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Morphology as evidence of maturity in Isopod Crustacea, as exemplified by Mesidotea entomon (L.)[1]

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Sexual dimorphism is conspicuous in *Mesidotea entomon*. In size mature males exceed females by about 130—140 %. During development the genital papillae lengthen in relation to the copulatory stylets, pointing ventrally until maturity but thereafter caudally. Males retain their mature appearance for the rest of their lives.

In females sexual maturation culminates in the formation of a ventral brood pouch. This comprises five pairs of oostegites, which develop as outgrowths from the base of the pereiopods. After giving birth to the young, the females moult, like females of some other Isopods. The oostegites are shed and the females revert to the appearance of young immature females.

The terminology for defining maturity in male and female Isopods like *M. entomon* is discussed.

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1. Introduction

In Crustacea the stage of sexual maturation can be precisely determined by studying spermato- and ovogenesis. It can also be estimated from the morphological characters differentiating the sexes. These characters are acquired at successive moults which allow the stepwise growth of the individual. Sexual dimorphism is conspicuous in the superorder Peracarida of the subclass Malacostraca. The superorder comprises seven orders, the two largest being the Isopoda and the Amphipoda.

The present article describes the morphology of the sexual characters in the valviferous Isopod *Mesidotea entomon* (L.), taking this scavenger, a species that is common in the Baltic Sea, as a representative of the order. This aspect of the species has previously been studied by KOVALEVSKII (1884), MCCRIMMON & BRAY (1962) and GRUNER (1965). Detailed descriptions of the morphology and mode of functioning of the reproductive organs in the Isopod *Asellus aquaticus* have been published by UNWIN (1920), HAEMMERLI-BOVERI (1926) and MAERCKS (1930).

2. Material and methods

The material was obtained with dredges and baited nets (see HAAHTELA 1978) in the waters close to Tvärminne Zoological Station, SW Finland. The animals (n = 15 000) were preserved in 10 % neutral formalin or 70 % alcohol, and the characters drawn under a dissecting microscope fitted with a camera lucida. For distinguishing the sexual characters, alcohol mixed with a little glycerol (and formalin) proved a much better preservative than formalin alone.

3. Sexual characters and maturity

A. Dimorphism

Sexual dimorphism is marked in *M. entomon*. Males grow larger than females, attaining a size of 130—140 % of the latter. At Tvärminne the maximum body length for males was 78 mm, for females 57 mm (see also HAAHTELA 1975). Males have a pair of genital papillae

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on the sternum of the 7th thoracic segment. When the males mature a pair of copulatory stylets (appendix masculina) develop on the 2nd pleopods (Fig. 1A—D).

In females no structures comparable to the genital papillae develop on the 7th thoracic segment. Individuals about to breed acquire at moulting a ventral brood pouch (marsupium), the dorsal wall of which is formed of the thoracic sterna and the ventral wall of five pairs of overlapping oostegites, plate-like outgrowths from the medial side of the pereiopods (Fig. 1E—J).

B. Development of male characters

The genital papillae develop as outgrowths from the sternum. In individuals born and kept in aquaria they could not be distinguished until the body reached a length of 17 mm (n = 47). In specimens 20 mm long the genital papillae were always visible under a dissecting microscope. Thus at this size the individuals could be sexed, many even with the naked eye. No protruding appendix masculina could yet be distinguished (Fig. 1A). In the Western Canadian Arctic Ocean sexual dimorphism is apparent at a body length of about 25 mm (McCrimmon & Bray 1962). In that population *M. entomon* grows larger than in the Baltic, males attaining a maximum size of more than 90 mm, females reaching about 80 mm.

During successive moults the genital papillae lengthen, pointing ventrally. When males reach a body length of about 30 mm the copulatory stylets are clearly visible at the medial border of the endopodites of the 2nd pleopods (Fig. 1B). Both papillae and stylets lengthen without any striking morphological changes (Fig. 1C) until the latter reach the caudal margin of the pleotelson. At the same ecdysis the genital papillae also come to point caudally instead of ventrally as before (cf. also McCrimmon & Bray 1962). The vas deferens is by now visible to the naked eye, being full of sperm (Fig. 1D). At this stage the male is mature, i.e. ready to inseminate the female. At Tvärminne it has attained a body length of at least 50 mm.

I found no exception to the relation between the position of the genital papillae and the length of the copulatory stylets among some 8 000 specimens from Tvärminne and some 10 000 specimens from elsewhere. It is thus unnecessary to examine the stylets when separating mature males from immature ones.

C. Development of the female characters

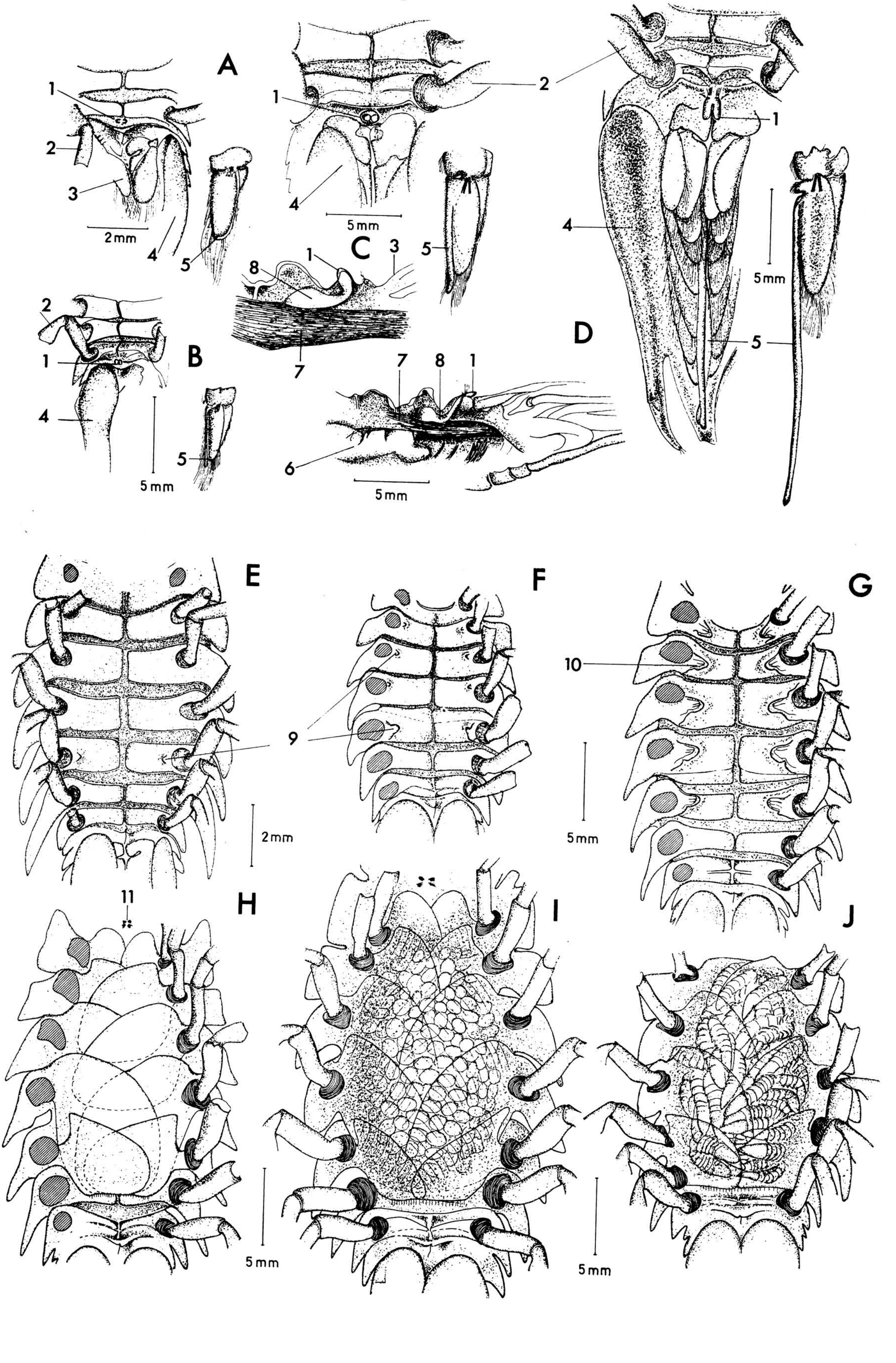
As mentioned, females have no structure comparable to the genital papillae of the male. An oviduct opens on the sternum at the base of the 5th pereiopod on each side. But the openings are not visible until the oostegites are formed (Fig. 2, see also Schöbl 1880, Maercks 1930). The first signs of the oostegites are distinguished at the base of the 5th pereiopods at a body length of about 17—20 mm, i.e. at the same size as sexual characters begin to appear in the male (Fig. 1E). As a result of the following moults similar lobes appear at the base of the 2nd — 4th pereiopods (Fig. 1F). As the female continues to mature, the lobes grow into triangular processes within which can be seen the folded oostegites (Fig. 1G). These are liberated at a moult called the parturial ecdysis (van Emden 1922, Gebelin 1939). The female is now ready to brood the embryos (Fig. 1H—J).

I have classified as mature those females which have a complete brood pouch, either empty or containing embryos, or females with the caudalmost pair of oostegites only.

4. General aspects of sexual maturity in Isopods

The definition of a mature female given above simplifies the terminology for classification, but is not quite correct. Of those Isopods which have more than one brood, some (e.g. *Idotea baltica*, Reidenbach 1971) retain their marsupium, whereas others (e.g. *Asellus aquaticus*), after liberating the young, go through a moult at which the brood pouch is shed (Unwin 1920, Haemmerli-Boveri 1926, Maercks 1930). Thereafter the female resembles a young, immature female. A new marsupium is formed as the female matures for the next brood. In *A. aquaticus* the formation of the marsupium is induced by an ovary filled with developing oocytes, but no longer by an ovary with fully ripe ovae (Haemmerli-Boveri 1926).

In Isopoda (with one known exception, see George 1972), in contrast to other Malacostraca, ecdysis, including the parturial ecdy-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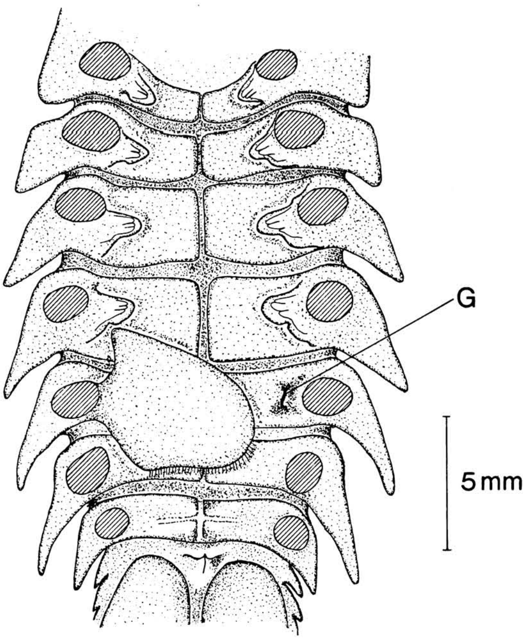

Fig. 2. Mature female (body length 39 mm). The first stage of maturity: abdomen newly moulted with a single pair of fully developed oostegites, of which the left one has been removed to show the genital opening (G). Orig.

sis, is biphasic. The abdominal portion, i.e. the cuticle of the three caudalmost pereiomeres and the abdomen, is shed first. As a result, the posteriormost pair of oostegites is formed (Fig. 2) before the others. The anterior half of the cuticle is shed after a period of hours to weeks, depending on the species concerned and the conditions.

In *M. entomon*, as in *A. aquaticus*, the brood pouch is shed. Hence females which have matured, reproduced and lost their brood pouches are classified as immature. But they have already reached maturity at least once, although they are now in an intergenerative phase of breeding.

The use of the terms "gravid" or "ovigerous" would have meant that females with empty brood pouches or with the last pair of oostegites only would be excluded from the category "mature". The former could be designated as "spent", because their ovaries were barely visible, containing only young oocytes. In my collection of thousands of *Mesidotea*, females which had a complete marsupium and ripe ovaries were extremely rare. To avoid errors, one could use the terms "parous female" or "female at the reproductive stage". I shall deal with this subject in a separate paper.

The present definition of a mature male is not identical with that of a mature female. I believe that mature males never lose their copulatory stylets, but remain morphologically mature for the rest of their lives. But Kovalevskii (1864) recorded *M. entomon* males which had emptied their sperm ducts in copulation and lost their copulatory stylets. Skorikova (1906) asked whether it is copulation that causes the stylets to break, and whether large males have to regenerate their appendices masculinae? She showed that the stylets develop from a group of cells at the base of the 2nd pleopods, their growth being independent of moults. Inagaki & Berreur-Bonnenfant (1970) showed that in *Ligia oceanica* the appendix masculina grows throughout life, even during

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Fig. 1. External sexual characters of *Mesidotea entomon*. A–D = Maturation in the male: pereion and pleon in ventral view (left), the same in median section (C and D below) and 2nd pleopod (right). E–J = Maturation in the female: pereion and pleon in ventral view.

A. Young immature male, body length 21 mm, B. Young immature male, 29 mm, C. Adult immature male, 53 mm, D. Mature male, 50 mm, E. Young immature female, 20 mm, F. Adult immature female, 31 mm: early stage of maturing, G. Adult immature female, 39 mm: late stage of maturing, H. Mature female, 39 mm: spent specimen with empty brood pouch (oostegites fully formed); could also be a newly moulted specimen immediately before the fertilized eggs enter the marsupium (rare), I. Mature female, 44 mm: gravid (ovigerous) specimen with spherical yellow embryos of stage 1, J. Mature female, 38 mm: gravid specimen with fully formed (manca stage) embryos.

1: genital papilla, 2: 7th pereiopod, 3: 1st pleopod, 4: uropod, 5: appendix masculina, 6: vas deferens, 7: longitudinal muscle, 8: ductus ejaculatorius, 9: early stage of oostegital process, 10: the same at a later stage with folded oostegites visible inside, 11: mouth. Orig.

senescence. They mention nothing about a relation to moulting or whether the organ can be regenerated. I have never observed this phenomenon.

Studies on the sexual characters of *M. entomon* have thus been published since at least 1864, so McCrimmon & Bray (1962:498) seem to have overlooked many earlier papers. In the present article most references are to older papers, just to show how long development of the sexual characters has been known in broad outline.

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