely on the first pleonic sternite. Finally, the glutinous material, resting along the anterior borders of the flanges, become almost perpendicular to the median body.

As the compound spermatophore is anchored to the female, gelatinous substance extends over the coxae of the third pereopods and under the wings, penetrates the area between the coxal plates of those pereopods and covers the posterior portion of sternite XII.

In *Penaeus stylirostris* the spermatozoa are apparently released by the rupture of the attached spermatophore. By some unknown means, the geminate body with adjoining flanges breaks away, leaving the wings, together with paired rounded masses of sperm surrounded by gelatinous substance, on the female. It seems that when the spermatophores are expelled, the spermatozoa and the gelatinous substance, which were previously within the sacs, are forced into, and then break through, the anterolateral bulges, finally becoming lodged in the thelycal concavities of sternite XIII. In the extruded spermatophores that I have examined—removed from impregnated females or obtained by forcing their expulsion from the terminal ampullae of males—the sacs retained but little sperm. The wings are torn from the geminate body along the line of union between their mesial extensions and the corresponding ventral wall, and the break continues across the lateral wall to the posterior ridge of the respective wing. The rupture does not occur along definite sutures, but it follows the pattern described. Once the geminate body breaks away, the spermatozoa are exposed to the surrounding water, in close proximity to the female gonopores.

On one of the females examined there was an entire spermatophore superimposed upon the remains of another, the latter represented by a pair of wings and remnants of a sperm mass. This indicates that the animal had copulated twice within a short period of time.

Material

MEXICO. 1 ♂ 2 ♀ [impregnated], USNM, off Guaymas, Sonora, 8 April 1940, Capt. Corona.- 2 ♀ [impregnated], USNM, off Guaymas, Sonora, 9 April 1940, E. F. Ricketts.- 2 ♂ 2 ♀, INIBP, Bahía de Altata, Sinaloa, 14 April 1959, commercial catches.- 4 ♂ 3 ♀, USNM, between Monte Alto and San José, Chiapas, 25 m, 8 August 1970, D. Palacios.

COSTA RICA. 3 ♀ [impregnated], USNM, Parrita, SE of Puntarenas, 27 m, 4 July 1974, B. R. Drummond.- 1♀ [impregnated], USNM, off Parrita, 11 m, 8 March 1975, B. R. Drummond. 2♀ [impregnated], USNM, off Parrita, 18 m, 8 March 1975, B. R. Drummond. 5♀, [impregnated], USNM, off mouth Río Coronado, 16 m, 10 March 1975, *María del Pilar*.

PANAMA. 4♂ 9♀, USNM, off Panamá Prov., 12-24 m, 16 February 1973, *Patricia*.- 14 ♂ 1♀, USNM, 4.5-7.5 m, of Juan Díaz, 26 February 1973.- 6♂, USNM, off Panamá Prov., 5 March 1973.- 4 ♀ [impregnated], USNM, off Panamá Prov., 6 March 1973, *Patricia*.- 1♂ 3♀, USNM, Isla Gorgona, 1 m, March 1973, fishermen.

ECUADOR. 1 ♂ 1♀, USNM, off Playas, 3 December 1963, San Andrés.- 1♂, USNM, Ensenada de Valdivia, December 1934, S. Camino.

PERU. 2 ♂ 2♀, USNM, off Puerto Pizarro, 11 May 1941.

Species Range

Punta Abreojos, Territorio de Baja California, and Gulf of California, México, to Tumbes, Perú.

Penaeus (*Litopenaeus*) *schmitti* Burkenroad 1936 Figures 1A, B, 13-15

Spermatophore

The compound spermatophore consists of a geminate body produced in a pair of anterolateral wings, flanked caudolaterally by flanges broadened posteriorly and bearing wide lateral flaps (Figure 13A, B).

Anteriorly, the thick, opaque ventral wall of each spermatophore is truncate and strongly inclined dorsally (Figure 14A); posteriorly, it is imperceptibly continuous with the thick portion of the lateral wall, both turning abruptly dorsad forming the fundus of the sac. The lateral wall bears a small, blunt to acute caudal projection, just before joining the flange. The flange is narrow and horizontal anteriorly, it becomes progressively broader posteriorly, and turning mesially is deflected ventrally becoming almost perpendicular to its anterior portion. The lateral wall is bounded dorsolaterally by a fine rib that serves as base for the anterior part of a long blade. The blade is divided by a deep horizontal incision. The anterior part is narrow and convex at its cephalic extremity, then broadens abruptly and reaches the flange where its free caudal margin overhangs (ventrally) the cephalic margin of the posterior part. The posterior part, in turn, is narrow and runs along the lateral border of the flange, tapering caudally. The flange bears a broad, lateral flap which is produced anteriorly in a narrow strip running laterally along the sac; the broad portion of the flap is strengthened by a subtriangular

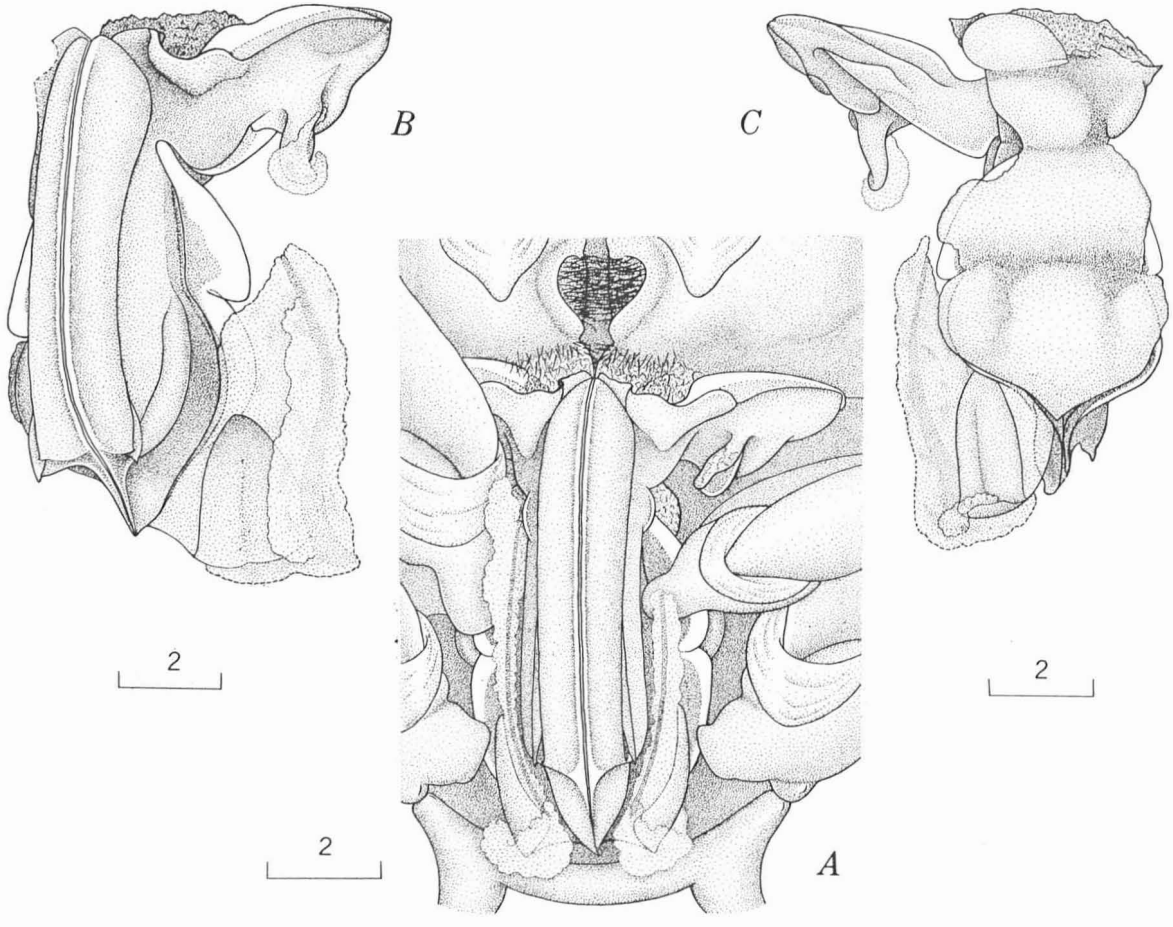

FIGURE 13.—*Penaeus* (*Litopenaeus*) *schmitti* Burkenroad. *A*, Compound spermatophore attached to female, ♀ 34 mm cl, off Tucuracas, Península de la Guajira, Colombia. *B*, Ventrolateral view of compound spermatophore dislodged from female, ♀ off Honduras. *C*, Dorsal view of same specimen (anterodorsal extremity missing).

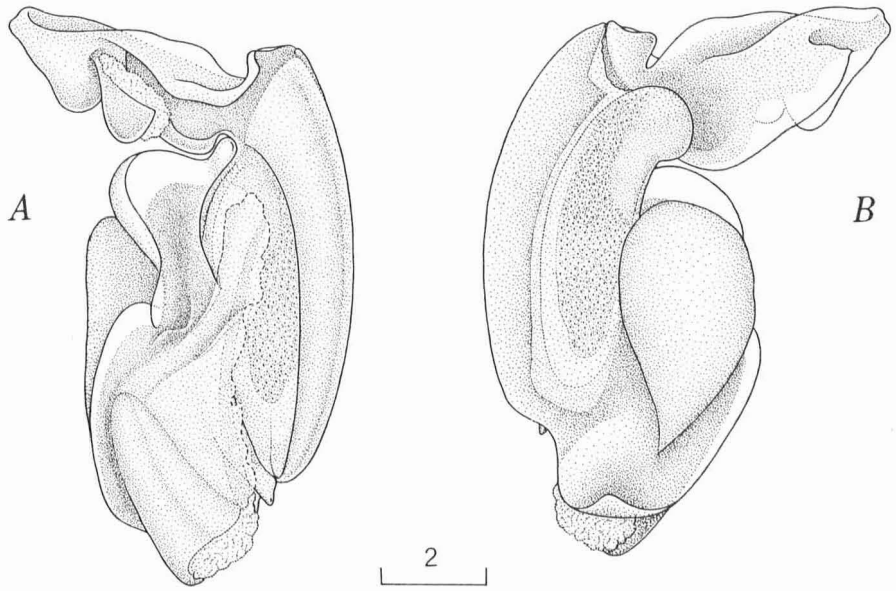

FIGURE 14.—*Penaeus* (*Litopenaeus*) *schmitti*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂ off Ubatuba, São Paulo, Brasil, *B*, Dorsomesial view of same specimen.

plate and a submarginal thickness somewhat stiffens the entire flap. A glutinous material rests against the flange, and adheres to the mesial surface of the flap.

The thin, translucent dorsomesial wall bulges conspicuously beyond its attachment along an oblique line extending from the anterior extremity of the mesial lapel to the posteroproximal end of the wing (Figure 14B; this bulge, occupied by the extremity of the sperm mass enclosed in the spermatophore, bears a triangular crest, rather similar to the subconical anterior extremity of the sperm sac in *P. stylirostris*. Posterior to the bulge, the dorsomesial wall, as in all the other spermatophores, is attached to the mesial lapel along its entire length, extending laterally to join the blade, and caudally to become affixed to the base of the flange.

The wing is long and irregular in contour, produced caudally in a broad proximal lobe, and tapers to a rounded excavated tip. The ventral surface is scabrous, bearing several projections: a rigid, rounded prominence on the anterior rib; an elongate, twisted process (its base situated slightly distal to midlength) that extends mesially in the form of a subovate to nearly semicircular lobule; and a distal shelf, obliquely flanking the process posterolaterally.

The dorsal plate (Figure 14B) is roughly tear-shaped, rounded anteriorly, tapering posteriorly, and relatively long, extending from the anterior end of the blade (at the base of the wing) almost to its posterior tip. The plate is intimately associated with the blade anteriorly, and practically fused to the flange posteriorly.

Thelycum (Figure 15)

Sternite XIV bears a pair of subparallel anterolateral ridges which extend posteriorly without turning mesially, to reach two rigid rounded or subconical prominences; a narrow median sulcus often divided by a slender longitudinal rib is present anterior to the prominences. Sternite XIII is rigidly sclerotized forming a strong plate produced posteriorly as an emarginate soft shelf overhanging sternite XIV; the anterior part of this sternite bears a pair of soft and naked transverse elevations flanking a tonguelike lamella bordered by setae. The lamella forms the roof of a concavity floored by a strong ridge from sternite XII. The ridge (a marginal thickening of platelike sternite XII and mostly hidden by setose, rounded, and relatively short coxal plates of the third pereopods) is produced into two pairs of convex projections, a small median pair and considerably larger lateral ones armed with long setae. The concavity of sternite

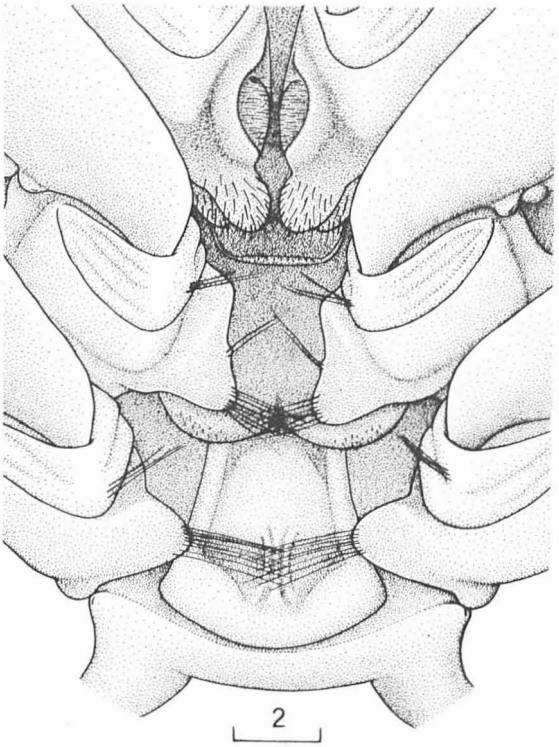

FIGURE 15.—*Penaeus (Litopenaeus) schmitti.* Thelycum, ♀50 mm cl, off Paramaribo, Surinam.

XIII serves to receive the sperm masses projecting through the ruptured anterodorsal bulges of the compound spermatophore, a function similar to that of paired concavities present on the same sternite in *P. stylirostris*.

Disposition of the Compound Spermatophore on the Thelycum

At mating, the compound spermatophore is applied to the thelycum with the anterior part of the geminate body lying on the mesial margins of the coxal plates of the third pereopods, in close proximity to the gonopores (Figure 13A). Basally, the wings extend over (ventrally) the coxal plates, their posterior lobes embrace laterally the sperm masses emerging from the sacs, and are attached caudal to the tonguelike lamella of sternite XIII, where they are almost contiguous; the anteromesial margins of the wings, however, are free, leaving a passageway between them and the body of the female, through which protrudes gelatinous substance. The wings are affixed distally to sternite XIII, with the twisted processes turned strongly posteromesiad and hidden by the articular (dorsal) membranes of the corresponding fourth pereopod. The sperm masses which emerge through the ruptured anterodorsal bulges of the spermatophore are lodged within the concavity roofed by the lamella of sternite XIII and floored by the strong ridge projecting from sternite XII. The sperm-filled concavity is lined by the gelatinous substance which surrounded the sperm while in the sac. Caudally, the geminate body extends to the posterior part of sternite XIV, where the posteromesial portions of the flanges meet on the sagittal plane and form a vertical shelf that is situated between the two thelycal protuberances. The broad anterior parts of the paired blades and the lateral (anterior) portions of the flanges are attached to sternite XIII and XIV successively, pressing against the dorsal plates. The broad flaps borne by the flanges conspicuously flank the geminate body, and the glutinous material—adhering to their mesial surfaces—enlarge, extending along the sides of the geminate body. The dorsal plates fuse in a single mass which is directly applied to sternites XIII and XIV, and which anteriorly abuts the indurate gelatinous substance enveloping the sperm masses within the concavity of sternite XIII (Figure 13C).

Several years ago, during the course of field work in Caribbean waters, I examined a few females carrying complete spermatophores as well as a few others bearing only those elements of the spermatophores which become affixed to sternite XIII. The latter specimens indicate that after the compound spermatophore is attached to the female, the geminate body is severed leaving behind only the wings and paired masses of sperm. Remarks on the rupture of the spermatophore in *P. setiferus*, which occurs in about the same manner as it does in *P. schmitti*, are presented on p. 481.

Material

Many specimens examined by me are recorded in Pérez Farfante (1969). Two females with spermatophores attached studied during the course of this investigation are in the lots listed below.

COLOMBIA. 6 ♂ 10 ♀, USNM, off Tucuracas, Península de la Guajira, 22 m, 6 October 1965, *Oregon* stn. 5674.

SURINAM. 1 ♀, USNM, E of Braams Point, 22 m, 30 May 1957, *Coquette* stn. 155.

A complete spermatophore dislodged from a female caught off Honduras was also examined. It is deposited in the USNM, and was presented by Eric J. Heald.

Species Range

Cuba to Guadeloupe, and along the continental coast from Belize (British Honduras) to Laguna, Santa Catarina.

Penaeus (*Litopenaeus*) *setiferus* (Linnaeus 1767) Figures 1C, D, 16-19

Spermatophore

The compound spermatophore consists of a geminate body which bears a pair of anterolateral wings, and is flanked posterolaterally by a pair of flanges which broaden posteriorly and bear broad flaps (Figure 16A, B).

Anteriorly, the thick, opaque ventral wall of each spermatophore is truncate and strongly inclined dorsally (Figure 17A); posteriorly, it turns abruptly dorsad, and merges indistinctly with the thick posterior portion of the lateral wall, which bears a small, acute or blunt caudal projection. The thin and translucent portion of the lateral wall is bounded dorsolaterally by a rib that serves as a base for the narrow, scalloped blade which extends caudally along the lateral margin of the flange. The flange is narrow and horizontal anteriorly, becomes progressively broad posteriorly, and turning mesially is deflected ventrally becoming almost perpendicular to its anterior portion. Laterally, the flange sustains a broad, ventromesially directed firm flap, produced anteriorly in a narrow, subrectangular projection; the flap is strengthened by a subtriangular thickening, and is continuous with a milky white, iridescent, resistant membrane. An extremely sticky, glutinous material lies against the flange and adheres to the mesial surface of the flap.

The thin, translucent dorsomesial wall, like that in the spermatophore of *P. schmitti*, bulges anteriorly beyond its attachment to the ventral and lateral walls along an oblique fine rib extending from the mesial lapel to the posteroproximal end of the wing (Figure 17B). The bulge, occupied by the extremity of the sperm mass enclosed in the sac, bears a triangular crest which abuts on the

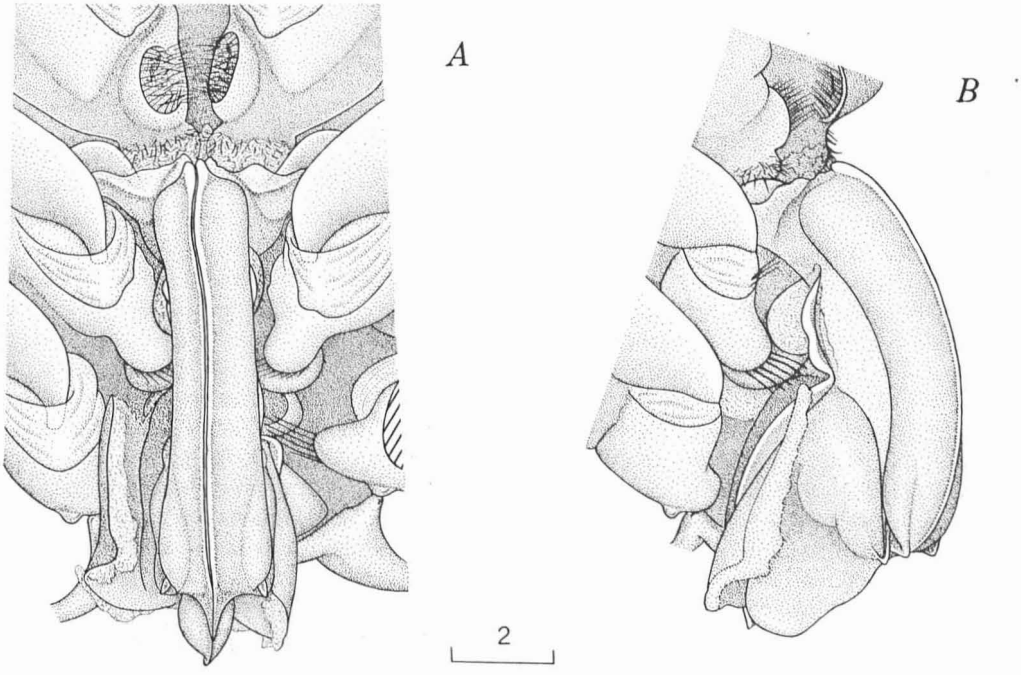

FIGURE 16.—*Penaeus* (*Litopenaeus*) *setiferus* (Linnaeus). *A*, Compound spermatophore attached to female, ♀32 mm cl, 0.8 km off Long Beach, N.C. *B*, Lateral view of same specimen.

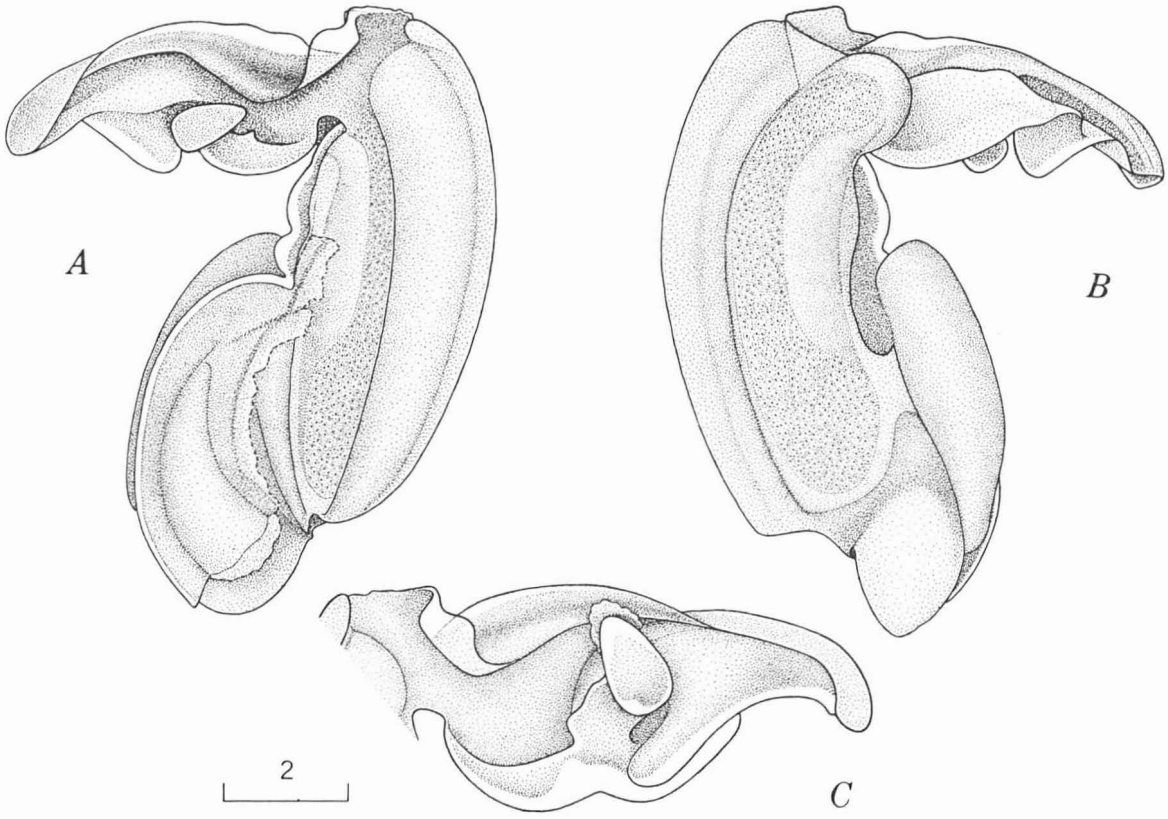

FIGURE 17.—*Penaeus* (*Litopenaeus*) *setiferus*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂SW of mouth of Sabine River, Tex. *B*, Dorsomesial view of same specimen. *C*, Ventral view of wing, left spermatophore, ♂off Melbourne Beach, Fla.

mesial lapel; posterior to the bulge, the dorsomesial wall extends laterally to join the lateral wall (along the base of the blade), and posteriorly merges with the flange.

The wing, long and irregular in contour, is produced posteriorly in a broad proximal lobe, tapering laterally to a rounded, excavated, short tip (Figure 17C). The ventral surface is very irregular, bearing several projections: a rigid subtriangular or rounded prominence on an anterior rib; an elongate twisted process, its base continuous with a posterior fold of the proximal lobe situated about midlength, extending mesially into a subovate to semicircular flap; and a subdistal shelf obliquely flanking the twisted process.

The dorsal plate is tear-shaped in outline, rounded anteriorly, tapering posteriorly, and moderately long, extending from slightly beyond the anterior margin of the flange to its posterolateral corner.

Thelycum (Figure 18)

Sternite XIV bears a pair of sharp crescentic anterolateral ridges the posterior portions of which converge mesially but do not meet, and are often separated by a median longitudinal rib; the posterior part of this sternite is provided with a pair of closely set fleshy lobes, usually separated by a fine median rib which may be continuous with the anterior one. Sternite XIII is heavily sclerotized, forming a strong plate produced posteriorly as a soft emarginate shelf overhanging sternite XIV; the anterior part of this sternite bears a pair of soft, naked, transverse elevations flanking a tonguelike lamella bordered by setae. The lamella forms the roof of a concavity floored by a strong ridge of sternite XII. The ridge (a marginal thickening of heavily sclerotized sternite XII, mostly hidden by setose, rounded and relatively short coxal plates of the third pereopods) is almost

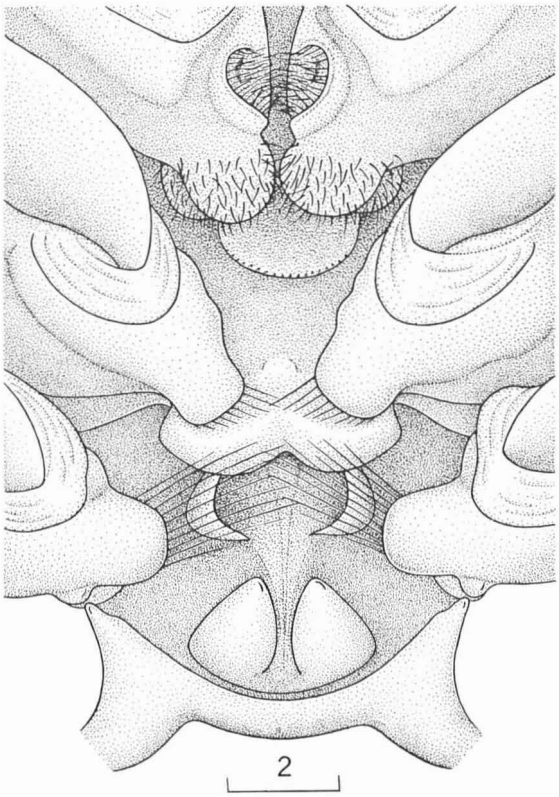

FIGURE 18.—*Penaeus* (*Litopenaeus*) *setiferus*. Thelycum, ♀40 mm cl, off Galveston, Tex.

straight or slightly emarginate along its median portion, and produced laterally in a pair of convex projections armed with long setae. The concavity of sternite XIII is most important in that it serves to lodge the sperm masses protruding anterodorsally from attached spermatophores.

Disposition of the Compound Spermatophore on the Thelycum

The compound spermatophore is anchored to the female much as it in *P. schmitti*. Anteriorly, the geminate body lies on the mesial portions of the coxal plates of the third pereopods (immediately posteroventral to the gonopores), with the sperm masses projecting anterodorsally through the ruptured bulges of the sacs, to lie in a gelatinous envelope fitting into the concavity of sternite XIII. The wings embrace the sperm masses and then extend over the coxal plates, leaving a passageway between them and the body of the animal. The wings are proximally attached to sternite XIII (just caudal to the thelycal lamella) by their posterior lobes, which are in close proximity, and distally affixed to the sternite, or partly to the latter and partly to the articular membranes of the third pereopods. Posterior to the wings, the lateral portions of the ventral walls are turned strongly mesially thus reducing somewhat the lumen of the sacs (Figure 1D). This action may be responsible in part for the transfer of the sperm masses from the sacs to the concavity of sternite XIII at the time of mating. The geminate body is elevated above the sternum so that between the wings and flanges it sometimes does not touch the animal, nor even do the accompanying paired blades, which become almost perpendicular to the sternum. Caudally, the geminate body reaches sternite XIV, where the vertical shelf formed by mesial portions of the flanges lies between the thelycal lobes, or farther beyond on the first pleonic sternite. The firm elongate flaps project ventromesially in conspicuous fashion on each side of the geminate body, whereas anterolateral portions of the flanges are horizontally applied to the dorsal plates, in turn attached to sternite XIV.

I have examined a few females carrying only those parts of the compound spermatophore which are firmly anchored to sternite XIII; the geminate body and adjoining structures have been lost. In all of them, parts remaining affixed to the thelycum (Figure 19) are almost identical: paired masses of sperm lie exposed in the concavity of sternite XIII, where each is contained in an indurate gelatinous substance which, in turn, is tightly embraced by the wings. It appears that in this species, as in *P. stylirostris*, when the spermatophores are released from the terminal ampullae of the male, the masses of sperm and jelly are transferred from the posterior parts of the sacs to the anterodorsal bulges which break under pressure allowing sperm, surrounded by jelly, to reach the thelycal concavity of sternite XIII. This gelatinous substance is directly applied to the concavity, there forming an envelope containing sperm. Eventually, the compound spermatophore splits, the geminate body falls, or is torn away, and the sperm is exposed.

In the impregnated females mentioned above, the compound spermatophore had split in the same fashion, leaving the sperm masses exposed to the surrounding water, suggesting that this rupture might be the means by which spermatozoa are

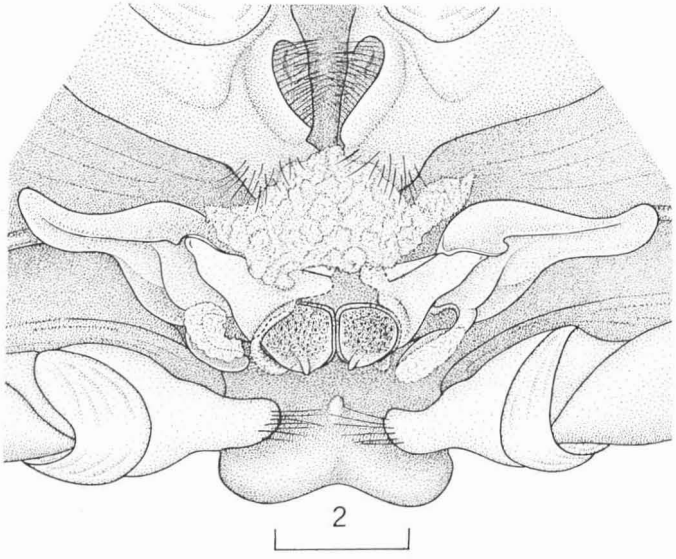

FIGURE 19.—*Penaeus* (*Litopenaeus*) *setiferus*. Sternites XII and XIII bearing wings and paired masses of sperm from a compound spermatophore the geminate body of which has been lost, ♀32.5 mm cl, off Long Beach, N.C.

released at the time of spawning. In some of these females, however, as well as in others with complete spermatophores, a part of each sperm mass protrudes anteriorly from the passageway between the wings and the body of the animal, and even extends onto sternite XII. This indicates that the spermatozoa might disperse anteriorly from the gelatinous envelops surrounding the paired sperm masses while the compound spermatophore is still attached to the female and otherwise intact. Thus, which of these methods is employed in the release of the sperm must await observations of live females immediately after copulation.

Material

The specimens examined by me are listed in Pérez Farfante (1969). Additional specimens follow.

UNITED STATES. 4 ♂ 3 ♀ [1♀ impregnated], UNC-IMS, 0.8 km off Long Beach, (3.2 km E of Lockwood's Folly), N.C., 6 m, 6 May 1949.- 3 ♂ 2 ♀ [impregnated], UNC-IMS, 0.8 km off Long Beach, N.C., 6 m, 6 May 1949.- 1 ♂ 2 ♀, [1♀ impregnated], UNC-IMS, Beaufort Bar (between Sea Buoy and Bar Buoy No. 1), N.C., 13-16 m, 6 July 1949, *Penny*.- 2 ♀ [impregnated], USNM, Apalachicola Bay, Fla., June 1974.- 1 ♀ [impregnated], USNM, SE of Freeport, Tex., 15 m, 26 July 1973.- 1 ♀ [impregnated], USNM, off Galveston, Tex., 1973.- 20 ♂, USNM, off Galveston, Tex., 25 June 1974.

Species Range

Fire Island, N.Y., to Saint Lucie Inlet, Fla.; in the Gulf of Mexico, from west Florida to the vicinity of Ciudad Campeche, Campeche.

ROLE OF COXAL PLATES IN RETENTION OF COMPOUND SPERMATOPHORE

In the females of the various species of *Litopenaeus*, the coxal plates of the last three pairs of pereopods exhibit specific variations which seem to be associated with the position of the affixed compound spermatophore and the function they serve in holding it in place. In *P. vannamei*, in which the spermatophore reaches anteriorly only to the median protuberance of sternite XIII, the coxae of the third pereopods are not produced posteriorly into well-defined coxal plates. In contrast, the fourth pereopods bear large, flattened coxal plates offering extensive support to the anterior parts of the sperm sacs. The coxal plates of the fifth pereopods are rather short, but prominent, and directed mesially providing a base of attachment for the ventrally elevated lateral portions of the dorsal plates; thus, they are responsible in part for keeping the posterior parts of the sacs raised well above the sternum.

In *P. occidentalis*, the coxal plates of the third pereopods are very elongate and strongly curved anteromesially and dorsally in scooplike fashion,

serving to receive the sperm immediately after its release through the openings of the sperm sacs which lie immediately posteroventral to them; the enclosure for the freed sperm is completed ventrally by the bases of the anterior lobes of the spermatophores which are applied to sternite XII. The coxal plates of the fourth and fifth pereopods are relatively short but are directed mesially, helping to keep the compound spermatophore in position by supporting its lateral blades which lie dorsal to them and which are firmly applied to the thelycum.

In *P. schmitti*, *P. setiferus*, and, particularly in *P. stylirostris*, the coxal plates of the third pereopods are large and directed posteriorly; thus, they appear to aid in keeping the sperm masses (projecting dorsally through the compound spermatophore) within the thelycal concavity of sternite XIII. This is suggested by the fact that in the former two species, in which the concavity lies on the anterior part of sternite XIII, the coxal plates are much shorter than in *P. stylirostris* in which the double concavity is located on the posterior part of the sternite. In *P. schmitti* and *P. setiferus*, the coxal plates of the fourth and fifth pereopods (longer in the latter) are directed mesially, supporting the lateral components of the spermatophore and pressing them against the thelycum. In *P. stylirostris*, these coxal plates are larger than in any of the other species, those of the fifth pereopods offering a broad base for the attachment of the anterior portions of the dorsal plates of the spermatophore to their ventral surfaces. The coxal plates of the fourth pereopods are directed posteromesially, lying ventrad to the subvertical shelf of sternite XIII, thus helping in holding the sperm masses within the thelycal concavities of the latter sternite.

Finally, in all five species, the coxal plates are provided with numerous long, mesially directed setae which, in impregnated females, become embedded in the dorsal plates or extend over the blades and flanges, thus contributing to maintaining the spermatophore in position.

COMPARISONS OF SPERMATOPHORES

The morphology of the spermatophores of two species of the subgenus *Melicertus* have been studied in rather considerable detail: that of *P.* (*M.*) *kerathurus* (Forskål 1775) by Mouchet (1931) and Heldt (1938a, b), and that of *P.* (*M.*) *japonicus* Bate 1888, by Kishinouye (1900), Hudinaga (1942) and, later, more meticulously by Tirmizi (1958). A brief illustrated account of the spermatophore of *P.* (*Farfantepenaeus*)[2] *duorarum duorarum* Burkenroad 1939, was presented by Eldred (1958). Recently, Malek and Bawab (1974a, b), conducted a thorough study of the formation of the spermatophore within the vas deferens in *P.* (*M.*) *kerathurus*; the hardened cover of the spermatophore that is contributed by the ampulla is now being investigated by them. The above studies, as well as those on the subgenus *Litopenaeus*, have revealed that in spermatophores of *Penaeus* the sperm mass is surrounded by a gelatinous, multilayered (Malek and Bawab 1974b) sheath which, in turn, is enclosed in a sperm sac; this usually bears an aliform process, and in members of *Litopenaeus* additional attachment structures are present.

The principal characteristics of the spermatophores of the five species of *Litopenaeus* are presented in Table 1 to facilitate a comparison of them.

The spermatophore of *P. vannamei* is the simplest. It lacks an anterolateral wing, is not produced into an anterior lobe, and does not bear a lateral blade.The fact that the ventral and lateral walls are both opaque and thus almost indistinguishable, contributes to the relatively simple appearance of this spermatophore. However, it exhibits by far the thickest lateral flap and the largest dorsal plate. Apart from the seemingly firm affixation of the anterior part of the sacs to the thelycum, the attachment of the compound spermatophore to the female is accomplished by the very elongate dorsal plates, which support the geminate body and the paired flanges. Finally, the compound spermatophore when applied to the female extends only to about the midlength of sternite XIII, instead of reaching sternite XII as do those of the other species. The short anterior extensions of the ventral walls are applied to the median protuberance of sternite XIII, and the prominent bulges of the sacs, where the sperm masses are concentrated, lie at the anterior part of sternite XIV. Consequently, the sperm is released farther away from the gonopores of the female than in the remaining species.

[2]The subgenus *Farfantepenaeus* was recently established by Burukovskii (1972) to include the grooved species of *Penaeus* (those with adrostral sulci extending posteriorly beyond midlength of carapace) from American waters, one of them also occurring off West Africa. These shrimps were previously placed by Pérez Farfante (1969) in the subgenus *Melicertus* Rafinesque 1814, together with the grooved *Penaeus* occurring from the eastern Atlantic eastward to the waters of Hawaii.

TABLE 1.—Characteristics of the spermatophores of five species of *Penaeus* (*Litopenaeus*).

Species	Sperm sac	Wing	Anterior lobe	Flange	Blade	Lateral flap: Along sac	Lateral flap: Along flange	Anterior lamina	Dorsal plate	Position on female
P. vannamei	Simple[1]	Lacking	Lacking	Long, caudal	Lacking	Broad, fleshy	Narrow, flexible	Lacking	Long, underlying most of sac and flange	Reaching about mid-length of sternite XIII
P. occidentalis	Simple	Small	Present	Short, caudal	Attached at edge, extending laterally; broad	Lacking	Broad, highly sclerotized	Present	Moderately long, underlying blade	Reaching posterior part of sternite XII, and embracing gonopore
P. stylirostris	Complex[2]	Large	Lacking	Long, caudolateral	Attached along midline, extending dorsomesially and ventromesially	Broad, membranous	Narrow, flexible	Lacking	Moderately long, underlying base of sac and flange	Reaching anteriormost part of sternite XIII
P. schmitti	Simple	Moderately large	Lacking	Long, caudolateral	Attached at edge, extending laterally; broad anteriorly	Narrow, firm	Broad, firm	Lacking	Long, underlying blade and flange	Reaching anteriormost part of sternite XIII
P. setiferus	Simple	Moderately large	Lacking	Long, caudolateral	Attached at edge, extending laterally; narrow throughout	Narrow, firm	Broad, firm	Lacking	Moderately long, underlying flange	Reaching anteriormost part of sternite XIII

[1]Lateral wall continuous with dorsomesial.
[2]Lateral wall overlapping dorsomesial wall laterally, forming free shield (see p. 473).

It seems noteworthy that *P. vannamei* is the only species of the subgenus *Litopenaeus* in which a strongly developed median protuberance (projecting from sternite XIII) is present on the thelycum. Females of the remaining species of *Litopenaeus* lack a median protuberance, unlike all of the other species of *Penaeus*. In the former females, the midposterior part of sternite XIII bears instead a simple, relatively small knob—in *P. occidentalis*—or is produced into a shelf which overhangs sternite XIII. This shelf is horizontal in *P. schmitti* and *P. setiferus*, and subvertical in *P. stylirostris*.

The spermatophore of *P. occidentalis* is considerably more elaborate than that of *P. vannamei*, although the sac is structurally similar in the two and simpler than that of *P. stylirostris*. The spermatophore of *P. occidentalis*, unlike that of *P. vannamei*, possesses a wing and, unlike all other species of *Litopenaeus*, bears an anterior lobe, and is produced caudally in a very short flange. Also, it bears the largest lateral blade to be found in any of them, the blade being divided in several sections and continuous with the typical stiffened ventromesial extension, ending in a rather flexible caudal lobe; that extension seems to correspond to the flap borne by spermatophores of the other species. In addition, the spermatophore of *P. occidentalis* possesses a unique transverse lamina on the anterior extremity of the sac, which is not intimately associated or even firmly attached to it or to the other contiguous components, i.e., the anterior lobe and the wing. In this spermatophore, however, the flange is inconspicuous, consisting of a short rigid shelf at the posterior end of the sac. Finally, the compound spermatophore of *P. occidentalis* is affixed to the female farther anteriorly than in the other species, the anterior lobes extending over (ventrally) the coxae of the third pereopods to become attached to sternite XII; this brings the openings of the sacs to the scooplike coxal plates of the third pereopods, almost directly opposite the female gonopores.

The spermatophore of *P. stylirostris* differs from all the others chiefly in the structure of the sperm sac, which is largely formed by the dorsomesial wall. This wall, after extending laterally, is bent mesially in such a way as to reach, ventrally, the base of the mesial flap; as a result, part of the ventral and lateral walls, apart from giving support to the sac, serve as a protecting shield. The spermatophore of *P. stylirostris* also possesses the broadest wing to be found within the subgenus,

and is armed with a blade, the anterior portion of which is directed both dorsomesially and ventromesially instead of laterally, in specimens removed from males. Along the sac, the lateral flap is almost as broad as that in *P. vannamei*, but thinner and not fleshy. Furthermore, in *P. stylirostris*, the paired dorsal plates affix only the posterior part of the spermatophore to the females, not directly supporting the midportion. The flanges become attached to the female almost perpendicular to the geminate body, instead of extending entirely caudad as in *P. vannamei* or somewhat caudad as in *P. schmitti* and *P. setiferus*.

The spermatophores of *P. schmitti* and *P. setiferus* are almost identical. They may be distinguished by the width of the lateral blade, the anterior portion of which is broad (except for a narrow portion at the base of the wing) in *P. schmitti* and very narrow in *P. setiferus*. Sperm sacs of both species are similar to those of *P. vannamei* and *P. occidentalis*; however, they bear wings, which are lacking in *P. vannamei*, and the wings are moderately large and scabrous, with various projections on the ventral surface, thus very different from the small wing with the margins extensively folded found in *P. occidentalis*.Also, the flanges extend considerably anteriad along the lateral walls of the sacs, whereas those in *P. vannamei* are virtually caudal and, unlike *P. occidentalis*, are produced posteriorly much beyond the sac instead of barely overreaching the fundus. Finally, flaps borne by the flanges are broad in the two Atlantic species, instead of narrow as in *P. vannamei*, and, although firm, are different in texture from the heavy sclerotized shelf sustained by the flange in *P. occidentalis*.

Despite the similarities of the various sacs, the mode of dehiscence varies–differences among the spermatophores are due more to the elements associated with the sac than to the sac itself. It seems that in *P. occidentalis*, the sperm is released through anterior openings of the sacs which become applied to the coxal plates of the third pereopods, and are well protected by the anterior lobes of the spermatophores. In *P. stylirostris* as well as in *P. schmitti* and *P. setiferus*, it seems that the compound spermatophore attached to the female splits longitudinally into two parts, the geminate body breaks away leaving paired masses of sperm on the thelycum freely exposed to the surrounding water. In *P. schmitti* and *P. setiferus*, however, there are certain indications that the sperm reaches the water through a passageway between the wings and the body of the female, the geminate body persisting. On the basis of the available material of *P. vannamei*, there is no indication as to how the sperm escapes from the spermatophore. Understanding of the precise manner in which spermatozoa are freed from spermatophores in all of the species must await direct observations.

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LITERATURE CITED

BURKENROAD, M.D.
1934. The Penaeidea of Louisiana with a discussion of their world relationships. Bull. Am. Mus. Nat. Hist. 68:61-143.
1939. Further observations on Penaeidae of the northern Gulf of Mexico. Bull. Bingham Oceanogr. Collect. 6(6):1-62.

BURUKOVSKII, R. N.
1972. Some problems of the systematics and distribution of the shrimps of the genus *Penaeus*. [In Russ.] Fisheries Research in the Atlantic Ocean. Tr. Atlant. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 42:3-21. (Translated by Israel Program Sci. Transl., TT72-50101.)

CÁRDENAS FIGUEROA, M.
1952. Descripción del espermatóforo de *Penaeus stylirostris* Stimpson. Rev. Soc. Mex. Hist. Nat. 13:9-16.

ELDRED, B.
1958. Observations on the structural development of the genitalia and the impregnation of the pink shrimp, *Penaeus duorarum* Burkenroad. Fla. State Board Conserv. Mar. Lab., Tech. Ser. 23, 26 p.

EWALD, J. J.
1965. Investigaciones sobre la biología del camarón comercial en el occidente de Venezuela. Inst. Venez. Invest. Cient., Segundo Informe anual al Fondo de Investigaciones Agropecuarias. 1-128, 137-147 p.

HEEGAARD, P. E.
1953. Observations on spawning and larval history of the shrimp, *Penaeus setiferus* (L.). Publ. Inst. Mar. Sci., Univ. Tex. 3(1):73-105.

HELDT, J. H.
1938a. De l'appareil génital des Penaeidae. Relations morphologiques entre spermatophore, thelycum et petasma. Trav. Stn. Zool. Wimereux 13:349-358.
1938b. Le reproduction chez les crustacés décapodes de la famille des pénéides. Ann. Inst. Oceanogr. 18:31-206.

HUDINAGA (FUJINAGA), M.
1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Jap. J. Sci. 10:305-393.

KING, J. E.
1948. A study of the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus). Biol. Bull. (Woods Hole) 94:244-262.

KISHINOUYE, K.
1900. Japanese species of the genus *Penaeus*. J. Fish. Bur. Tokyo 8:1-29.

MALEK, S. R. A., AND F. M. BAWAB.
1974a. The formation of the spermatophore in *Penaeus kerathurus* (Forskål, 1775) (Decapoda, Penaeidae). I. The initial formation of a sperm mass. Crustaceana 26:273-285.
1974b. The formation of the spermatophore in *Penaeus kerathurus* (Forskål, 1775) (Decapoda, Penaeidae). II. The deposition of the main layers of the body and of the wing. Crustaceana 27:73-83.

MOUCHET, S.
1931. Sur l'appareil génital mâle de *Penaeus trisulcatus* Leach. Bull. Soc. Zool. Fr. 56:458-467.

PÉREZ FARFANTE, I.
1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

TIRMIZI, N. M.
1958. A study of some developmental stages of the thelycum and its relation to the spermatophores in the prawn *Penaeus japonicus* Bate. Proc. Zool. Soc. Lond. 131:231-244.

WEYMOUTH, F. W., M. J. LINDNER, AND W. W. ANDERSON.
1933. Preliminary report on the life history of the common shrimp *Penaeus setiferus* (Linn.). Bull. U.S. Bur. Fish. 48:1-26.