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**A New Genus and Species of
Sphaeromatidae
(Crustacea: Isopoda) with
Experiments and Observations
on Its Reproductive Biology,
Interspecific Interactions and
Color Polymorphisms**

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Abstract

The new genus, *Paraleptosphaeroma*, is distinguished from the morphologically similar genus *Leptosphaeroma* by the fusion of the pleonites, the shape of the peni, the attachment of appendix masculina, and the presence or the absence of an endopod on the first pleopod. The term *cingula* is introduced to refer to lateral margins fringed with setae and the distinction is drawn between setal and membranous forms of the cingula.

Paraleptosphaeroma glynni (sp. nov.) occurs on cobble in tidal pools and is associated with three sessile species, two bryozoans and a coralline alga. Experiments demonstrate the isopod to be a sequential hermaphrodite with a socially mediated sexual transformation. Brood mortality is very low. Observations of feeding and analysis of gut contents show anascan bryozoans to be the principal food sources of *P.*

glynni. The principal color polymorphisms of juveniles are illustrated. The apparent concordance between these patterns and those produced by the boring activities of phoronids and barnacles is tested, with results suggesting that the color patterns are adaptations to concealment from fish predators. This interpretation is further supported by morphological evidence and experiments demonstrating the poor swimming ability of *P. glynni*.

Key Words

Bryozoa, color polymorphism, protogynous sex change, *Paraleptosphaeroma*.

Introduction

The occurrence of sequential hermaphroditism is known in the isopod suborders Anthuridea, Flabellifera, and Epicaridea, but has yet to be reported in the flabelliferan family, Sphaeromatidae. We herein describe a new sphaeromatid genus and species, *Paraleptosphaeroma glynni*, which undergoes a protogynous sex change. Unlike the occurrence of sequential hermaphroditism in many other taxa (e.g., labrid fishes), very little is known of the ecological circumstances which may favor sex change in the isopods. Observations and experiments are provided on the repro-

ductive biology, feeding behavior, swimming behavior, and color polymorphisms of *P. glynni*.

Paraleptosphaeroma gen. nov.

Type Species *Paraleptosphaeroma glynni* sp. nov.

Diagnosis Body oval, strongly depressed, fringed with translucent membrana cingula. Two proximal articles of first antenna expanded anteriorly into flat plates which completely enclose the anterior margin of the cephalon. Rostrum short, clypeus not visible dorsally. Inner margin of maxilliped palp articles 2 to 4 not markedly produced into lobes. Mandible with strongly developed molar process and elongate, toothed incisor. Coxal plates broadly expanded laterally. Pleotelson dorsally fused into a single piece. Peni considerably longer than wide, basally fused. Pleotelson completely enclosed by expanded endopod of uropods; exopod short, fitting into lateral margin of endopod. Endopod lacking on first pleopod. Endopod reduced on pleopod 2, appendix masculina attached near apex. Pleopods 4 and 5 lacking transverse folds. Protogynic hermaphrodites; sexual dimorphism not evident in dorsal view except for size.

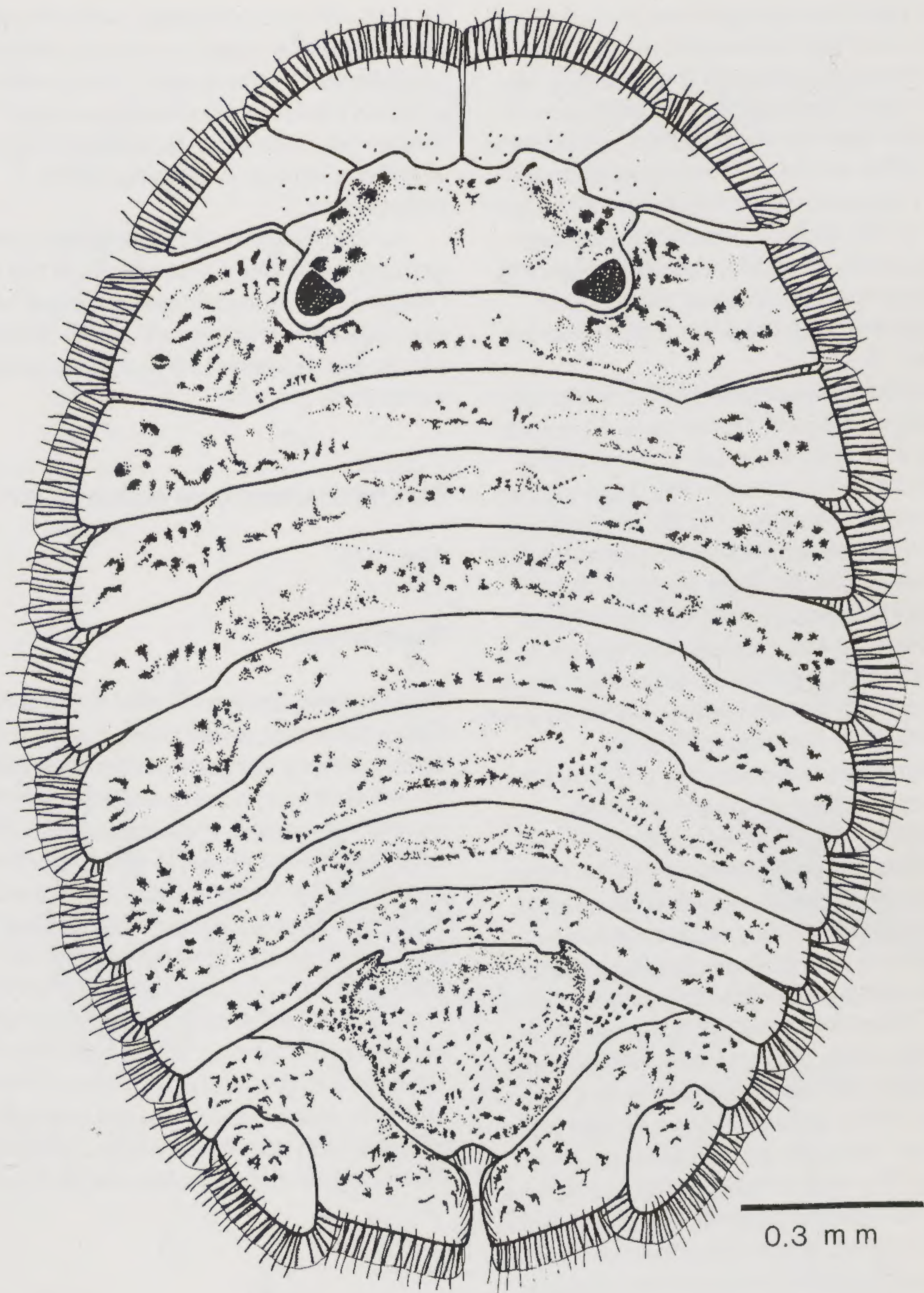
Remarks

Hansen (1905) revised the family Sphaeromatidae (i.e., his subfamily Sphaeromanae), dividing it into three groups: Eubranchiatae, Hemibranchiatae, and Platybranchiatae. The absence of folding on the fourth and fifth pleopods places *Paraleptosphaeroma* in the group Platybranchiatae. Hansen's group names have recently been raised to subfamily standing (e.g., Eubranchiatinae, Hemibranchiatinae, and Platybranchiatinae) by Hurley and Jansen (1977). Article 11e of the International Code of Zoological Nomenclature (Stoll et al., 1964) states that when a family group name is first proposed it must be based on a then valid generic

name. As these subfamily names were not based on generic names, they are nomina nuda. For this reason we follow Hansen's classification without proposing properly formed names as revisionary work is in progress by one of us (EWI).

The genus *Paraleptosphaeroma* bears a very close morphologic resemblance to the Platybranchiate genus, *Leptosphaeroma* Hilgendorf, 1885, and also to the Eubranchiate genus, *Amphoridella* Baker, 1908. These genera all show a remarkably similar body morphology which may represent convergent adaptation. *Leptosphaeroma* is the most closely related genus to *Paraleptosphaeroma* morphologically and perhaps phylogenetically. The genus *Amphoridella* differs from both *Paraleptosphaeroma* and *Leptosphaeroma* primarily in having transverse folds on the exopod and endopod of the fourth and fifth pleopods. Further, the first pereonite of *Amphoridella* is modified into gnathopod.

Paraleptosphaeroma differs from *Leptosphaeroma* in the following characters. In *Leptosphaeroma* there are three medially fused pleonites that comprise the anterior segment of the pleon, each of which reaches the lateral body margin. In *Paraleptosphaeroma* there appears to be complete fusion between these pleonites, as suture lines are not visible dorsally. In *Paraleptosphaeroma* the lobes of the peni are elongate and fused basally, whereas in *Leptosphaeroma* the peni are very short, apically broadly rounded, and basally widely separated. The appendix masculina of *Paraleptosphaeroma* differs from the usual case in sphaeromatids, and isopods in general, by attaching near the apex of the endopod. In *Leptosphaeroma*, like most other isopods, the appendix masculina attaches at the base of the endopod. Brusca and Wallerstein (1979) reported that the valviferan isopod, *Cleantioides occidentalis*, and Glynn (1970) that the sphaeromatid isopod, *Cerceis carinata*, have the appendix masculina attaching near the middle of the endopod. In addition to the above characters, the apparent loss of the endopod on

**Fig. 1**

Paraleptosphaeroma glynnigen, gen. and sp.
nov., holotype male, dorsal view. YPM 7191.

the first pleopod distinguishes this genus from all other sphaeromatids except the genus *Ancinus*. Although the endopod appears to have been lost during evolution, it is possible that the endopod has a tendency to fall off the animal in the course of preservation. However, the reduced size of the endopod on the second pleopod of *Paraleptosphaeroma* and the reduced size (width) of both the first and second pleopods in *Leptosphaeroma* suggests that this is not the case.

From the literature several sphaeromatid genera (e.g., *Striella*, *Dynamene*, *Dynamenoides*, and others) appear to have lateral margin fringed with setae. We propose that this structure be called a *cingula* (Latin for girdle). In the cases where it is composed of simple setae, we propose the term *setal cingula*. However, in the case of *Paraleptosphaeroma* and *Leptosphaeroma* this structure takes the form of a number of uniformly spaced, parallel setule-like structures embedded in a translucent flexible membrane-like structure. We propose the name *membrana cingula* in this case.

Scanning electron micrographs (Fig. 4) reveal that the *membrana cingula* in *Paraleptosphaeroma* is composed dorsally of an upper row of widely separated setae. Below this is a row of evenly spaced setae-like structures embedded in a membranous sheet. These riblike supports are visible in the dorsal view, but not in the ventral view. In between the supporting setae, the membranous sheet appears furrowed parallel to the setae. Ventrally on the pleonites and uropods, the lateral margin of the cuticle extends into a series of small, flattened, multi-pointed spines. The composition of the membranous sheet is not known, but the absence of glandular openings around the lateral body margin suggests that it is not secreted. However, the membranous sheet and embedded setal supports are easily torn with forceps giving a ragged appearance in some preserved specimens. Often the embedded setal supports remain intact in the matrix, or may break free and remain attached to the animal. Large sections can

be torn off the coxal plates, with the embedded setule-like supports usually remaining undisturbed in the matrix. The *membrana cingula*, like other modifications for a limpet-like body plan, probably serves to assist the animal in clinging to the substratum.

An examination of *Leptosphaeroma gottschei* revealed that although the lateral margin was figured as being fringed with discrete setae (Nishimura, 1976) this species is also bordered by a well-developed *membrana cingula*.

***Paraleptosphaeroma glynni* sp. nov.**

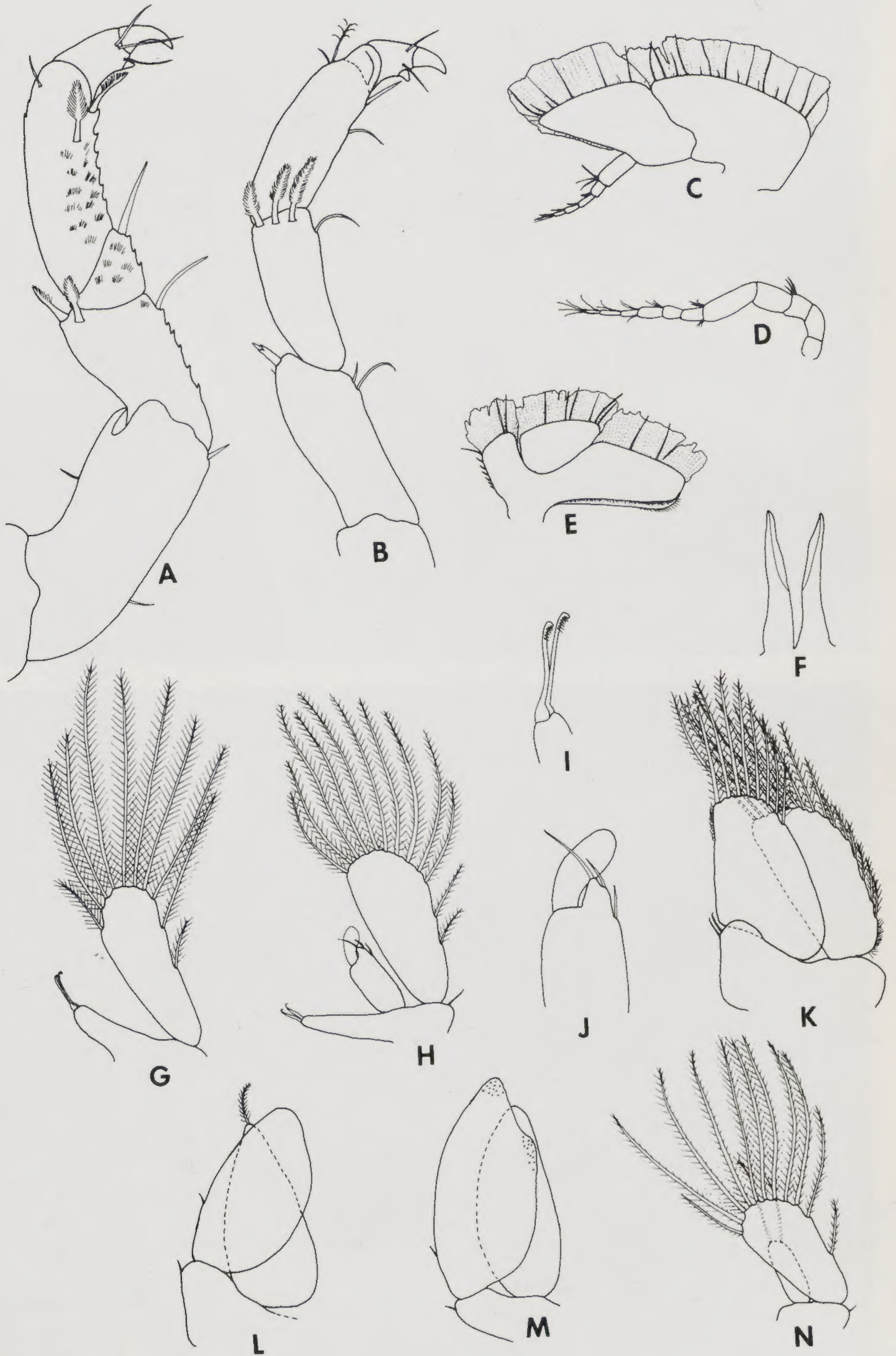
Figs. 1-3

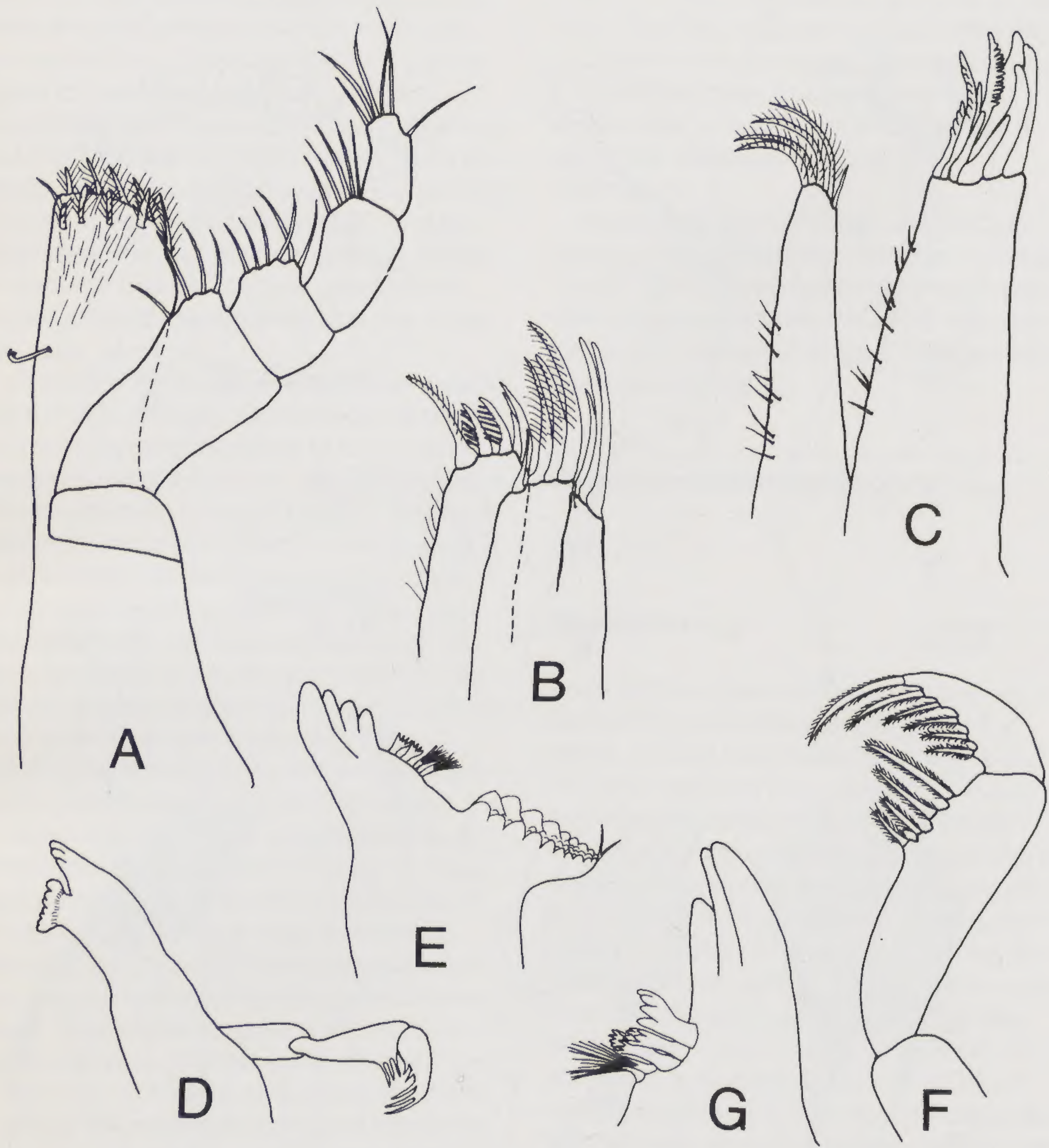
Description

Body lacking obvious dorsal sculpturing. Cephalon small, anteromedial region of dorsal surface somewhat concave, raised on either side into low swelling. Eyes not excessively raised, with about 16 to 20 ocelli each. First antenna short, reaching the middle of the first pleonite; flagellum of 3 to 4 articles. Second antenna exceeding the posterior margin of the first pereonite; flagellum of 6 to 7 articles. Clypeus not excessively produced anteriorly, arms slender, enclosing the labrum. Right mandible: incisor with 3 to 4 cusps, setal row of 3 to 4 complex setae, molar process strongly developed with numerous cusps; second article of palp with 3 to 4 plumose setae, third

Fig. 2 ►

Paraleptosphaeroma glynni gen. and sp. nov., male: A, pereopod 1; B, pereopod 7; C, antenna 1; D, antenna 2; E, uropod; F, penis; G, pleopod 1; H, pleopod 2; I, comb seta of pleopod 2 basis; J, pleopod 2 endopod (note curved appendix masculina); K, pleopod 3; L, pleopod 4; M, pleopod 5; N, pleopod 2, female.



**Fig. 3**

Paraleptosphaeroma glynnigen, gen. and sp. nov. *A*, maxilliped; *B*, maxilla 2; *C*, maxilla 1; *D-F*, right mandible: *D*, mandible; *E*, incisor and molar processes; *F*, palp; *G*, left mandible showing incisor process, lacinia mobilis and setal row.

Fig. 4 ▶

Scanning electron micrograph showing detail of membrana cingula bordering lateral margin of *P. glynni*. Top, dorsal view; bottom, ventral view.



article shorter than second, and with 5 to 6 plumose setae. Left mandible: incisor with 3 to 4 cusps, lacina mobilis with 4 cusps, setal row of 3 to 4 complex setae. Inner lobe of first maxilla with 4 curved pectinate setae and 1 simple seta; outer lobe with 3 to 4 dentate spines and 5 to 6 smooth spines arranged in two rows. Second maxilla inner lobe with 2 pectinate setae between an inner comb seta and an outer group of simple setae; inner lappet of outer lobe with 3 long pectinate and one short setae, outer lappet with 3 setae.

Pereopod 1: inner margin of propodus, carpus and merus variable, usually armed with several small spines in male; inner distal margin of propodus with a single comb seta, and a pectinate seta somewhat proximal to the first; carpus and merus with a single large simple seta at inner distal edge; outer distal margin of merus with 2 pectinate setae. Pereopod 7: propodus, inner margin variable, usually lacking small spines; carpus with a distal row of about 3 pectinate setae.

Pleotelson wider than long; anterodorsal surface with a slight longitudinal swelling (best seen in lateral view) along the midline; posterodorsal surface with 2 submedial, low, longitudinal swellings. Pleotelson apex somewhat upturned, ventrally grooved, so that an aperture, visible from behind, is formed between the margin of the pleotelson and uropodal endopods. Peni long, tapering to a narrowly rounded apex. Pleopod 1: exopod at least twice as long as broad, fringed with 7 to 10 plumose, marginal setae (PMS), the longest exceeding the length of the exopod; basis medially expanded into a narrow process tipped with 2 slender, comb setae. Pleopod 2, male: exopod at least twice as long as wide, 12 to 13 PMS, the longest exceeding the length of the exopod; endopod reduced, with 3 to 5 simple setae; apex of appendix masculina broadly rounded and curved toward lateral margin of endopod. Pleopod 2, female: endopod reduced in size, 2 PMS. Pleopod 3: not excessively lengthened, shaped normally; exopod with 14 to 16 PMS; endopod

with 6 to 8 PMS; length of PMS equal to or less than length of rami. Pleopod 4: without transverse folds; outer margin of exopod rami inflated; exopod apically with a single short PMS. Pleopod 5: without setae or transverse folds; outer margin of rami inflated; endopod with 2 squamiferous patches. Uropodal endopod long; outer margin thin; inner margin somewhat thickened and bifurcated by longitudinal groove into which the lateral margin of the pleotelson fits. Anterior to the insertion of exopod, endopod broadly reaching lateral body margin.

Measurements

Holotype (male), body length (BL) 2.26 mm, total length (TL) 2.54 mm. The mean BL of 449 males was 2.37 mm (range: 2.14–2.58, SD: 0.07). The mean BL of 582 nongravid females was 1.92 mm (1.66–2.30, 0.13). The mean BL of 298 gravid females was 1.98 mm (1.66–2.38, 0.12) and of 716 prereproductive individuals was 1.34 mm (0.86–1.82, 0.22). The mean BL of 10 newly released young was 0.80 mm (0.78–0.83, 0.03).

Type Locality

Punta Paitilla, Panama, a rocky intertidal shore some 5 km south of the Pacific entrance to the Panama Canal (79°31'W, 8°54'N), on bryozoan-encrusted cobble in tidal pools.

Material Examined

Monthly collections from the type locality, each numbering at least 50 individuals, were made over the period February–August 1978. The holotype was collected in April 1978 from a tide pool at +0.1 m tidal height. The male holotype has been deposited in the Yale Peabody Museum of Natural History (YPM) under catalogue number 7191. Paratypes have been distributed as follows: 1747 paratypes under catalogue number 7192 at the Yale Pea-

body Museum, 81 under catalogue number 782 at the Allan Hancock Foundation, University of Southern California, 28 under catalogue number 180266 at the United States National Museum.

Etymology

The generic name *Paralepto-sphaeroma* refers to the close similarity of this genus to *Leptosphaeroma* (Hilgendorf). It is our pleasure to name this species after Dr. Peter Glynn, a student of isopods, of corals, and a marine biologist of outstanding stature.

Distribution

Paraleptosphaeroma glynni has been collected from only two localities, Punta Paitilla and Isla Taboguilla, both in the Bay of Panama. At both localities it was found inhabiting rocks in tide pools and channels. *Paraleptosphaeroma glynni* is found most commonly on cobbles encrusted by one or more of three sessile species, the anascan bryozoans *Antropora tinctoria* (Hastings) and *Onychocella alula* (Hastings), and the coralline alga, *Neogoniolithum rugulosum*

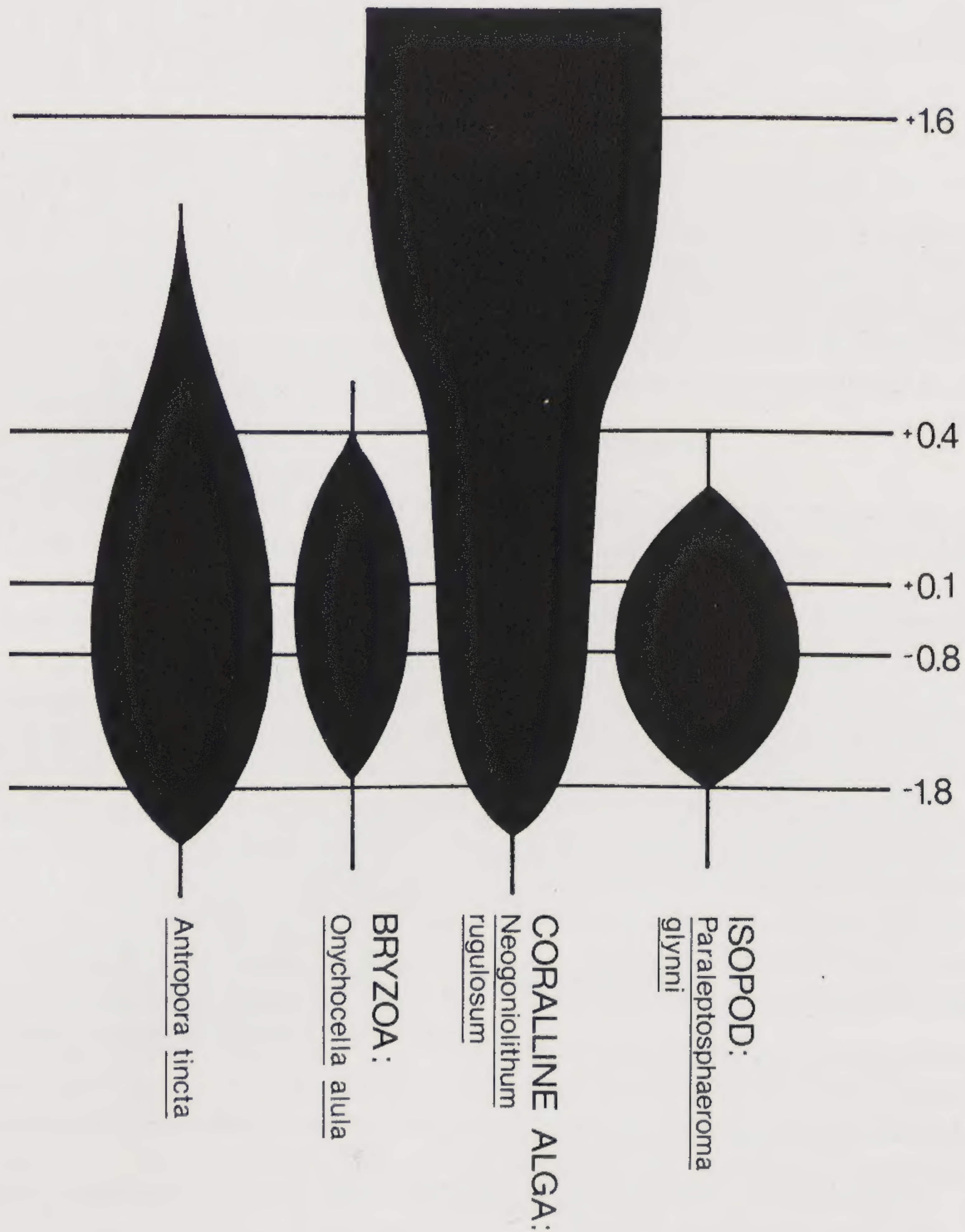
(Adey). One hundred cobbles collected randomly at Punta Paitilla in June 1978 at +0.1 meters tidal height showed *P. glynni* to have a strong positive association with cobbles inhabited by these three species (Table 1, $p < 0.001$, 2 X 2 Contingency Table with Yate's Correction). *Antropora tinctoria* and *N. rugulosum* are common cobble-dwelling organisms found on most intertidal hard substrata in the Bay of Panama. *Onychocella alula*, although found at low frequencies on some shores, was found abundantly only at Punta Paitilla and Isla Taboguilla, the two localities where *P. glynni* was found.

In June 1978, 200 cobbles from each of 5 pools of differing tidal height at Punta Paitilla were examined and scored for the presence or absence of *P. glynni*, *O. alula*, *N. rugulosum*, and *A. tinctoria*. Results are presented in Figure 5.

All species except *N. rugulosum* reach their maximum abundance at a tidal height of +0.1 m. None of these species extends its range subtidally and both *P. glynni* and *O. alula* are restricted to tidal heights less than +0.8 m. The close association of *P. glynni* and these three sessile species (especially *O. alula*) on both a local and regional scale is suggestive of some degree of functional interdependence between them.

Table 1 Association between *P. glynni* and the Dominant Components of the Sessile Fauna.

		<i>P. glynni</i>		
		Present	Absent	
<i>O. alula</i> , <i>A. tinctoria</i>	Present	58	2	60
& <i>N. rugulosum</i>	Absent	14	26	40
		72	28	100

**Fig. 5**

Tidal height distribution of *P. glynni*, *A. tincta*, *O. alula*, and *N. rugulosum* at Punta Paitilla, Panama. Width of band proportional to percentage of individuals present on 200 rocks at each of five tidal levels. Tidal height in meters.

Sequential Hermaphroditism

Hermaphroditism is well known in several groups of isopods. For example, most (if not all) members of the subfamily Anthuridae are protogynic hermaphrodites (Burbanck and Burbanck, 1974). Like *P. glynni* they undergo a sex change from female to male. The opposite change from male to female (protandric) occurs in the suborder Epicaridae and the flabelliferan family Cymothoidae (Brusca, 1978a,b). The occurrence of hermaphroditism in the flabelliferan family Sphaeromatidae has not, to our knowledge, been previously reported. It is significant to note that the free living isopods (Anthuridae, Sphaeromatidae) in which hermaphroditism has been reported are protogynic, while parasitic forms (Epicaridae, Cymothoidae) are protandric.

From February to August 1978 a total of 2040 *P. glynni* were collected at Punta Paitilla, Panama, sexed and measured. Figure 6 shows the relationship between total length, sex, and female reproductive condition. Although a large number of individuals were measured, a conspicuous absence of males smaller than 2.14 mm and of females larger than 2.30 mm was observed. This relationship suggested the occurrence of sequential hermaphroditism in this species. This hypothesis was tested by placing 4 females on each of 10 replicate cobbles. Each cobble was encrusted with a bryozoan food source and was maintained in a running seawater system throughout the experiment. Each cobble was so positioned that the isopods were not able to crawl between adjacent cobbles (see swimming behavior below). All of the females used in

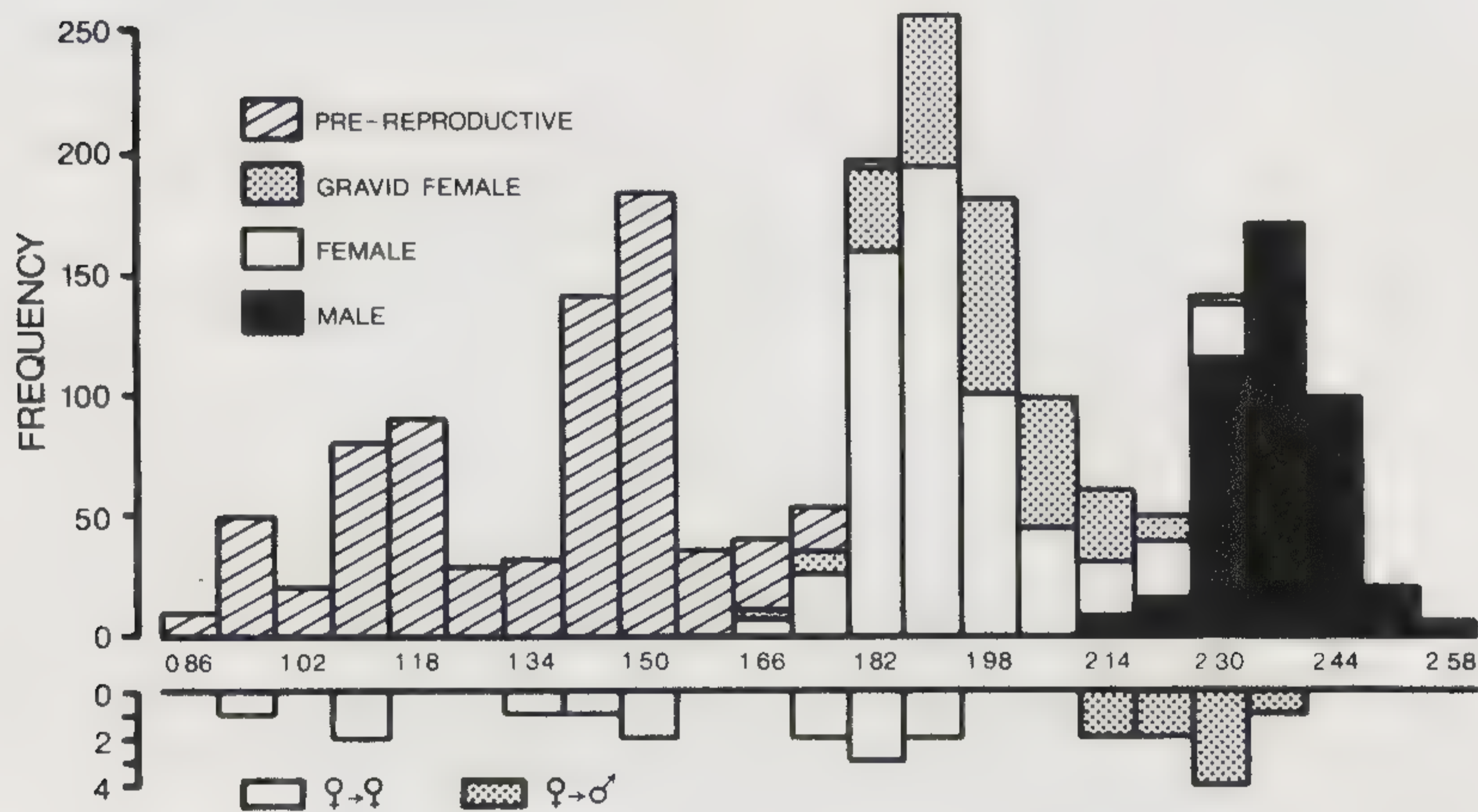


Fig. 6. Size-frequency distribution of male and female *P. glynni* (top) and size-frequency distribution of intermoult individuals (bottom). Length in millimeters.

this experiment had recently released a brood. After 2 months, the isopods were collected and the number of males and females recorded. In 6 of the 10 replicates the cobble was occupied by 3 females and 1 male. In one case, the cobble was occupied by 3 females and 1 individual in the process of moulting. This individual was observed to have male sexual characteristics on its posterior half suggesting that the transition from female to male occurs (superficially) in one moult. In the 3 remaining replicates, each cobble contained the original condition of 4 females. In all 7 replicates where a sex change had or was occurring, the female which underwent the sex change was the largest on that particular cobble at the initiation of the experiment.

Socially mediated sex change has been suggested for the protandric isopods (Brusca, 1978a,b). To examine this possibility in *P. glynni*, the above experimental procedure was repeated using 10 cobbles, 5 containing 1 male and 4 females and 5 containing 4 females only. After 2 months, 3 of the 5 female-only treatments had one individual with male characters. None of the individuals in any of the male+female treatments had undergone a sex change. These data suggest that *P. glynni* is a protogynic hermaphrodite in which sexual transformation is socially mediated.

The moult from female to male appears to be terminal. Of the 23 intramoult individuals found in the field (Fig. 6), none of them were moults from male to male. In the laboratory, males maintained for up to 7 months did not undergo a moult, whereas females maintained under similar conditions for the same period during the study underwent from 1 to 3 moults. Given that the moult from female to male is terminal, it is of interest that males represent only 21.7% of the total population. The low number of males recorded in the Punta Paitilla population suggests that mortality rates of the larger individuals (males) are greater than those of the smaller individuals (females).

In living *P. glynni* the paired testes are

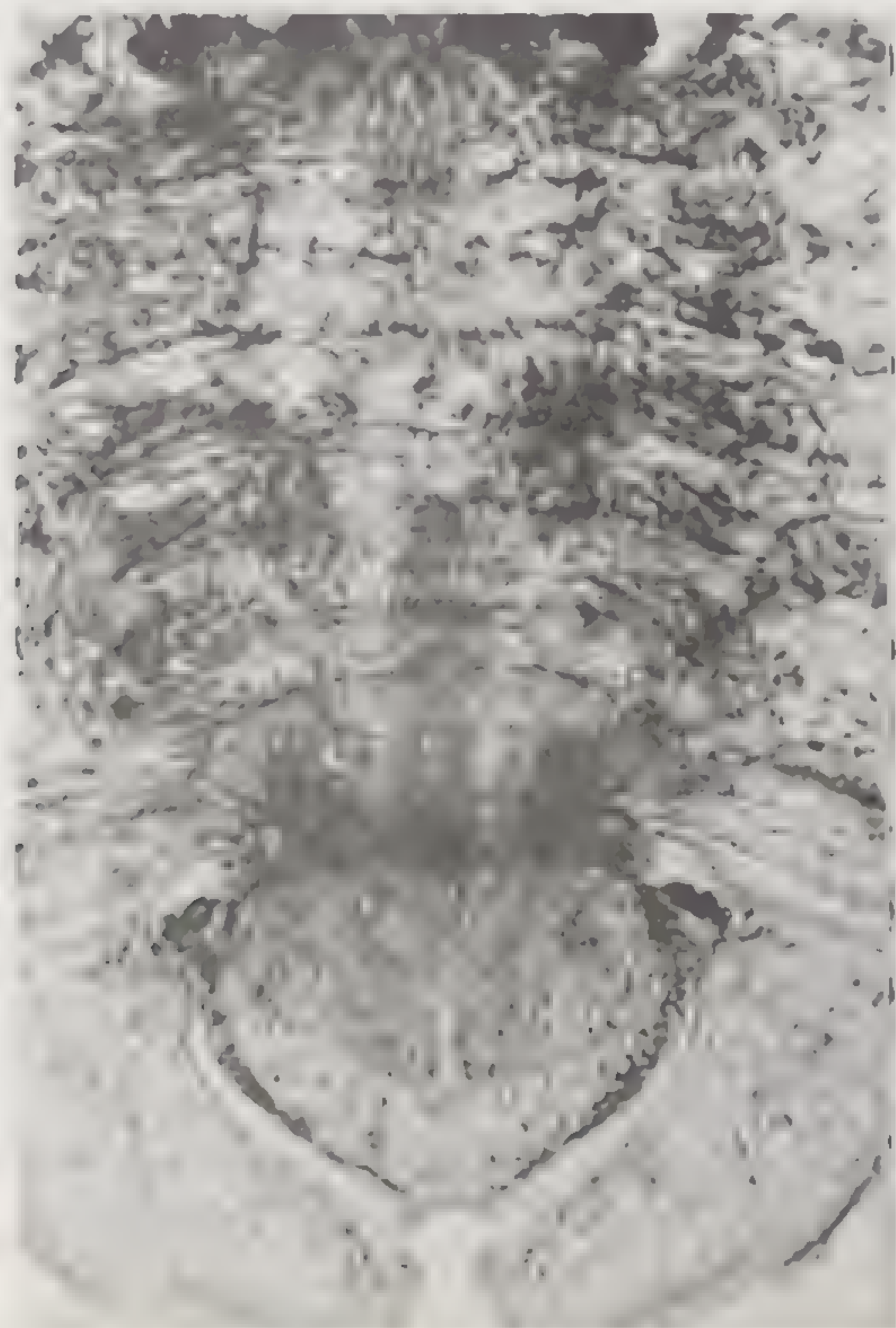
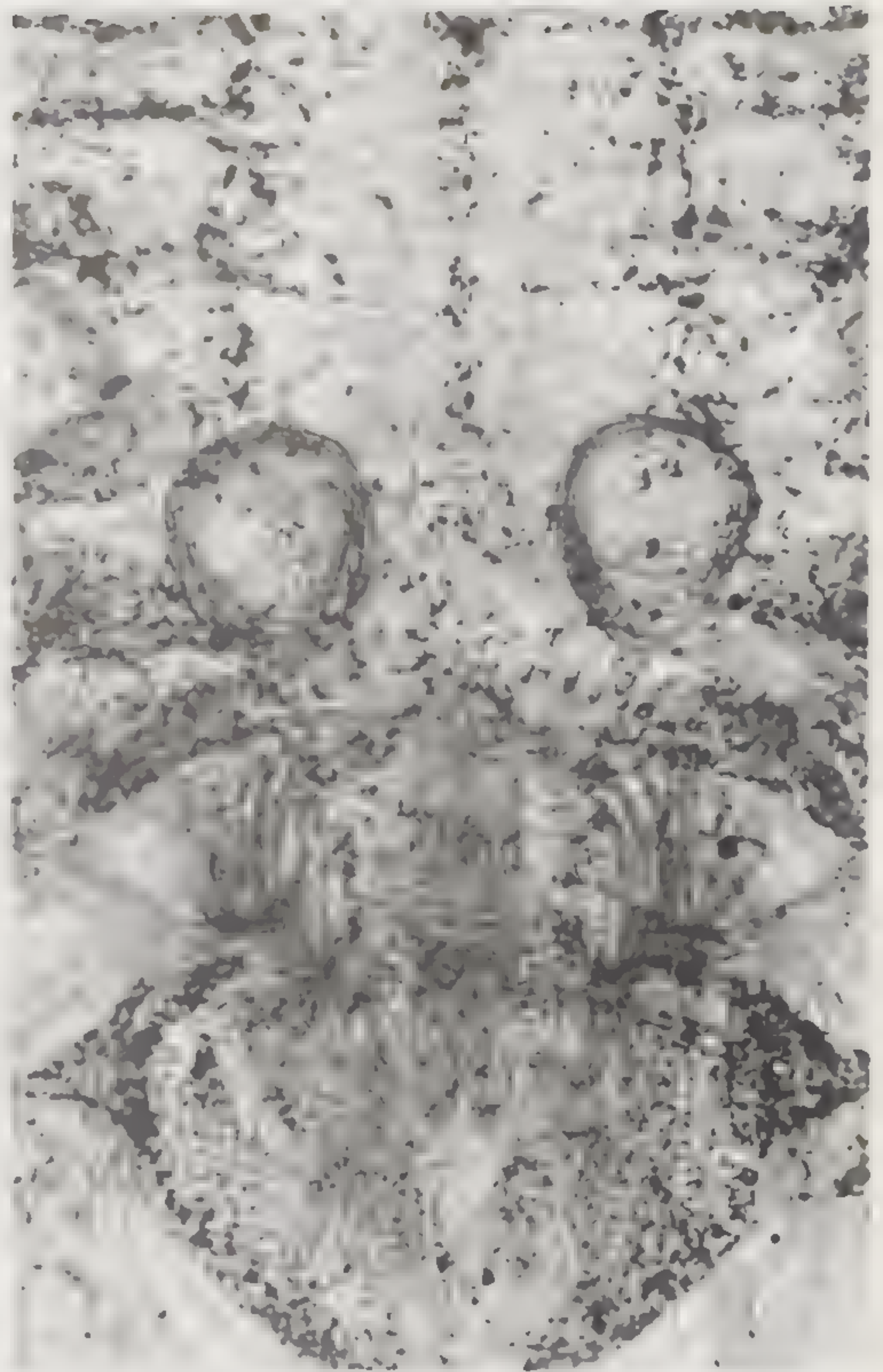
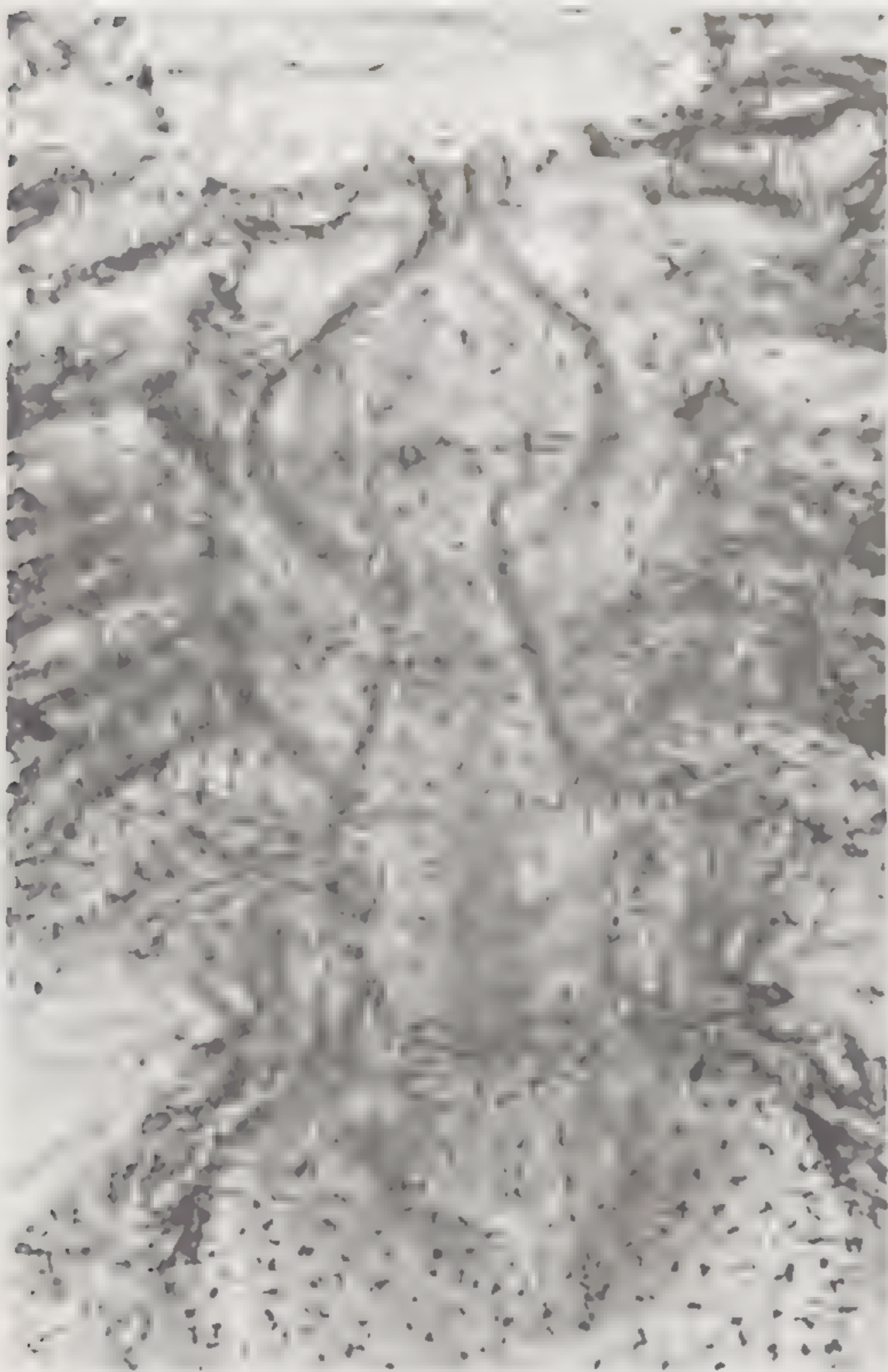
easily recognizable in the dorsal view through the cuticle by their white color and are formed of 1 to 3 pairs of elongate wavy bundles of testicular tissue (Fig. 7C). The development of testes in *P. glynni* presumably occurs either just before or during the moult from female to male. The testes are first noticeable in *P. glynni* as hollow circular objects (Fig. 7B) in individuals undergoing the transition from female to male. Histological investigations into the exact time of differentiation of premordial cells or the point at which the testes become functional were not undertaken.

Reproductive Biology

There is little information about the copulatory behavior of sphaeromatids. The ability of the female to roll up into a ball seems, however, to dictate the manner in which the male attempts copulation. Since most sphaeromatids are able to roll more or less completely into a ball, copulation probably proceeds in a manner roughly similar to that reported by Bowman and Kuhne (1974) for *Cymodetta gambosa*. Iverson (unpublished data) has observed similar behavior in *Gnorimosphaeroma*, *Exosphaeroma*, and *Paracerceis*. A male *C. gambosa* grasps the female with his pereopods, while the female responds by rolling into a ball. The male next rolls the female over several times, presumably determining the female's receptiveness before attempting copulation. A few sphaeromatids (e.g., *Ancinus*, *Tecticeps*, and others) do not roll up into a ball, but rather fold in the middle. Glynn and

Fig. 7 ►

Stages in the development of the testes in *P. glynni*. Bottom: immature female, lacking evidence of differentiating testes (TL= 1.44 mm); top, right: intermoult from female to male with presumably nonfunctional testes (TL= 1.88 mm); top, left: adult male with functional testes (TL= 2.39 mm).



Glynn (1974) reported observing the male *Ancinus* grasp a small female and place her underneath him with her dorsal surface to his ventral surface.

In the case of *P. glynni*, when a male encounters a nongravid female, the male will grasp the female with the anterior pereopods. The male then flips her over while moving her underneath him, venter to venter. The male will usually carry the female in this position for several minutes prior to initiating copulation. This positioning represents an unusual behavior in isopods, which to our knowledge has not been previously reported. It is possible that this behavior evolved as a result of acquiring a progressively more limpetlike body shape and tendency not to leave the substratum.

Males were observed to attempt to copulate with females regardless of the female moulting condition. It is not known whether or not copulation with intramoult females were successful. In the laboratory, copulation was never observed between males and females of approximately equal size. This may be due to the inability of the male to hold a large female underneath and still remain securely attached to the substratum.

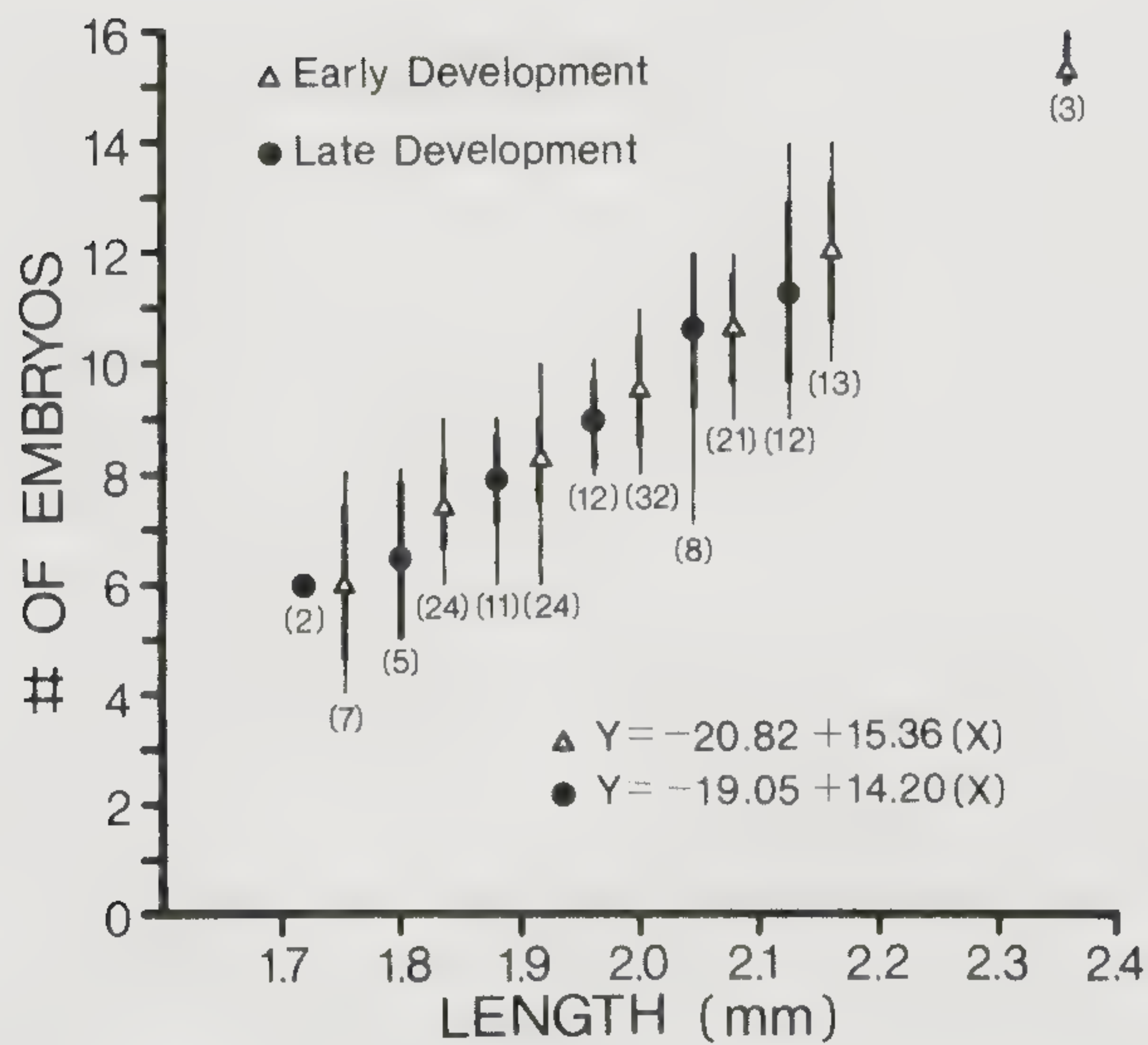
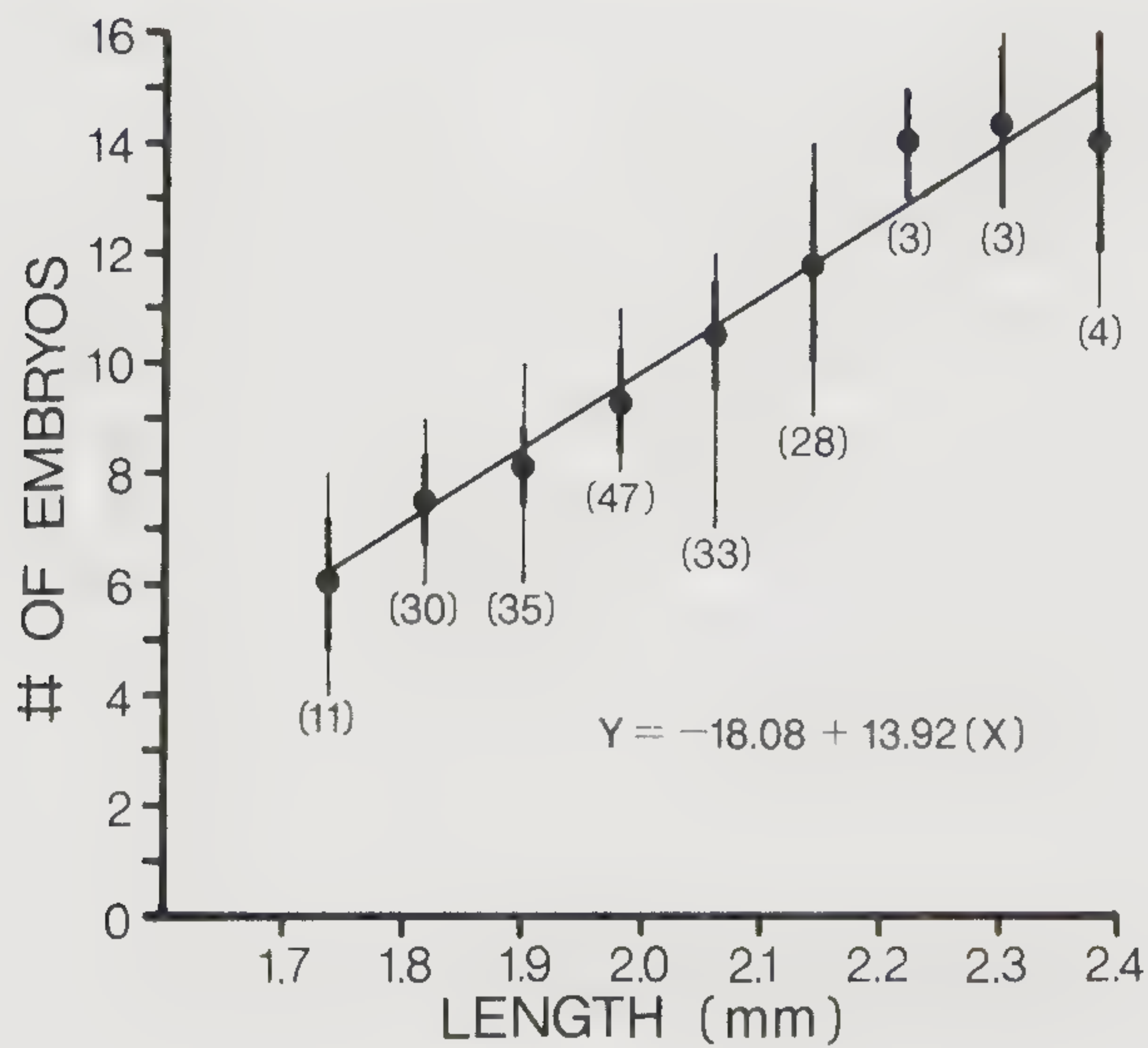
Temperate species of the family Sphaeromatidae are thought, in most cases, to produce a single brood of young (Fincham, 1974; Hoestlandt, 1969) and to live about one year, with males living slightly longer. A preliminary experiment was performed to examine the possibility of multiple broods in *P. glynni*. Five females (all recently having released manca) were placed on five different cobbles and isolated from contacts with males for a period of three months. None of these individuals developed a brood or underwent the moult from female to male. A control group of 5 females, which had also recently released manca, were allowed contact with males. All produced eggs and a brood within 4 weeks. Although these results are inconclusive, they do suggest that sperm storage does not occur in *P. glynni*. Menzies (1954) and Holdich (1968) reported the absence of

sperm storage organs in *Sphaeroma* and *Dynamene*, respectively.

Female *P. glynni* mature sexually after the third moult, which occurs when they reach a total length of between 1.66 mm and 1.82 mm (Fig. 6). In the field, females on any given cobble do not breed synchronously. Breeding appears to be continuous throughout the year as ovigerous females with varying stages of brood development were collected in each month from June 1978 to June 1979. Since quantitative sampling was not carried out over the entire year, it is unknown whether or not there are seasonal peaks in reproductive activity. It is also not known exactly how long individuals live. Males, however, were kept in the laboratory for up to 7 months before they were accidentally lost.

The first step in the production of eggs in *P. glynni* is the appearance of a large quantity of undifferentiated yolk in the body cavity. The appearance of this yolk precedes the appearance of the oostegites. As in most other isopods, the eggs are yellow in color, and are ovate in shape (0.49 mm x 0.36 mm, $n=10$). The number of eggs produced by individual females is strongly positively correlated with length ($r=0.84$, Fig. 8A). Development of the embryos was observed to occur synchronously within the brood pouch. As development proceeds, there is a drastic increase in the size of the brood pouch, such that gravid females rarely have food in their guts. This may be due to compression of the body organs, a tendency for gravid females not to eat, or both. At the time of release, manca average 0.80 mm in total length.

Despite the large increase in embryo size during development, mortality in the brood pouch is a rare event. The number of newly differentiated eggs and near terminal manca are plotted against female length in Figure 8B. The points fall on virtually the same line and are not significantly different (F test), demonstrating a low mortality rate. This is in sharp contrast to the high mortality (up to 36%) reported by Holdich (1968) for *Dynamene bidentata*.

**Fig. 8**

Top, fecundity of *P. glynni* as a function of female size. Values are means, thin bars represent ranges, and thick bars represent standard deviations. Parentheses enclose sample sizes. Bottom, *P. glynni* brood mortality. The number of eggs (triangles) are compared with the number of late manca stage embryos (circles). Notation as in A.

Feeding Behavior

Almost nothing is known about the feeding mechanisms or diet selections in sphaeromatid isopods. In the case of *P. glynni* observations reveal that it consumes zooids of the two bryozoans with which it occurs sympatrically (*A. tincta* and *O. alula*). Only autozooids are eaten and only one zooid is consumed at any one feeding (Fig. 9). The skeleton is left undamaged, the chitinized operculum dislodged, and the soft parts consumed. The only clearly identifiable materials in gut smears of 30 isopod individuals, over a range of sizes, were bryozoan soft parts. Although distributed primarily with *O. alula* and *A. tincta*, individuals of *P. glynni*, when maintained in the laboratory in the absence of these foods, fed on the anascan bryozoans, *Membranipora hastingsae* and *M. savartii*. They did not feed on the anascan *Antropora granulifera*, possibly because of the extensive cryptocyst of this species. Feeding was not observed on any of five species of ascophoran bryozoans offered (*Hippoporella gorgenensis*, *Microporella marsupiata*, *Parasmittina crosslandi*, *P. trispinosa*, *Rhynchozoon rostratum*).

Direct observation of feeding were obscured by the dorsum of the feeding individual. The feeding mechanism which we propose is inferred from the repeated observations of individuals approaching a healthy autozooid, remaining over it from 2 to 5 minutes, and leaving behind a zooid emptied of all tissues. Attempts to observe the actual mechanism of feeding by allowing individuals to feed upon bryozoans grown on glass substrata (while observing the colony from beneath) were unsuccessful. The cement secreted by the bryozoan in attaching itself to the substratum obscured such observations. Further understanding of the feeding mechanism is based upon examination of partially consumed zooids from which feeding individuals had been gently removed.

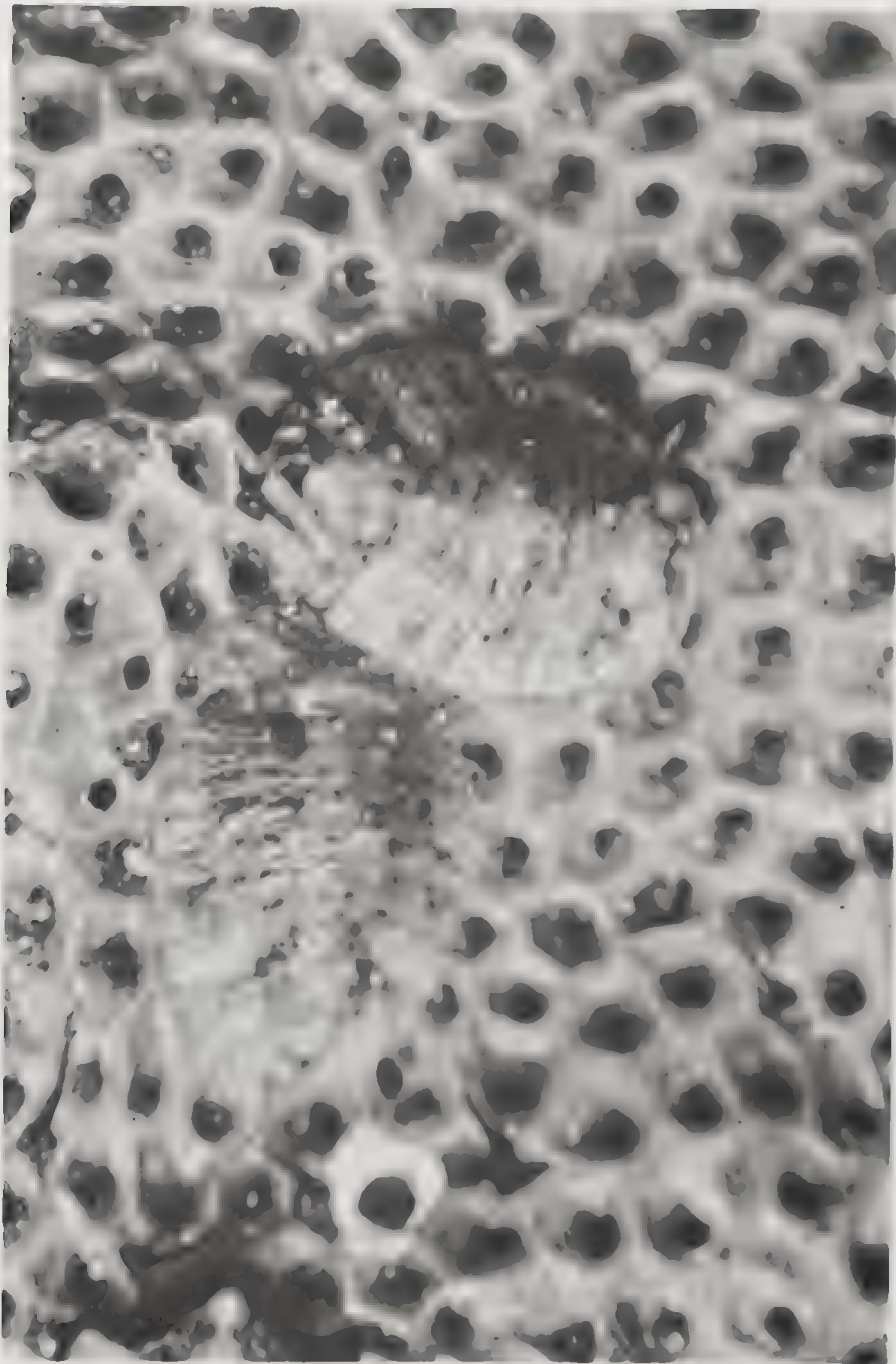
Antropora tincta is characterized by a roughly oval autozooid without a well developed cryptocyst. Partially consumed

zooids commonly exhibited punctures in the frontal membrane. These incisions were not localized in any particular region and no incisions were found in any of the bryozoan musculature. *Onychocella alula* is characterized by a roughly hexagonal autozooid with a broad cryptocyst which extends up to two-thirds the length of the opesia. Partially consumed zooids exhibited incisions just beyond the distal edge of the cryptocyst and proximal to the base of the operculum. Severed occlusor muscles were noted in several instances. These observations suggest that individuals of *P. glynni* gain access to *A. tincta* by severing the frontal membrane and to *O. alula* by first severing the frontal membrane, then severing the occlusor musculature, an act that releases the operculum and exposes the bryozoan tissue.

The mechanism is supported circumstantially by the observation that no individual of *P. glynni* smaller than 2.08 mm was ever found to feed on *O. alula*, whereas individuals of all sizes fed on *A. tincta*. If the mechanism suggested above is correct, the appendage of an individual feeding on *O. alula* must be sufficiently large to reach through the severed frontal membrane, beyond the cryptocyst, to the point of attachment of the occlusor muscles to the operculum. It would be expected, then, that only larger individuals of *P. glynni* would be capable of feeding on *O. alula* whereas feeding on *A. tincta* would involve no such restriction. Also consistent with this mechanism is the observation that *P. glynni* does not feed upon ascophoran bryozoans (which possess calcified frontals) and that the anascan upon which *P. glynni* does not feed possesses an extensive cryptocyst.

Swimming Behavior

Unlike other isopods which exhibit rhythmic swimming through the water column in response to tidal and photic stimuli (Fincham, 1974; Fish, 1970; Jones and Naylor, 1970; and others), *P. glynni* was never ob-

**Fig. 9**

Two individuals of *P. glynni* upon a colony of *O. alula*. Note the recently consumed zooid (white) in the upper right.

served to swim off of cobble in the laboratory. Since swimming is commonly associated with the search for food (Fincham, 1974), we initiated a laboratory experiment to determine whether *P. glynni* would swim under such conditions. Five *P. glynni* were placed on each of 5 replicate cobbles that were free from any encrusting bryozoan food sources. Five cm from each of these cobbles was placed on approximately equal-sized cobble that was heavily encrusted with colonies of both *A. tincta* and *O. alula*. After one week, each of the barren cobbles still had all 5 *P. glynni* per cobble. A control experiment was performed by placing pairs of barren and encrusted cobbles from the previous experiment in physical contact with each other. Within 12 hours, in all 5 replicates, at least 4 and in some cases all 5, individuals had moved from the barren cobble to the encrusted cobble. The rarity of swimming in *P. glynni* was further demonstrated by suspending 5 cobbles encrusted with *A. tincta* and *O. alula* off of the substratum so that migration to these cobbles could only be accomplished by swimming. These cobbles, as well as 5 control cobbles (placed in contact with other cobbles) had all individuals of *P. glynni* removed from them. After a period of one week, all of the control cobbles had acquired at least one individual of *P. glynni*, whereas none of the suspended cobbles had been colonized.

Color Polymorphism

Polymorphism in the coloration of the dorsum is a common phenomenon in the Sphaeromatidae. Holdich (1969) recognizes two types of polymorphism. The first is that caused by diet and the second, that due to aggregations of stable chromatophores on the dorsal surface. Although particular coloration patterns are known to be heritable in some species (e.g., *Sphaeroma serratum*, Bocquet, et al., 1951; *S. rugicauda*, West, 1964; *Dynamene bidentata*, Holdich, 1969), the adaptive significance of color

patterns is not always clear. Color polymorphs have been shown to possess differing tolerances to temperature and salinity stresses and the frequencies of these forms have been shown to correlate with seasonal and geographic variation in temperature (e.g., *Isocladus armatus*, Jansen, 1971). These results are consistent with the hypothesis that color patterns are linked pleiotrophically with some unidentified physiological characteristics and do not represent adaptive characteristics in and of themselves. In other cases, though, color polymorphisms appear to be adapted as cryptic coloration (e.g., *Ancinus panamensis*, Glynn and Glynn, 1974), with color patterns closely matching that of the substratum.

The population of *P. glynni* at Punta Paitilla, R.P., exhibits a wide variety of dorsal color patterns. The 6 principal color patterns found in prereproductive individuals (moult 1-3) are described below. The description is limited to juvenile forms because an ontogenetic change in coloration coincident with maturation often occurs. Crosses were not made and hence it is unknown whether these patterns are heritable.

Color notes are based on individuals of *P. glynni* examined live over a three-month interval (May-June 1979). Figure 10 represents the dominant pigmentation patterns observed. Color identification was made under reflected light from a Dyonics fiber optic illuminator at 25X magnification. We follow Glynn and Glynn (1974) in referring to pattern as the distribution of pigment on the dorsum, and ground color as the dominant background color of the individual. The relative frequency of each of these morphs in a single sample of 250 individuals is presented in Table 2.

Uniform A. Without conspicuous pigmentation on dorsum. Ground color grey to nearly colorless and translucent, revealing the coloration of the substratum upon which it rests. This form appears similar to the grey form of *Sphaeroma rugicauda* (fig. 1a of West, 1964), the uniform form of *Ancinus basilensis* (fig. 12k of Glynn and

Table 2 Distribution of Dorsal Color Patterns. $n=250$ individuals.

Pattern	%	Pattern	%
A	3.6	D	24.4
B	6.8	E	28.4
C	35.2	F	1.6

Glynn, 1974), and the albicans form of *Sphaeroma serratum* (fig. 1(1) of Teissier, 1969).

Uniform B. Pigmentation is nearly uniformly distributed over the dorsum. The dominant color is dark grey to black. This form is clearly visible on a light colored substratum, but rather cryptic on a dark colored one. This form is similar to the albicans morph of *Sphaeroma serratum* (fig. 1(2) of Teissier, 1969) and the uniform type of *Aricinus panamensis* (fig. 12a of Glynn and Glynn, 1974).

Pattern C. This form is variable, but characterized by a circular to roughly T-shaped patch in the anterior region. The patch color is black and the dominant ground color similar to Uniform A. This form is very similar to that described as pattern in *Sphaeroma rugicauda* (fig. 1d of West, 1964).

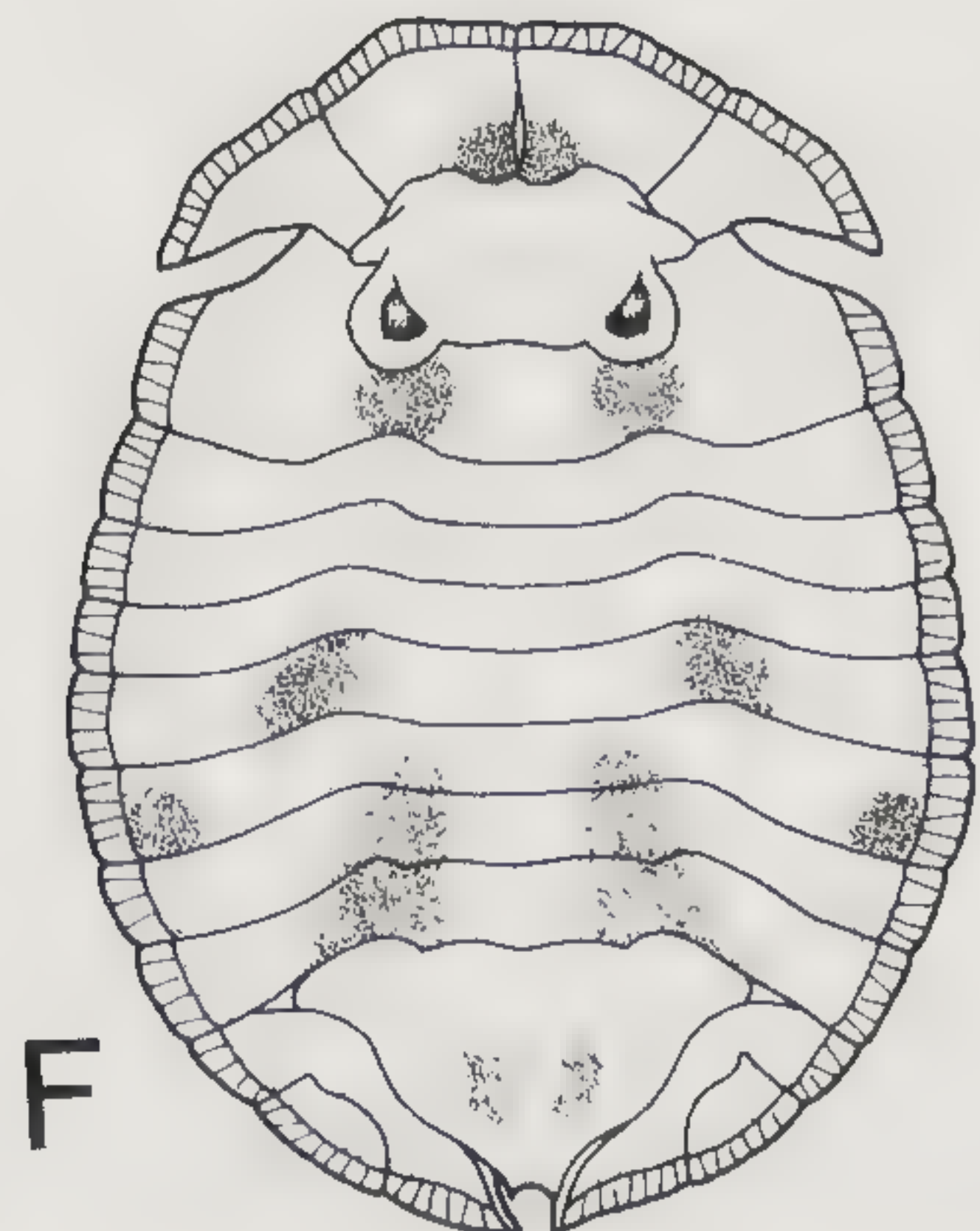
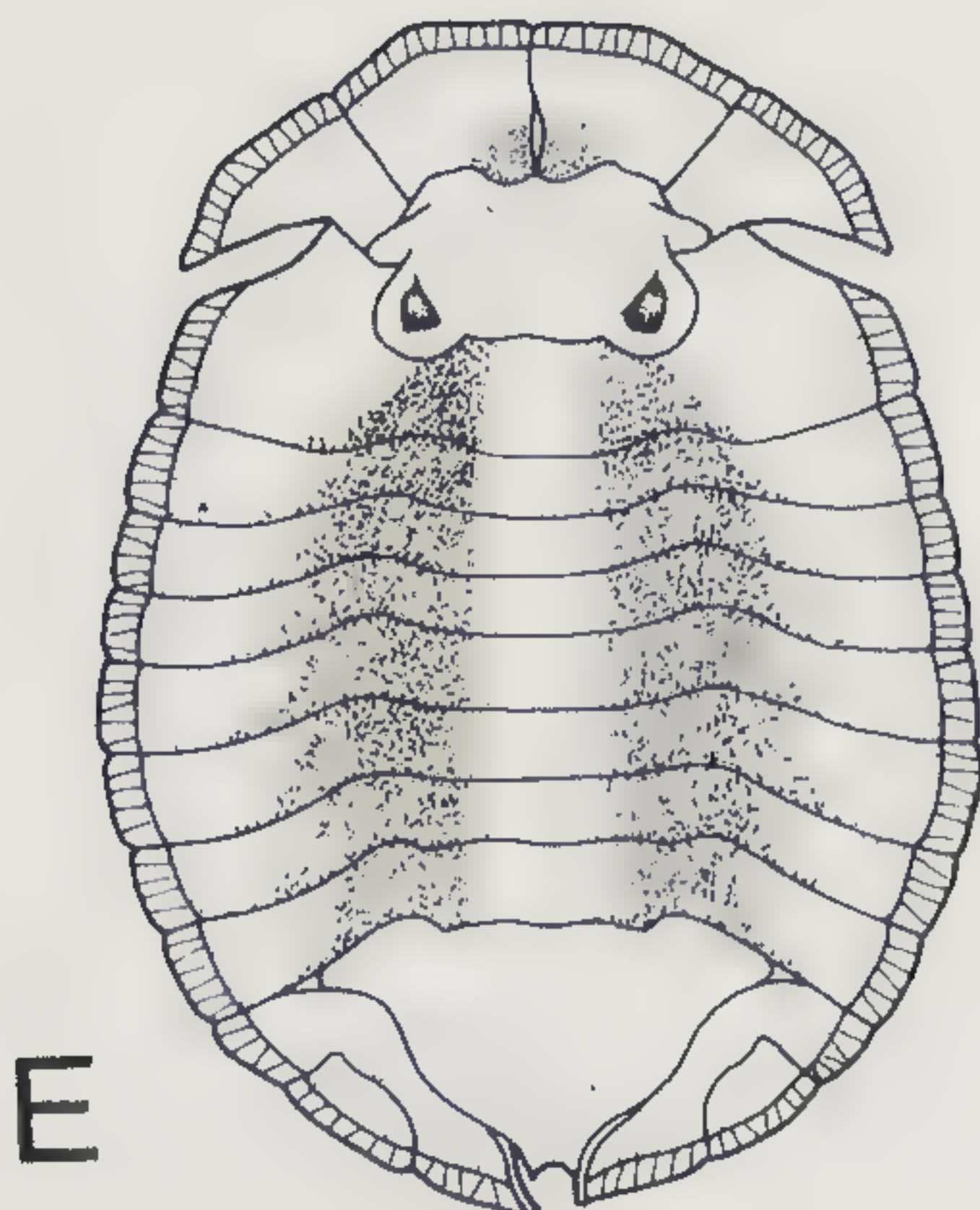
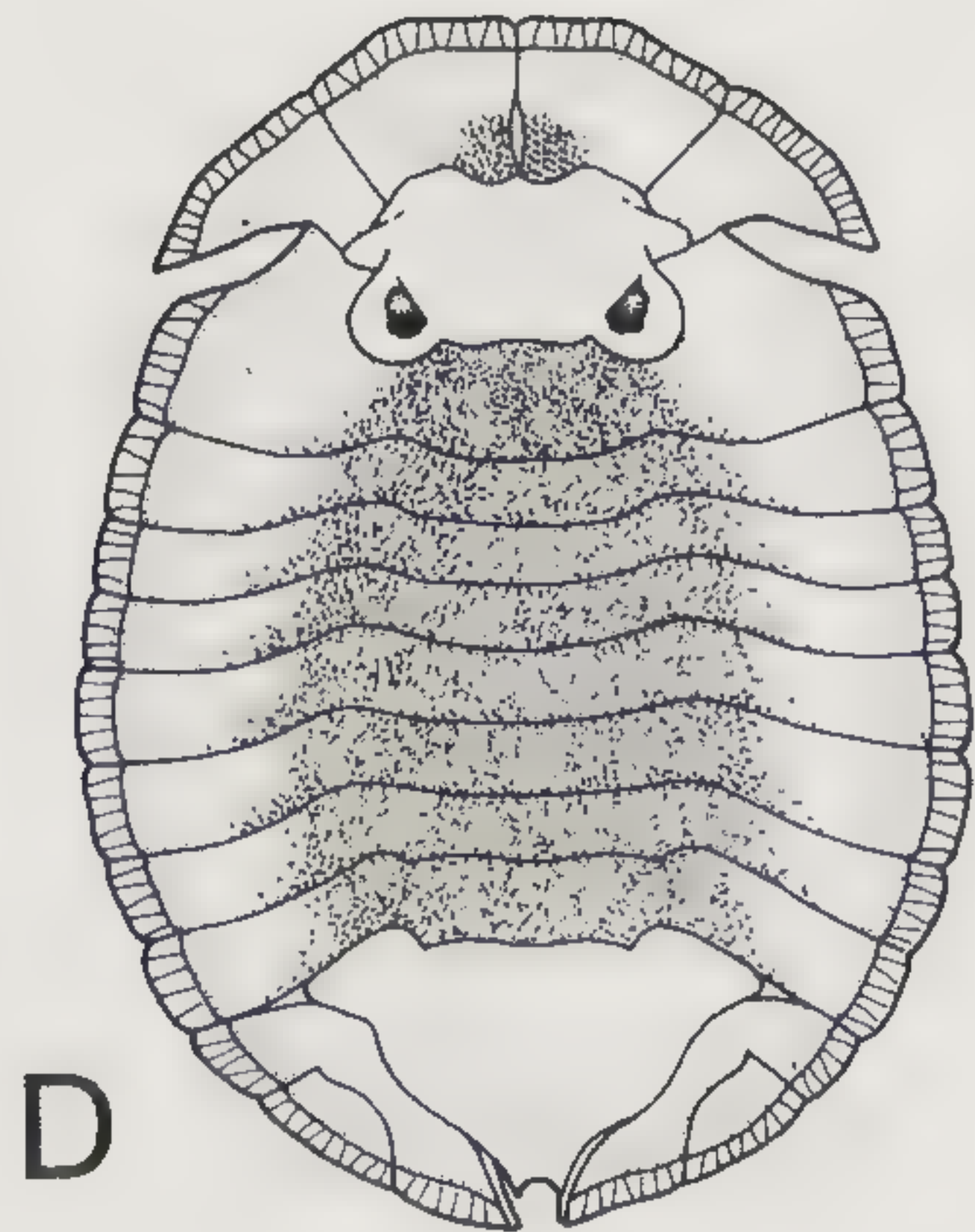
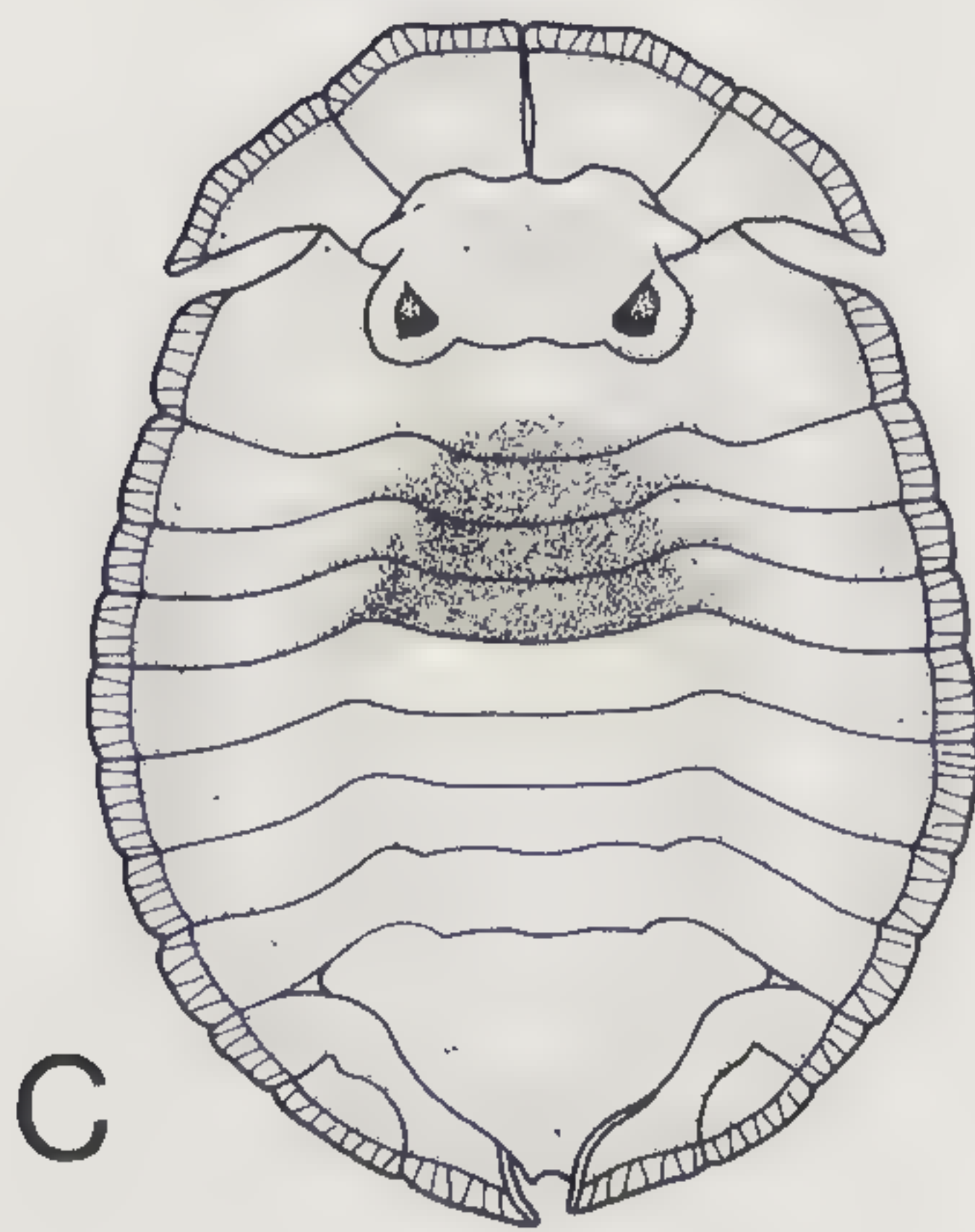
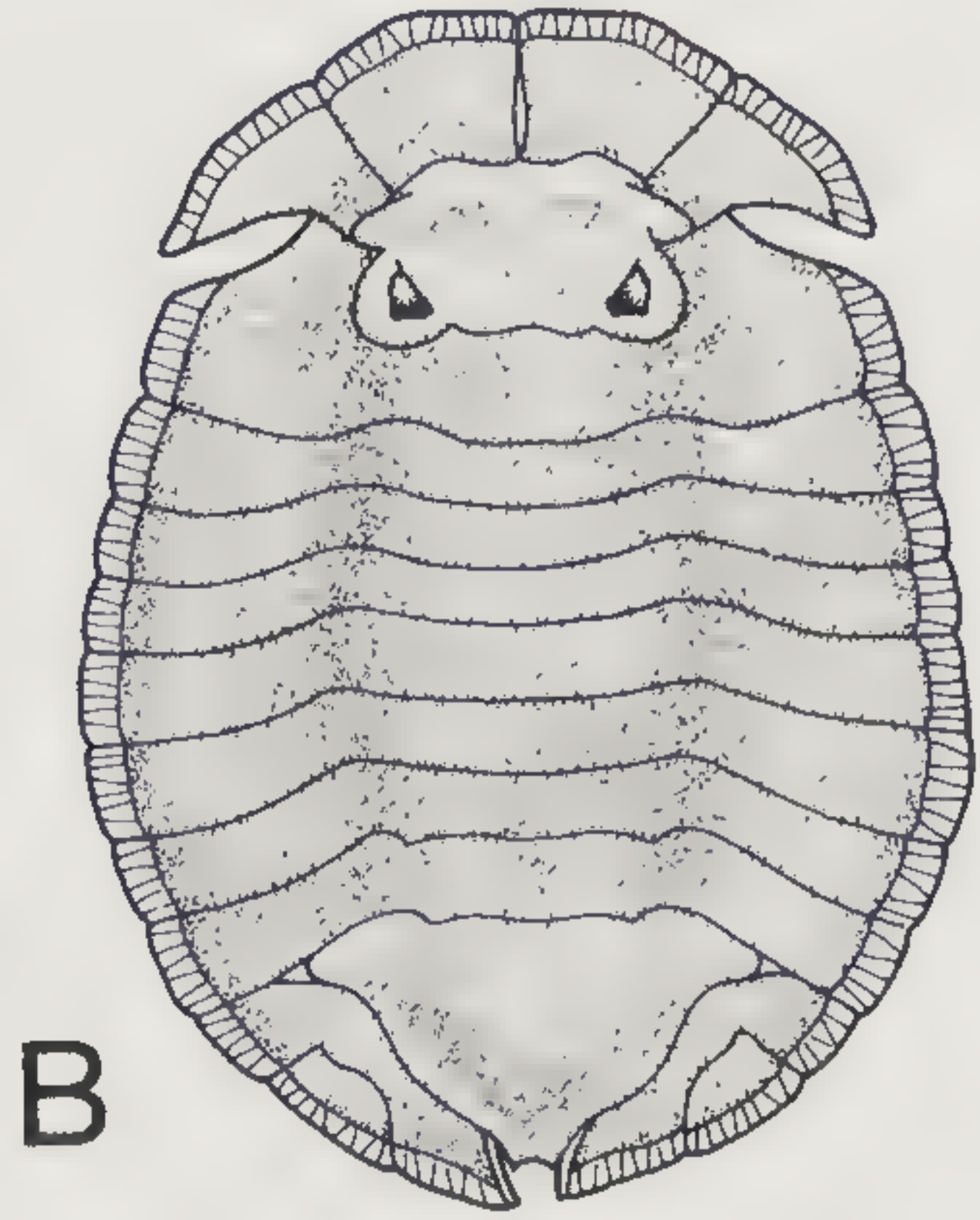
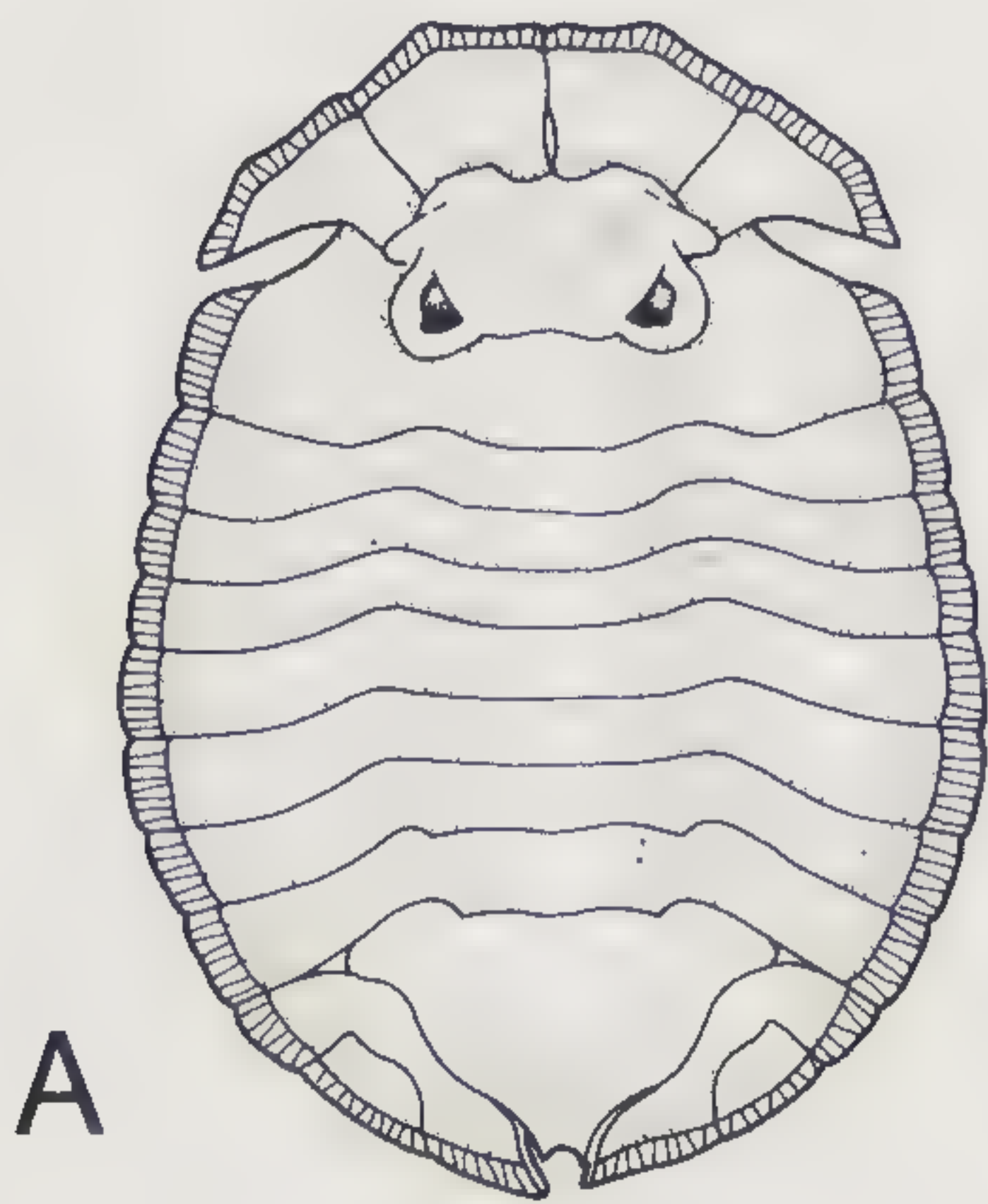
Pattern D. Characterized by dense pigmentation toward the center of the dorsum, gradually lessening toward the outer margin. Variations include a tapering of pigmentation anteriorly, posteriorly, or both. Pigmentation is black and ground color grey to colorless.

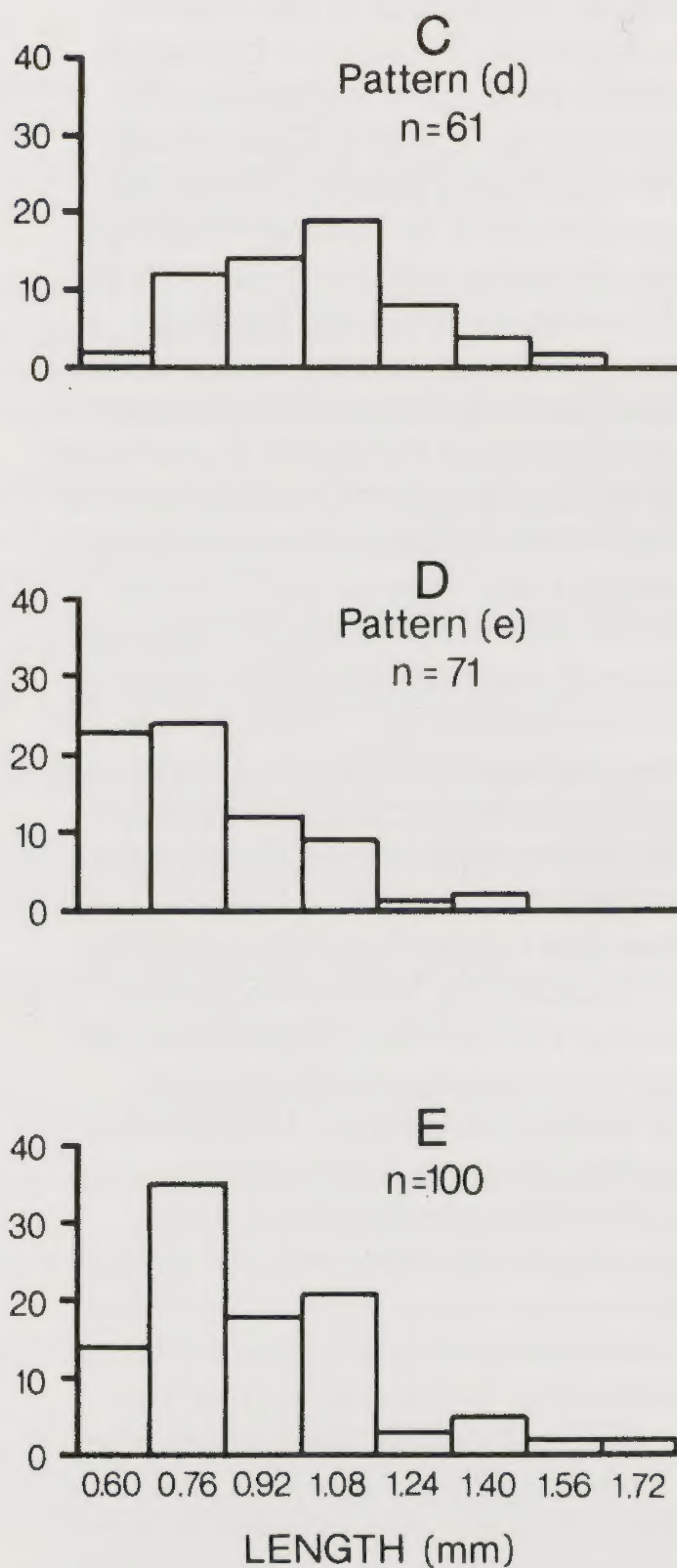
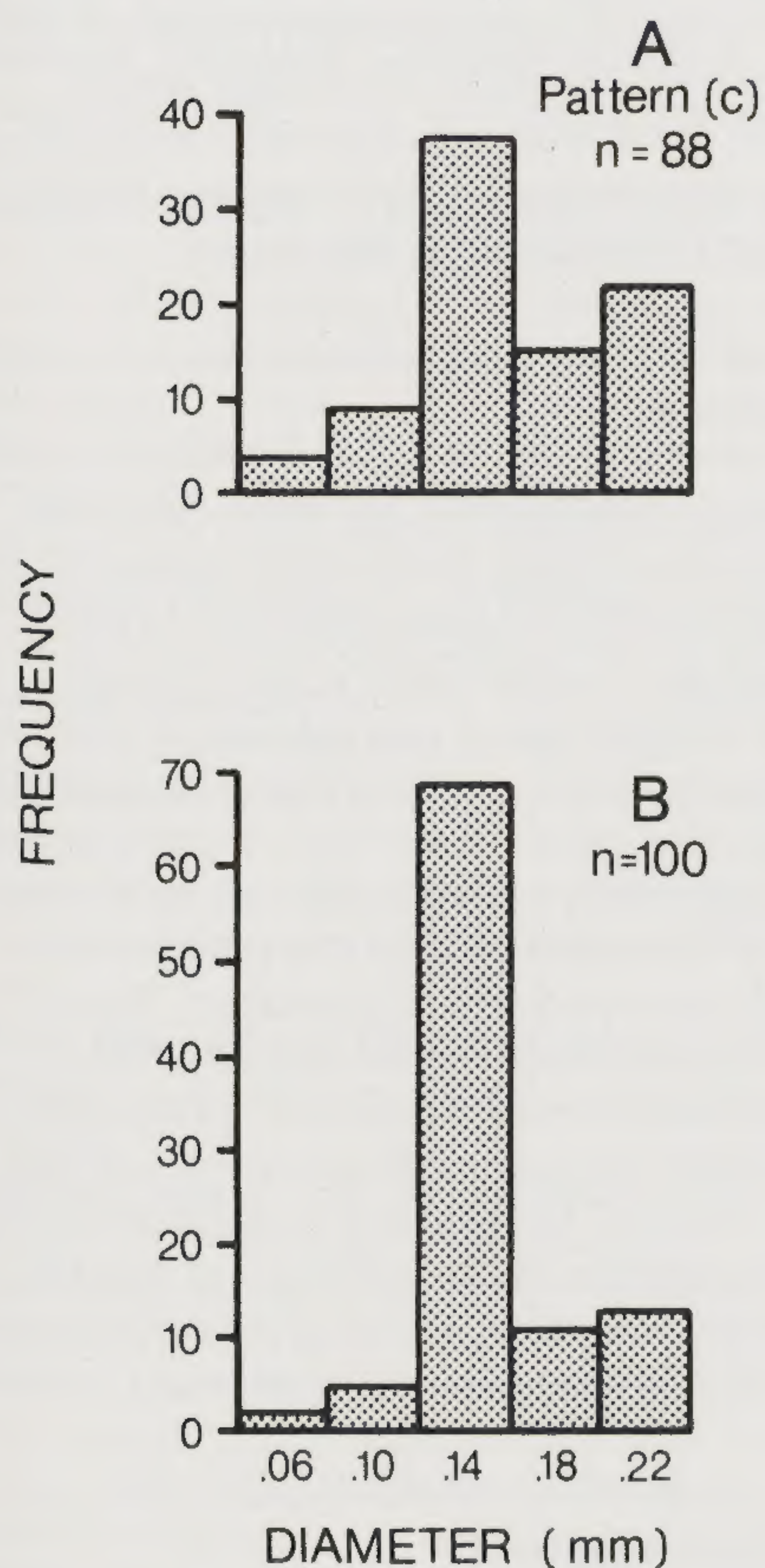
Pattern E. Characterized by a pigment-free area running the length of the dorsum, otherwise identical to Pattern D. Variations include those noted for Pattern D as well as the occasional occurrence of yellow to orange pigments in the central regions. Ground color light grey to colorless. This

form appears most similar to the signatum type of *Sphaeroma serratum* [fig. 1(6) of Teissier, 1969] and the stripe type of *S. rugicauda* (fig. 1f of West, 1964).

Composite F. Due to its rarity in juvenile forms, this variable type cannot be completely described. There occur characteristically pigment-free areas interspersed with less frequent pigmented areas, but no repeated pattern was noted in their distribution. Ground color grey to colorless, with dark grey to black hues prominent. However, yellow, red, and orange pigments are often found interspersed with the darker colors. This type is the most similar to color patterns seen in adults of *P. glynni*.

Of the six patterns, Patterns C, D, and E constitute 87.8% of all individuals classified. These patterns are suggestive of those occurring in the habitat in which the isopod is found. Juvenile isopods are found most commonly on the living surfaces on the coralline alga, *Neogoniolithum rugulosum* (Adey). The alga is commonly bored by phoronids and barnacles. When viewed from above, the coralline algae appear irregularly perforated with black dots, black elliptical slits and black elliptical slits with orange interiors. These are phoronid bore holes, barnacle bore holes and living barnacles, respectively. The roughly circular patch of dark pigment characterizing Pattern C appears similar to a phoronid bore hole. Patterns D and E appear similar to markings





◀ **Fig. 10.** Color patterns of juvenile *P. glynni*. *A-B*, uniform; *C-E*, pattern; *F*, composite. See text for description of each color morph.

Fig. 11 Comparison of the size-frequency distributions of juvenile *P. glynni* dorsal coloration and of the aperture of bore holes made in *N. rugulosum* by boring phoronids and barnacles. *A*, diameter-distribution of Pattern C marks; *B*, diameter-distribution of phoronid bore-holes; *C*, length distribution of Pattern D marks; *D*, length distribution of Pattern E marks; *E*, length distribution of barnacle bore slits.

produced on the surface of the coralline alga by the boring activities of barnacles. Only after several months of experience was the senior author able to distinguish with the naked eye between juvenile isopods from phoronid and barnacle borings.

If the coloration patterns of juvenile isopods do mimic phoronid and barnacle markings, one would expect a close correspondence between the size of the bore holes and the size of the patch of coloration. Figures 11A and B present the frequency of color patch sizes and phoronid bore hole sizes, respectively. Figures 11C, D, and E present the same information for color patterns D and E and barnacle slits. In each of these comparisons (Fig. 11, A vs B, C vs E, D vs E) the distributions are quite similar, with no significant differences found between the mean sizes of coloration patches and barnacle/phoronid markings (t-test).

These data suggest that coloration Patterns C, D and E (Fig. 10) are adapted for concealment of juveniles inhabiting coralline alga from visually-oriented, water-column-dwelling predators. The tidal channels in which *P. glynni* are found also support several planktivorous fish species, many of which will consume isopods if offered in the laboratory. Some of these species, primarily chaetodonts, guard schools of planktivorous fry by backing them up against pieces of cobble. We suggest that these fry may represent a selection pressure for cryptic coloration in juvenile *P. glynni*.

Color Patterns A, B, and F (Fig. 10) are not obviously related to any surface features of the coralline alga pavement. The beach at Punta Paitilla, where these organisms were collected, has suffered over the past ten years from increasing levels of pollution from Panama City. The resident fish population has declined substantially in both diversity and abundance over this period (R. Rubinoff, personal communication). It is unknown whether the increased pollution levels have relaxed selection for cryptic coloration, but the matter clearly merits further attention.

The color patterns noted for *P. glynni* are

similar to those recognized in several other species. The possibility that these polymorphs may be adapted to conceal isopods from water-column-dwelling predators also merits consideration. This possibility, of course, is not mutually exclusive with the apparent pleiotrophic link between coloration and physiological tolerances.

Summary

Paraleptosphaeroma glynni inhabits the surfaces of cobble, to which it appears to be limited by its poor swimming ability and potentially intense fish predation. Upon these cobbles occur two species of anascan bryozoans and a coralline alga. *Paraleptosphaeroma glynni* feeds upon the bryozoans and apparently utilizes markings on the surface of the coralline alga as a refuge from water-column-dwelling predators. These observations imply some degree of functional dependence between *P. glynni* and the sessile encrusting fauna of the cobbles they inhabit. The nature of this dependence and its relation to the evolution of sequential hermaphroditism in *P. glynni* will be explored in further communications.

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Literature Cited

- Bocquet, Charles, Claude Levi** and **Georges Teissier**. 1951. Recherches sur le polychromatisme de *Sphaeroma serratum* (F.). Arch. Zool. Exp. Gen. 87: 245-297.
- Bowman, Thomas E.** and **Helmut Kuhne**. 1974. *Cymodetta gambosa*, a new sphaeromatid isopod (Crustacea) from Australia, with notes on its mating behavior. Rec. Austr. Mus. 29: 235-244.
- Brusca, Richard C.** 1978a. Studies on the cymothoid fish symbionts of the Eastern Pacific (Isopoda, Cymothoidae) I. Biology of *Nerocila californica*. Crustaceana (Leiden) 34: 141-154.
- . 1978b. Studies on the cymothoid fish symbionts of the Eastern Pacific (Isopoda, Cymothoidae) II. Systematics and biology of *Lironeca vulgaris* Stimpson 1857. Occas. Pap. Allan Hancock Foundation. 2: 1-19.
- Brusca, Richard C.** and **Barry R. Wallerstein**. 1979. The marine isopod crustaceans of the Gulf of California II. Idoteidae: new genus and species, range extensions, and comments on evolution and taxonomy within the family. Proc. Biol. Soc. Wash. 92: 253-271.
- Burbanck, Madeline P.** and **William D. Burbanck**. 1974. Sex reversal of female *Cyathura polita* Stimpson 1855 (Isopoda, Anthuridae). Crustaceana (Leiden) 26: 110-113.
- Fincham, Anthony A.** 1974. Rhythmic swimming of the isopod *Exosphaeroma obtusum* (Dana). N.Z.J. Mar. Freshwater Res. 8: 655-662.
- Fish, Susan**. 1970. The biology of *Eurydice pulchra* (Crustacea: Isopoda). J. Mar. Biol. Assoc., U.K. 50: 753-768.
- Glynn, Peter W.** 1970. A systematic study of the Sphaeromatidae (Crustacea: Isopoda) of Isla Margarita, Venezuela, with descriptions of three new species. Mem. Soc. Cienc. Nat. La Salle 30: 1-45.
- Glynn, Peter W.** and **Carmen S. Glynn**. 1974. On the systematics of *Ancinus* (Isopoda, Sphaeromatidae), with the description of a new species from the tropical Eastern Pacific. Pac. Sci. 28: 401-422.
- Hansen, Hans J.** 1905. On the propagation, structure, and classification of the family Sphaeromatidae. Q. J. Micro. Sci. 49: 69-135.
- Hoestlandt, Henri**. 1969. Sur un Sphaerome nouveau de la cote pacifique americaine, *Gnorimosphaeroma ravi*, n. sp. (Isopode, Flabellifere). C. R. Acad. Sc. Paris 268: 325-327.
- Holdich, David M.** 1968. Reproduction, growth and bionomics of *Dynamene bidentata* (Crustacea: Isopoda). J. Zool. (London) 156: 137-153.
- . 1969. Polychromatism in the genus *Dynamene* (Crustacea: Isopoda). Pubbl. St. Zool. Napoli 37: 18-27.
- Hurley, Desmond E.** and **Kevin P. Jansen**. 1977. The marine fauna of New Zealand: Family Sphaeromatidae (Crustacea: Isopoda: Flabellifera). N. Z. Oceanogr. Inst. Mem. 63: 1-95.
- Jansen, Kevin P.** 1971. Ecological studies on intertidal New Zealand Sphaeromatidae (Isopoda: Flabellifera). Mar. Biol. 11: 262-285.
- Jones, David A.** and **Ernest Naylor**. 1970. The swimming rhythm of the sand beach isopod *Eurydice pulchra*. J. Exp. Mar. Biol. Ecol. 4: 188-199.
- Menzies, Robert J.** 1954. The comparative biology of reproduction in the wood-boring isopod crustaceans *Limnoria*. Bull. Mus. Comp. Zool. 112: 364-388.
- Nishimura, Saburo**. 1976. Redescription of *Leptosphaeroma gottschei* Hilgendorf (Isopoda, Sphaeromatidae), with some biological notes. Publ. Seto Mar. Biol. Lab. 23: 169-177.
- Stoll, N. R., R. Ph. Dollfus, J. Forest, N. D. Riley, C. W. Sabrosky, C. W. Wright, and R. V. Melville** (Editorial Committee). 1964. International Code of Zoological Nomenclature. London, Int. Trust for Zool. Nomenclature. 176 pp.
- Teissier, Georges**. 1969. Génétique des populations de *Sphaeroma serratum*, Isopoda littoral. Pubbl. St. Zool. Napoli 37: 135-145.
- West, David A.** 1964. Polymorphism in the isopod *Sphaeroma rugicauda*. Evolution 18: 671-684.

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