

FIG. 12. — **a-c**, *Dynomene hispida* Guérin-Ménéville, 1832, ♂ 11.6 x 9.2 mm, Somalia, Gesira, stn 12, intertidal coral (MZUF): **a**, tip of right second pleopod; **b**, inner surface of exopod and base of left second pleopod showing location of secretory tegumental gland; **c**, close up of secretory tegumental gland shown in previous figure. — **d**, *Dynomene praedator* A. Milne Edwards, 1879, ♂ 10.8 x 8.5 mm, Somalia, Gesira, stn 14, intertidal coral (MZUF): tip of right second pleopod. — **e-f**, *Dynomene pilumnoides* Alcock, 1900, ♂ 23.5 x 19.0 mm, New Caledonia, SMIB 3, stn 18, 338 m: **e**, tip of right first pleopod, note that the apical plate has been curled and deformed by processing for the SEM; **f**, tip of right second pleopod. (All pictures taken with scanning electron microscope.)

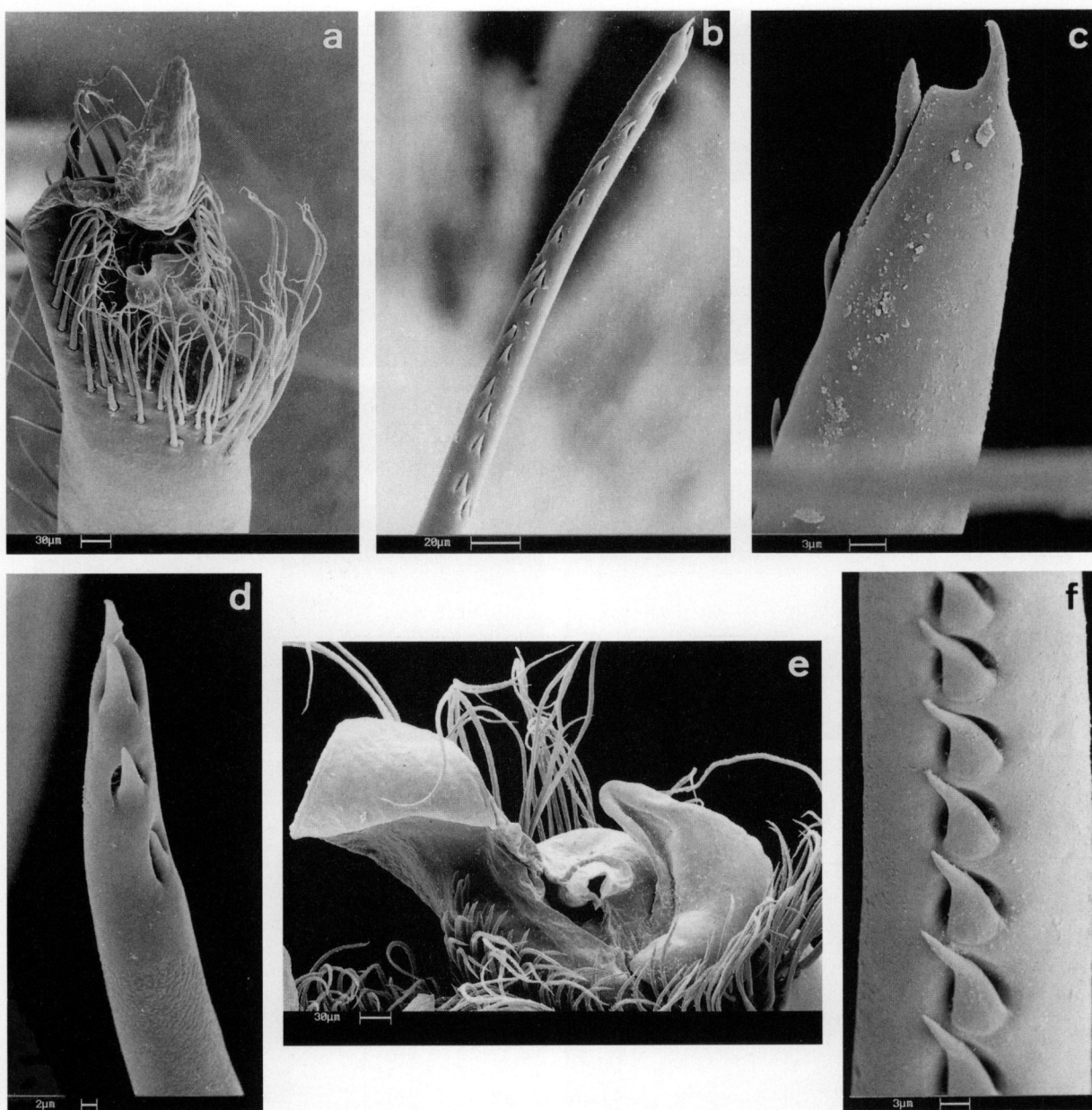


FIG. 13. — **a-b, d:** *Hirsutodynamene spinosa* (Rathbun, 1911), ♂ 19.6 x 14.5 mm, Western Australia, Exmouth Gulf, intertidal (AMS-P19118): **a**, tip of left first pleopod; **b**, right second pleopod; **d**, tip of left second pleopod. — **c, e-f:** *Metadynamene tanensis* (Yokoya, 1933), ♂ 16.5 x 15.8 mm, New Caledonia, SMIB 3, stn DW 25, 437 m: **c**, tip of second pleopod; **e**, tip of left first pleopod, note that the apical plate has been deformed by processing for the SEM; **f**, subdistal spines from second male pleopod. (All pictures taken with scanning electron microscope.)

The first male pleopod consists of two articles: the base of the proximal article forms a flattened plate, lying beside the genital opening of the coxa, while the distal article is narrower and forms a semi-rolled tube accessed by the second pleopod on the medial side. The distal article ends in an oval-shaped flattened plate, borne on the medial corner, which is surrounded by a dense fringe of long setae. The aperture for sperm delivery lies at the base of the plate, amongst the setae. The second pleopod is about as long as the first, and is borne on a sternal plate which is produced anteriorly at the corners. The basal article of the second pleopod bears an exopod and an endopod.

The proximal article of the exopod is very short while the distal article is longer, narrowing to a blunt point and has a setose lateral margin. The proximal article of the endopod is broad but very short while the distal article is much longer and narrows quickly to a needle-like shaft. When both pleopods are in their natural position, the extended coxa ("penis"), bearing the gonopore, opens between the plates formed by the proximal article of the first pleopod (above) and the flattened basal articles of the second pleopod (below). The exopod of this pleopod, lying in front of and below the genital opening, has an important role in channeling the sperm from the genital opening into the base of the first pleopod. Meanwhile, a conical swelling on the extension of the sternal plate at the base of the second pleopod, closes the posterior limit of the chamber into which the sperm is delivered. The action of the spines on the anterior surface of the needle-like part of the second pleopod may propel the spermatophores into the first pleopod where they are delivered through the setose tip into the female spermatheca. The oval medial plate on the first pleopod may help to guide the sperm into the spermatheca. Thus the exopod of the second pleopod, far from being vestigial, may be an integral part of the sperm delivery process. Near the base of the endopod of the second pleopod is the opening of a prominent tegumental gland. The role of this accessory sex gland may be to provide extra seminal fluid aiding sperm transfer. MINIGAWA (1993) has reported the presence of secretory glands in both the first and second pleopods of *Ranina ranina*. These glands normally secrete mucopolysaccharides and could also be present in the first male pleopod of dynomenids, but to establish this would require sectioning and staining. It is interesting to note that in *Chionoecetes opilio* (Majidae) rosette type accessory sex glands only appear in mature crabs and are concentrated in the proximal region of the first pleopod, with ducts leading to the ejaculatory canal (BENNINGER *et al.*, 1995).

TABLE 1. — Morphological variation in male second pleopods.

	Terminal spines	Subterminal spines	Direction of subterminal spines
<i>Dynomene hispida</i>	2 straight spines	5 arranged sinuously over 180°, none overlapping	Apical
<i>Dynomene praedator</i>	3 straight spines	5 arranged sinuously over 90°, none overlapping	Apical but with tips curved laterally
<i>Dynomene filholi</i>	1 straight spine	10 arranged sinuously over 90°, none overlapping	Apical
<i>Dynomene pilumnoides</i>	2 curved spines	15 arranged sinuously over 180°, none overlapping	Apical
<i>Hirsutodynomene spinosa</i>	2 straight spines	16 curving from anterior to posterior surface and back again, some overlapping	Apical
<i>Hirsutodynomene ursula</i>	2 curved spines	20 curving from anterior to posterior surface and back again, some overlapping	Apical
<i>Metadynomene tanensis</i>	2 curved spines	24 along anterior surface of pleopod, none overlapping	Apical but with tips curved laterally
<i>Paradynomene tuberculata</i>	2 straight spines	14 along anterior surface of pleopod, none overlapping	Apical

In most groups of the Brachyura the male pleopods show wide variation and differences between species which have proved taxonomically valuable. However there is little variation in structure of the first pleopods of different dynomenid species. Under the normal light microscope the second male pleopods simply appear to be needle-like, but examination at higher magnifications, using the scanning electron microscope, reveals some fine detail and variation in structure. The fine structure of the second pleopods of eight out of the thirteen species (representing four of the genera) have been examined (see Table 1). The basic plan for dynomenid pleopods consists of a shaft bearing a row of tiny inset spines running along the length and ending with two or three

terminal spines. The main sources of variation are the number of subterminal spines, their disposition to each other, and their direction. The number of spines ranges from 5 to 24, which can be arranged in a straight line or variously curving around the shaft axis, and in some cases the spines overlap so that two adjacent spines can be side by side. In most cases the spines are directed apically but in two species (*Dynomene praedator* and *Metadynomene tanensis*) they are curved towards one side. The differences between the genera are not dramatic: in *Dynomene* there tend to be fewer spines (usually directed apically) than in the other genera, whereas in *Metadynomene* there are a large number of quite curved spines. In the cases of two pairs of species which, for other reasons, are believed to be closely related, viz. *Dynomene filholi* - *D. pilumnoides*, and *Hirsutodynomene spinosa* - *H. ursula*, the only difference between them is in the number of subterminal spines. The species of *Hirsutodynomene* have a unique arrangement of spines and it is the only genus in which spines overlap. In spite of its dromiid-like features, *Paradynomene tuberculata* has pleopods which are typical of dynomenids (see Discussion under this species). The second pleopods of two dromiids, *Stindromia lamellata* (Ortmann, 1894) and *Epigodromia gilesii* (Alcock, 1899), examined in the same way, show no evidence of ornamentation. The distal part of the second pleopod of *Dicranodromia felderi* has minute scattered spinules (MARTIN, 1990, his fig. 3g). As far as is presently known, the dynomenids are the only dromiaceans with ornamented second male pleopods.

The tube (i.e. "penis") carrying sperm to the base of the pleopods is well developed in podotreme crabs. Dromiid males have a long soft penis extending from the coxal article but in dynomenids this is absent. Instead the corner of the coxal article itself is extended to carry the sperm to the pleopods (see Fig. 14 f). Thus the dynomenids could be said to have a calcified "penis" and they share this character with the homolodromiids (GUINOT, 1995), although the shape is a little different. Using the implied vertebrate analogy, the name "penis" is not really very accurate since it is not this structure which is responsible for introducing sperm into the female. The so-called "penis" of all crabs is analogous to the vas deferens and should perhaps be called the "sperm duct". The first male pleopod should be referred to as the pleopod or "penis".

Male dynomenids have rudimentary pleopods on segments three to five. In the species that have been examined closely, the last three pairs of pleopods are biramous. Only *Dynomene praedator* has uniramous pleopods. The exopod is usually longer and connected to the basal article by a joint. However, the other article is not jointed and appears to simply be an extension of the basal article. If it is regarded as representing the endopod, then we must assume that the joint has been lost as a result of fusion. In *Metadynomene tanensis* both articles are about the same length and fused to the base. The presence of rudimentary male pleopods is also found in homolodromiids and some dromiids. GUINOT (1995) recorded rudimentary pleopods in both *Homolodromia* A. Milne Edwards, 1880, and *Dicranodromia* A. Milne Edwards, 1880 where they varied in size between species, and sometimes asymmetrically on each segment, but in all cases they were uniramous. Dromiids with rudimentary male pleopods include *Sphaerodromia* Alcock, 1899, *Exodromidia* Stebbing, 1905, and some species of *Dromia* Weber, 1795 where they are symmetrical and uniramous (McLAY, 1993). Retention of these pleopods in males must be regarded as a plesiomorphic character.

The first female pleopod is vestigial and consists of a proximal calcified basal article, attached to the sternum, and a distal article which is soft and flexible, bearing long marginal setae and narrowing to a blunt tip. This pleopod does not carry eggs and when the abdomen is closed it overlies the sternal suture 7/8 which harbours the spermatheca. Their proximity to the spermathecae may mean that these pleopods have some role in ensuring that eggs from the coxal gonopore, and sperm from the spermathecae, come into contact with each other. Since possession of vestigial first pleopods by females is a character of all podotremes, a similar role could be hypothesized for these pleopods in other families where there is close proximity of spermathecae, gonopores and first pleopods. This could be true in primitive dromiids like *Sphaerodromia* and *Eodromia* for example, but in more derived dromiids the spermathecae are moved to a much more anterior position in front of the gonopores, making this liaison unlikely. The other four pleopods in female dynomenids are biramous, the basal article is very reduced, and both the exopod and endopod consist of six articles. The endopods have long filiform setae for egg attachment while the exopods have dense fine setae (as on the first pleopod) along the margins for brood protection.