NOTES

INTERSEX ANOMALIES IN SHRIMP OF THE GENUS *PENAEOPSIS* (CRUSTACEA: PENAEIDAE)

While examining a relatively large collection of *Penaeopsis* (40 lots containing 196 specimens) taken by the U.S. steamer *Albatross* during the Philippine Expedition, 1907-10, I found three specimens having external characteristics of both males and females. Each specimen had a fully developed thelycum, a moderately well-developed petasma (about two-thirds the length of the petasma of males of corresponding size), small appendices masculinae, and genital apertures on the coxae of the fifth pair of pereopods. The shrimps were poorly preserved—the exoskeletons were soft, rostrums and telsons broken, and internal organs macerated; however, most of the features of the carapace were clearly distinct and the external genitalia intact.

The discovery of these shrimp elicits several questions: to which species do they belong? What is their functional sex? Do they represent a transitional stage in a protandrous hermaphroditic species? If not, have their intersex-appearing anomalies resulted from parasitism? Although none of these questions is answered definitively, all are discussed following a brief description of the external genitalia of the shrimp.

The specimens are deposited at the National Museum of Natural History: USNM 170581, 23 mm cl (carapace length), Bohol Strait, between Bohol and Cebu, 291 m, 25 March 1909, *Albatross* stn 5418. USNM 170582, 24.5 mm cl, Bohol Strait, 320 m, 25 March 1909, *Albatross* stn 5419. USNM 170583, 19 mm cl, Gulf of Davao, SE Mindanao, 247 m, 18 May 1908, *Albatross* stn 5247.

Description

Petasma (Figure 1B-C) with length about two-thirds that of petasma of males of *P. rectacuta* of comparable size, and twice as long as endopod of first pair of pleopods in females of *P. rectacuta* (Figure 1A) and all other congeners. Dorsomedian lobule with distinct distomedian projection and well-formed proximal plate. Dorsolateral lobule with supporting rib (in two of three specimens) ending proximally in subelliptical process. Ventral costa tapering distally, forming free, inwardly excavate, blunt projection directed dorsomesially at broadly obtuse angle with shaft of petasma.

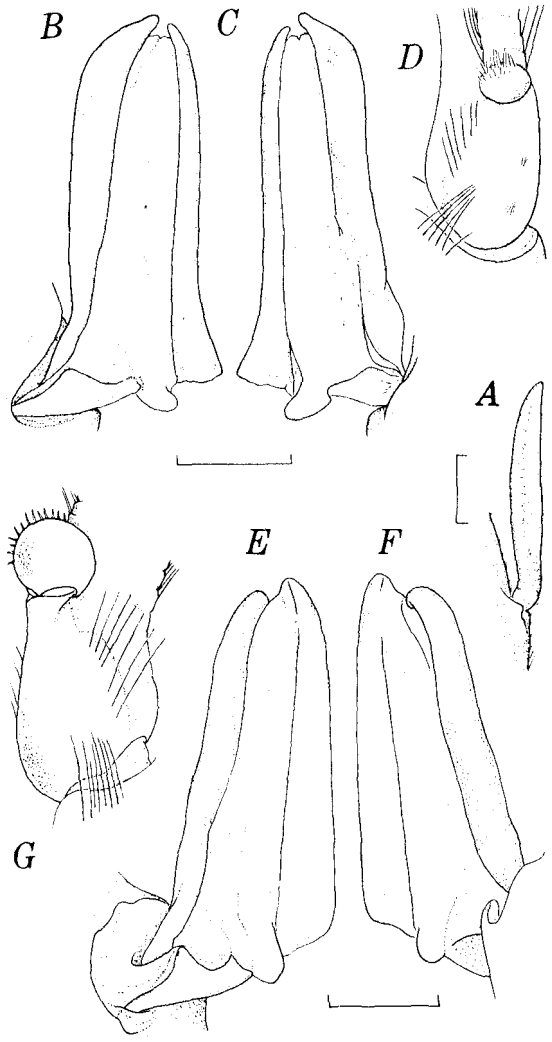

FIGURE 1.—A, *Penaeopsis rectacuta*, USNM 170586, ♀ 23.5 mm cl (carapace length), off Palompon, Leyte, Philippines, endopod of left first pereopod, dorsal view. B, *Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419, petasma, dorsal view of left half. C, Ventral view of same. D, Left appendix masculina, dorsal view, same specimen. E, *Penaeopsis rectacuta*, USNM 170587, ♂ 13 mm cl, off Mindanao, Philippines, *Albatross* stn 5518, petasma, dorsal view of left half. F, Ventral view of same. G, Right appendix masculina, dorsal view, same specimen. 0.5 mm indicated.

Appendix masculina (Figure 1D) minute, somewhat oval, bearing distal patch of setae; thickening at its base, inconspicuous.

Thelycum (Figure 2A-C) with anterolateral borders of plate of sternite XIV varying from slightly concave to convex, and separated by posteromedian projection of sternite XIII; plate strongly slanting dorsomesially, its surface flat or each side biconvex ventrally. Lateral borders slightly concave, strongly converging posteriorly, not reaching posterior ridge but separated from it by deep depression, latter extending anteriorly adjacent to median rib and merging with anteromedian depression; median rib broadest basally, gently tapering toward, but not reaching, posteromedian projection of sternite XIII. Median plate of XIII trilobed to cordiform, slightly to pronouncedly elongate, covered with setae (most lost in specimen illustrated in Figure 2C) except for naked central concavity, setae directed anteriorly except on base of posteromedian projection where directed caudally; posteromedian projection short, with caudal margin straight or shallowly emarginate. Sternite XII bearing small posteromedian tooth and pair of sharp ridges, extending posterolaterally from base of tooth.

Discussion

In several features the three specimens are markedly similar to members of *P. rectacuta* (Bate 1881). The rostrum (Figure 3) is straight and its second tooth is located in line with the orbital margin, the anteroventral angle of the carapace is approximately 90°, and the moderately long branchiocardiac carina is conspicuous, its anterior extremity not nearly reaching the posterior end of the hepatic sulcus. Also the relative length of the pereopods and—in the two smaller animals—the shape of the median plate of sternite XIII are similar to those in *P. rectacuta*. Furthermore, the three shrimps were collected together with specimens of the latter species, all three in localities where the only other *Penaeopsis* occurring in the area (*P. eduardoi* Pérez Farfante 1977) was not taken—another indication that these shrimp probably belong to *P. rectacuta*.

The petasma and the thelycum of these shrimp are different from those of other species of *Penaeopsis*, including those of *P. rectacuta*. The ventral costae of the petasma (Figure 1B-C), tapering distally into a short projection disposed at an obtuse angle to the shaft, differ from those of adult males of *P. rectacuta* in which the ventral costae turn abruptly at right angles and bear a thin marginal border that is bent inward. In the three specimens the petasma somewhat resembles that of large juveniles (with a carapace length of about 13 mm) of *P. rectacuta* (Figure 1E-F); however, in the latter the distomedian projections are less distinct than they are in my specimens or in adult *P. rectacuta*. Also, in juveniles of *P. rectacuta* the ventral costae do not taper distally into free projections, instead the tips are broad and turned

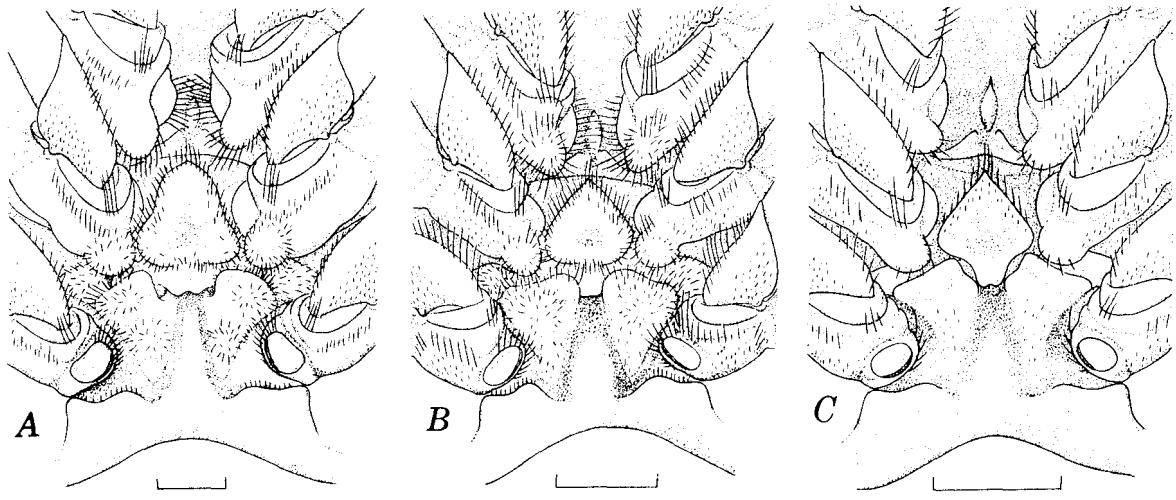

FIGURE 2.—*Penaeopsis* sp. Thelyca. A, USNM 170582, 24.5 mm cl, Bohol Strait, *Albatross* stn 5419. B, USNM 170581, 23 mm cl, Bohol Strait, *Albatross* stn 5418. C, USNM 170580, 19 mm cl, Gulf of Davao, Mindanao, Philippines, *Albatross* stn 5247. 2 mm indicated.

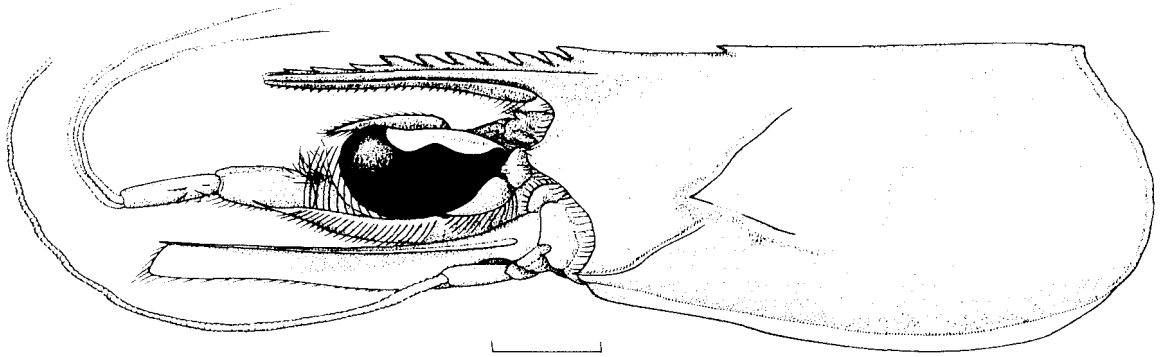

FIGURE 3.—*Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419. Cephalothorax, lateral view. 5 mm indicated.

at right angles to the shaft. The appendices masculinae (Figure 1D) are considerably less well developed in the present specimens than in juvenile males of *P. rectacuta*, in which they are circular (Figure 1G), and bear only marginal setae. The thelyca of the three specimens differ from those of *P. rectacuta* in that the lateral borders of the plate of sternite XIV converge strongly (rather than gradually) toward the posterior thoracic ridge and are separated from the ridge by a deep groove, a unique characteristic; the median plate of sternite XIII, although trilobed in one specimen, is cordiform in the other two, the latter resembling that of *P. rectacuta*.

The functional sex of the three specimens cannot be ascertained because their gonads had disintegrated. It is unlikely that they were hermaphrodites for each bears only one pair of gonopores. Because they have a completely developed thelycum one would expect ovipores to occur on the coxae of the third pair of pereopods, but whereas these coxae are similar in outline to those of female *P. rectacuta*, they lack openings and are covered by a hardened cuticle (Figure 2A-C) like those of males; instead, the coxae of the fifth pair of pereopods exhibit a membraneous cuticle with an opening on the proximomesial border. Although the latter aperture is situated on the last pereopod, it occurs on the coxa (Figure 4A) rather than on the bulging articular membrane as it does in typical males (Figure 4B). Furthermore, no terminal ampullae—the ectal muscular region of the vasa deferentia—appear to have been present, even though the skeletal muscles are rather well preserved.

Many anomalies of the secondary sexual characters of decapod crustaceans have been recorded, e.g. in lobsters (Chace and Moore 1959, among others) and crayfishes (Turner 1924, 1929, 1935). Recently Zongker (1961) described many sexually aberrant individuals within a population of *Cambarus montanus acuminatus* Faxon 1884. Among the aberrant individuals she found were females (sex identified by examination of the gonads) lacking ovipores on the coxae of the third pair of pereopods, but with "male openings" on those of the fifth, an anomaly similar to that exhibited by my specimens. In these shrimp, the apertures are not typical of penaeoid males because of their location on the coxae rather than on the articular membranes. Being present on the coxae, they resemble female openings; however, ovipores are typically subcircular rather than slitlike and, furthermore, they are characteristically situated on the mesial surface of the coxa, dorsal to the coxal plate, instead of on the ventral face as in my specimens.

Individuals of the superfamily Penaeoidea bearing both a thelycum and a petasma have not been recorded previously in the literature. Based on size distribution and characters of the endopod of the first pair of pleopods in females, Heegaard (1967, 1971, 1972) suggested the possibility that protandrous hermaphroditism occurs in *Solenocera membranacea* (Risso 1816) and also in *Penaeus kerathurus* (Forskål 1977), but no individuals with both petasma and thelycum were found by him. The external genitalia in my three specimens causes one to suspect that they might be transitional forms and that therefore at least some members of the genus *Penaeopsis* exhibit protandrous hermaphroditism (protandrous because at their size the thelyca are fully developed whereas the petasmata are relatively small). Their rather

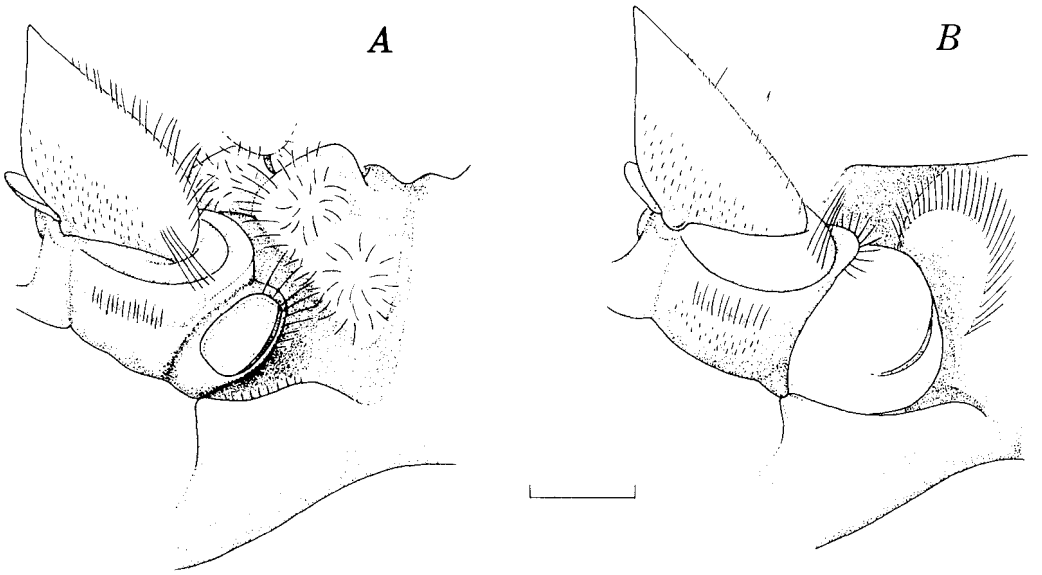

FIGURE 4.—Right fifth pereopod. A, *Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419. B, *Penaeopsis rectacuta*, USNM 170586, ♂ 24.5 mm cl, off Palompon, Leyte, Philippines, *Albatross* stn 5403. 1 mm indicated.

large size, however, makes it unlikely that they are in a transitional stage. Furthermore, hermaphroditism has not been recorded in any species of the genus *Penaeopsis*, consequently its occurrence in these specimens would be exceptional.

Effects of parasitism in a species of *Metapenaeopsis*, a genus closely allied to *Penaeopsis*, were reported by Hiraiwa and Sato (1939). These authors observed conspicuous changes in the petasmata of males and the gonopores of males and females in the shrimp *Penaeopsis akayebi* Rathbun 1902 (= *Metapenaeopsis barbata* de Haan 1850) parasitized by the bopyrid isopod *Epipenaeon japonica* Thielemann 1910. In males, the petasmata were considerably smaller than those in normal individuals of corresponding size and their two parts were unjoined; the gonopores were barely noticeable, and the papillae, at the tips of which the gonopores are situated in normal individuals, were lacking. In the females, the ovipores were obscured, but the thelycum was not apparently affected by the presence of the parasite. In the extensive material examined, however, none of the specimens bore both a petasma and a thelycum. Among the specimens of *P. rectacuta* collected in the waters of the Phillippines, I found a few that were parasitized by bopyrids (one of them was taken at Bohol Strait, in a locality near those at which two of my three individuals were obtained). The parasitized specimens had normal external genitalia, thus lending no support to an assumption that the anomalies in the genitalia of these three individuals were induced by a bopyrid parasite. Nevertheless, parasitism offers the only clue as to the possible origin of the anomalies present in these shrimp.

Acknowledgments

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Literature Cited

CHACE, F. A., JR., AND G. M. MOORE.
1959. A bicolored gynandromorph of the lobster, *Homarus americanus*. Biol. Bull. (Woods Hole) 116:226-231.

HEEGAARD, P.
1967. On behaviour, sex-ratio and growth of *Solenocera membranacea* (Risso) (Decapoda, Penaeidae). Crustaceana 13:227-237.
1971. *Penaeus kerathurus* Forskal, a protandric hermaphrodite. Bull. Inst. Océanogr. Pêche (Salambô) 2:257-266.
1972. Sexual dimorphism in some Mediterranean penaeids and their spawning grounds. Thalassia Jugosl. 8:5-13.

HIRAIWA, Y. K., AND M. SATO.
1939. On the effect of parasitic Isopoda on a prawn, *Penaeopsis akayebi* Rathbun, with a consideration of the effect of parasitization on the higher Crustacea in general. J. Sci. Hiroshima Univ., Ser. B, Div. 1, 7:105-124.
THIELEMANN, M.
1910. Beitrage zur kenntnis der Isopodenfauna Ostasiens. Beitr. Naturgesch. Ostasiens. Ahb. Math-Phys. Kl. K. Bayer. Akad. Wiss. II. Suppl.-Bd. 3 Abh., 109 p.
TURNER, C. L.
1924. Studies on the secondary sexual characters of crayfishes. I. Male secondary sexual characters in females of *Cambarus propinquus*. Biol. Bull. (Woods Hole) 46:263-276.
1929. Studies on the secondary sexual characters of crayfishes, IX. Females of *Cambarus* with aberrant female characters. Biol. Bull. (Woods Hole) 56:1-7.
1935. The aberrant secondary sex characters of the crayfishes of the genus *Cambarus*. Am. Midl. Nat. 16:863-882.
ZONGKER, J.
1961. Monoecious tendencies in a population of *Cambarus montanus acuminatus* Faxon. M.A. Thesis, Univ. Virginia, Charlottesville, 30 p.

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ON THE ROLE OF THE DIFFERENT FIBRE TYPES IN FISH MYOTOMES AT INTERMEDIATE SWIMMING SPEEDS

In most fishes the myotomal locomotor musculature is made up of two main fibre types: a superficial layer of red fibres overlies the white fibres which form the main mass of the myotome. A spectrum of such differences as mitochondrial content, enzyme activities, blood supply, and innervation (as well as color) distinguishes these two fibre types.The electrophysiogical properties of the two fibre types have only been investigated in a few species, but in all of these the white fibres have been found to propagate muscle action potential, whereas only local nonpropagated activity is seen from red fibres (which are invariably multiply innervated). In many (but not all) fishes, there are also other less abundant fibre types in the myotomes, in some respects intermediate between the red and the white fibres (e.g., Patterson et al. 1975).

There is general agreement that at low sustained swimming speeds only the red fibres are employed and that the white fibres are active during short bursts of maximum speed, which cannot be long sustained. However, agreement has not yet been reached about which fibres are active during sustained swimming at speeds above the minimum cruising speed. Indirect evidence from a number of teleost species (e.g., Greer Walker and Pull 1973) indicated that the white fibres are active at these intermediate swimming speeds, as did the direct electromyographic investigations of Hudson (1973). More recently, several workers have suggested that fibres of intermediate type are recruited as swimming speed rises from the minimal cruising speed, before white fibres are activated and the fish attains its maximal sustained speed. In this note, we report electromyographic observations on various teleosts swimming at controlled speeds in a tunnel respirometer, which show that the activity of the myotomal fibre types during sustained swimming is different in different fishes.

Material and Methods

We studied herring, carp, and trout. Juvenile Pacific herring, *Clupea harengus pallasi* Valenciennes, 15-17.5 cm FL (fork length) were caught by seining in the Georgia Straits, B.C., and held in circulating seawater at the Department of Zoology, University of British Columbia, until swum in a tunnel respirometer (Brett 1964). Herring are delicate fish and did not settle quietly in the respirometer at flow lengths below 2-3 body lengths per second (BL/s). Instead, they darted upstream and fell back again in an irregular manner, so that it was necessary to force them to swim at such speeds from their first entry to the apparatus, without the acclimation period usual when working with other fishes.

Varnished copper wire (40 standard wire gauge) electrodes bared at the tips were placed in the postanal myotomes. The fish were anaesthetized with MS-222[1] (Sandoz) and the electrodes sutured to the dorsal surface before being led downward and backward to enter the myotomes. After recovery for 30 min or so in a bucket of seawater, the fish were introduced to the respirometer and muscle potentials recorded on a Gould Brush 220 pen recorder via Tektronix 122 preamplifiers. It proved difficult to record from electrodes whose tips lay amongst the white muscle fibres, but activity from

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.