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Notes on the Morphology and Sexuality of the Terrestrial Nemertean, Geonemertes palaensis[1]

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A collection of 24 specimens of *Geonemertes palaensis* Semper which the writer has had the opportunity of studying through the courtesy of Bernice P. Bishop Museum includes a series of sexual phases which are thought to be typical of the normal sexuality of the species. Consequently the collection is of much interest. A complete account of these phases has not been possible hitherto because of lack of suitable material. A few details of other anatomical features supplementary to those previously reported can also be supplied at this time.

This collection was made by Y. Kondo, a member of the Micronesian Expedition in March, April, and May 1936, and of the Henry G. Lapham Expedition in July 1938, at the following localities:

Palau Islands: Anguar (near hospital), Koror and Komakam (northeast corner of island), Peleliu; Caroline Islands: Yap (Mount Matade, Okau district), Ponape, Jokaj Islet, Nanpilo [Nanepil]; Samoan Islands: Pago Pago.

This species has been collected previously from the Palau, Celebes, Kei, and Samoan Islands at various situations from sea level to nearly 700 meters elevation. It is reported as common in Samoan forests. A closely similar species (*G. arboricola*) has been found on the Seychelles Islands in the Indian Ocean. The ten other terrestrial species at present known are endemic in Rodriguez Island, Bermuda, New

[1] Micronesian Expedition Publication 4.

[2] Contributions from Scripps Institution of Oceanography New Series, no. 80.

Zealand, Australia, New Guinea and Auckland Islands. Two of these species have been introduced into greenhouses in Germany.

In addition to the investigations of Von Kennel (1878), Dendy (1893), Böhmig (1898), Coe (1904), Schröder (1918), and others on the morphology and biology of various species of terrestrial nemerteans, Hett (1928) and Stammer (1934) give brief synopses of the characteristics and known distribution of each of the 12 described species.

Waterston and Quick (1937) have recently found an Australian species (*Geonemertes dendyi*) living beneath stones and fallen branches in damp situations at several localities near Swansea, Wales, where it has evidently become acclimated. The worms were observed to feed by sucking the juices of minute bugs and *Collembola.* Only females have been found, but some of these deposited clusters of eggs which developed by the direct method and liberated the young worms in about three weeks.

Geonemertes palaensis was described by Semper in 1863 from individuals found on the Palau Islands. The specimens in the present collection are all rather small, measuring only 10 to 28 mm. in length after preservation, the largest being less than half as long as some of the others that have been previously collected. The smallest ones represent young individuals, and these are of special interest in that they show the early sexual conditions necessary for the elucidation of the sexual phases of the entire life history. Most of the specimens previously studied have been considered females.

These specimens allow the following supplementary details to be added to the morphological characteristics previously recorded for the species by Von Kennel (1878), Böhmig (1898), Schröder (1918), Hett (1928), and earlier investigators.

Ocelli: They have one pair of large dorsal ocelli and from 1 to 3 pairs of small ocelli.

Proboscis: Most of these specimens have only two pouches of accessory stylets, but several of them have four. They have from 16 to 21 proboscidial nerves.

Nerve cords: The lateral nerve cords have well differentiated dorsal cores of fibers arising from the dorsal ganglia.

Nephridia: The nephridial system as described by Schröder (1918) and supplemented by Coe (1929) consists of thousands of

independent protonephridia, the system extending in the parenchyma from the tip of head to the posterior end of body. In the brain region and immediately anterior thereto the flame cells are massed about the cephalic blood vessels into veritable nephridial "glands" with several hundred flame cells in a single transverse section of the head (fig. 1). The preservation was not sufficiently perfect to allow the delicate efferent ducts as described for *G. agricola* (Coe, 1929) to be distinguished. The crowding of the flame cells is naturally greatest when the blood vessels are empty.

Sexuality of other species: According to the published descriptions there is great variation in the sexual conditions of the 12 known species of terrestrial nemerteans. Three species (*G. australiensis* Dendy, *G. rodericana* (Gull.), and *G. hillii* Hett) are described as of separate sexes, with the males smaller than the females. Three others (*G. dendyi* Dakin, *G. graffi* Bürger, and *G. novae-zelandiae* Dendy)

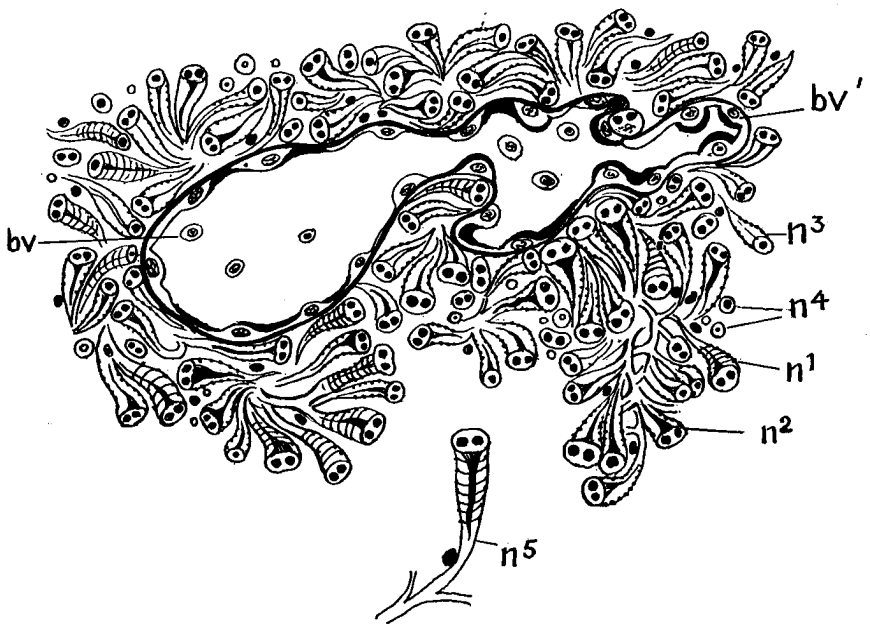

FIGURE 1.—Section of cephalic blood vessel with surrounding nephridial gland; *bv*, distended portion of vessel; *bv'*, contracted portion of vessel, showing darkly stained endothelial cells which act as valves when vessel is contracted; n^1, flame cells, surface view, showing the two terminal nuclei; n^2, same in section; n^3, same, showing but one of the two terminal nuclei; n^4, transverse sections of flame cells; n^5, single flame cell more highly enlarged.

have been thought to be of separate sexes, although no males have been found. One species (*G. spirospermia* Darbishire) is known only from a single male and another (*G. caeca* Darbishire) from a single female. Because of the scanty material which has been available for the study of these 8 species the evidence that hermaphroditism, either functional or sequential, does not occur in at least some of them is far from satisfactory. The remaining 4 species (*G. agricola* Will.-Suhm, *G. arboricola* Punnett, *G. chalicophora* Graff, and *G. palaensis* Semper) are undoubtedly hermaphroditic.

Reproductive organs: The sexual conditions in *G. palaensis* have hitherto been in some doubt, since all but one of the specimens studied have been considered to be females. The species now proves to be irregularly protandric, as suspected by Schröder (1918) and hermaphroditic, as reported by Von Kennel (1878), with alternating male and female functional sexual phases. The female phases, however, are usually complicated by the precocious development of a few or many ripe spermaries of the normally following male phase before the ova are fully mature (figs. 2, 3). Likewise in the primary male

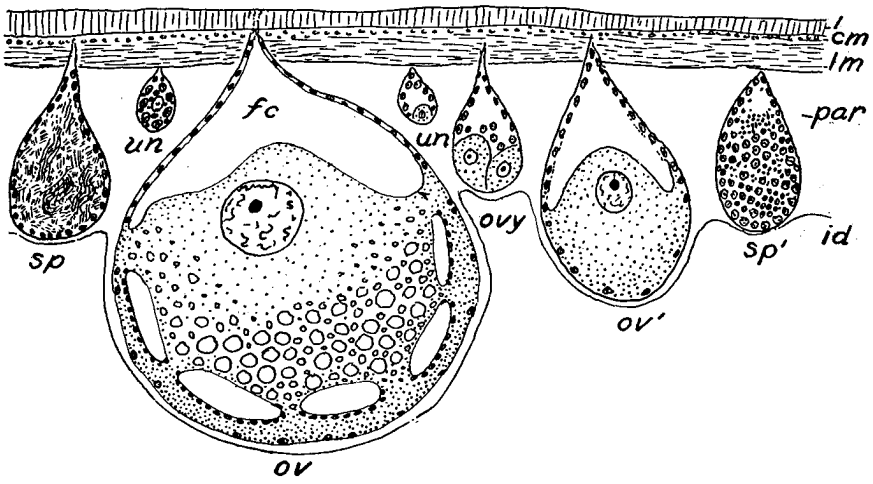

FIGURE 2.—Portion of horizontal section of body, dorsal to nerve cord, of functionally hermaphroditic individual; *ov,* ripe ovary with its single ovum, oviduct and fertilization chamber (*fc*); *ov'*, immature ovary; *ovy,* young ovary with two ovocytes; *sp,* ripe spermary; *sp'*, immature spermary; *un,* two sexually undifferentiated gonads; *i,* epithelium of body wall; *id,* intestinal diverticula; *cm* and *lm,* circular and longitudinal musculatures of body wall, respectively; *par,* parenchyma. (Slightly diagrammatic.)

phase of the young individual at first sexual maturity the ovaries often begin development before the sperm are discharged (Coe, 1939). The terminal portion of the female phase is therefore usually functionally hermaphroditic and self-fertilization in isolated individuals may be assumed as highly probable.

The primary functional male phase of the young worm is thus followed by successive, more or less regularly alternating, female and male phases, although the female phase, as stated above, is usually functionally hermaphroditic at the time of ovulation. Since each gonad functions but once and new gonads are constantly forming as the older ones are being emptied, the proportion of male and female gonads at different times in the same individual is highly variable. Moreover the evidence from a related species (*G. agricola*), of which a large number of living individuals have been studied, indicates that there are individual, perhaps hereditary, differences in respect to the relative dominance of male and female characteristics (Coe, 1904).

The sexual life history of a typical individual may be summarized as follows: primary male phase, with cross fertilization, followed by female hermaphroditic phase, with provisions for self-fertilization in isolated individuals. After a period of recuperation a secondary male phase begins a new sexual cycle, also with intergrading sexual phases, and this may be repeated.

The sexual condition of preserved specimens can only be determined with accuracy by examining sections throughout the entire gonadal region, for it often happens that localized groups of gonads are in a different sexual condition than those in other parts of the body. Consequently the conclusion that all except one of the specimens of this species previously examined were females may be accepted with some hesitation. It is highly probable that the three functional females in the present collection represented a temporary female phase only. No collector, so far as is known, has yet secured sufficiently young individuals to show the very first stages of sexual maturity. The two functional males in this collection were already provided with immature ovaries.

Of the 24 specimens in this collection, 2 were functional males at the time of collection, with ripe spermaries and immature ovaries, as mentioned; 3 were functionally female, with ovaries showing various early stages of ovogenesis but no spermaries; 9 were unripe sexually,

with small ovaries and undeveloped spermaries, and 10 were functional hermaphrodites with large ova and ripe or nearly ripe spermaries. The 9 sexually unripe individuals were not young but evidently represented a stage immediately following a period of sexual activity during which both ovaries and spermaries were completely emptied.

The new gonads which are constantly forming during the entire lifetime, following first sexual maturity, originate from a band of primordial sexual cells which extends throughout the gonadal region of the dorsal side of each of the nerve cords. In exceptional individuals, one or more spermaries, but not ovaries, may be formed on the ventral side of the nerve cord or even ventral to the lateral blood vessel. The young gonads are at first sexually undifferentiated and essentially ambisexual in nature. Antecedents of both types of sexual cells are present (figs. 2, 3). As the one type becomes activated, the other type gradually disappears by cytolysis.

The conditions which determine whether the young gonad is to form an ovary or a spermary are not known. In general, a spermary develops when numerous large ovaries are nearby, the spermary then forming from an undifferentiated gonad between the ovary and the nerve cord. Hence it may be suggested that unfavorable nutritive conditions may contribute to the differentiation of a spermary, since the

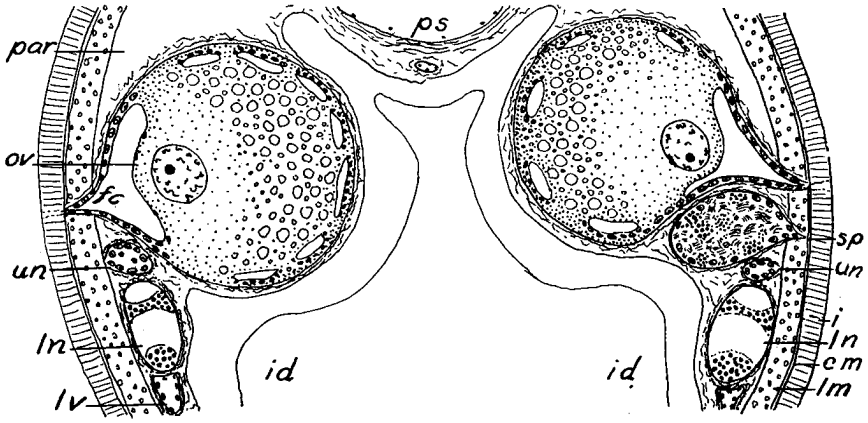

FIGURE 3.—Portion of transverse section of body of functionally hermaphroditic individual; *ov,* ripe ovaries with oviducts and fertilization chambers (*fc*); *sp,* ripe spermary; *un,* two undifferentiated gonads; *ln,* lateral nerve cord with dorsal and ventral fibrous cores; *lv,* lateral blood vessel; *ps,* proboscis sheath; *i,* epithelium of body wall; *id,* intestinal diverticula; *cm* and *lm,* circular and longitudinal musculatures of body wall, respectively; *par,* parenchyma.

rapidly growing large ova may exhaust the available nutritive material in the vicinity. In support of this hypothesis it may be mentioned that gonads in abnormal positions are always spermaries. It is also conceivable that the growing ova or their associated cells may secrete a substance of a hormonal nature to which the primary spermatogonia are chemically sensitized and thereby activated.

Ovaries are usually much more numerous than spermaries, the ratio being in some individuals upwards of a hundred to one. This may be another reason why nearly all the specimens previously collected have been classed as females. Also the spermaries come to maturity much more rapidly than do the ovaries.

Fertilization in all the terrestrial species, insofar as is known, is internal and the intimate association of two or more sexually mature individuals has been observed in other species (Dendy, 1893; Coe, 1904).

G. palaensis is presumably usually, if not invariably, oviparous, since no evidence of viviparity has been observed and an egg cluster was found attached to a specimen studied by Hett (1928). Only one species (*G. agricola*) is definitely known to be viviparous (Coe, 1904).

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