FIG. 9. — **a-b**, *Hirsutodynomene ursula* (Stimpson, 1860), ♀ ovig. 15.0 x 12.2 mm, Ecuador, La Plata Id, *"Askoy"*, stn 80 (LACM): **a**, dactyl spines from right fifth pereopod; **b**, propodal spines from right fifth pereopod. — **c**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♀ 23.8 x 17.8 mm, Cocos Keeling Ids, 0-28 m (WAM 723-89): dactyl spines from left fifth pereopod. — **d**, *Metadynomene tanensis* (Yokoya, 1933), ♂ 16.5 x 15.8 mm, New Caledonia, SMIB 3, stn DW 25, 437m: lateral view of tip of left fifth pereopod. — **e**, *Metadynomene tanensis* (Yokoya, 1933), ♀ 16.2 x 15.3 mm, New Caledonia, SMIB 8, stn DW 198, 414-430 m: propodal spines from right fifth pereopod. — **f**, *Acanthodromia erinacea* A. Milne Edwards, 1880, ♀ 9.5 x 11.5 mm, Yucatan, *"Albatross"*, stn 2354, 238 m (USNM 9547): dactyl from right fifth pereopod with marginal spines. (All pictures taken with scanning electron microscope.)
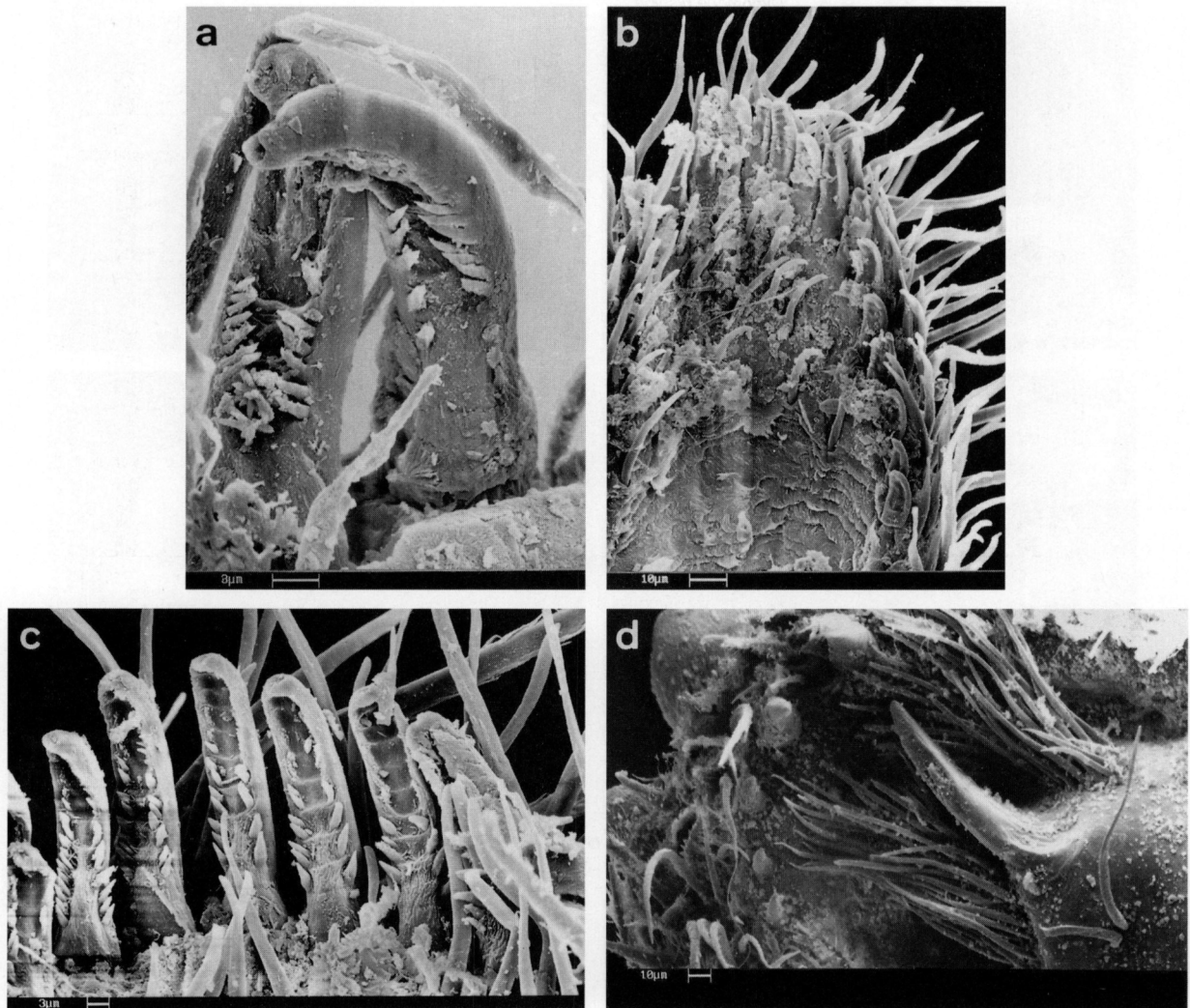
FIG. 10. — **a**, *Acanthodromia erinacea* A. Milne Edwards, 1880, ♀ 9.5 x 11.5 mm, Yucatan, *"Albatross"*, stn 2354, 238 m (USNM 9547): propodal spines from right fifth pereopod. — **b-c**, *Paradynomene tuberculata* Sakai, 1963, ♀ 21.5 x 21.2 mm, Loyalty Ids, MUSORSTOM 6, stn DW 406, 373 m (MNHN-B 25249): **b**, dactyl from right fifth pereopod with marginal spines; **c**, propodal spines from right fifth pereopod. — **d**, *Paradynomene tuberculata* Sakai, 1963, ♂ 22.0 x 22.8 mm, New Caledonia, SMIB 3, stn 14, 246 m: lateral view of tip of left fifth pereopod. (All pictures taken with scanning electron microscope.)

Comparison of the last two pereopods for males of all species shows that on average the fifth pereopod is only 31.2% of the length of the fourth pereopod (Fig. 11). Comparing individual articles between these limbs shows that there are no differences for most articles except for the coxae and dactyli. On average the coxae of the last limb occupy 19.6% of the length but on the preceding leg it is only 10.8%. For the dactyli the reverse is true with the dactyli of the fourth pereopods occupying 17.0% while those of the fifth only occupy 5.3%. Thus except for the articles at each end of the limb the fifth pereopod is just a scaled down version of the preceding limb. The coxa carries the male gonopore, and perhaps cannot be reduced by the same amount as the whole limb and still be functional, while the dactyl is part of a novel subchelate structure. The last pereopod of dynomenids is not reduced as much as found in the cymonomid *Elassopodus stellatus* Tavares, 1993, where both of the last two pairs of pereopods are reduced to tiny stumps, almost concealed by the abdominal segments. It seems that there is scope for a lot of redundancy in the posterior pereopods of decapods.
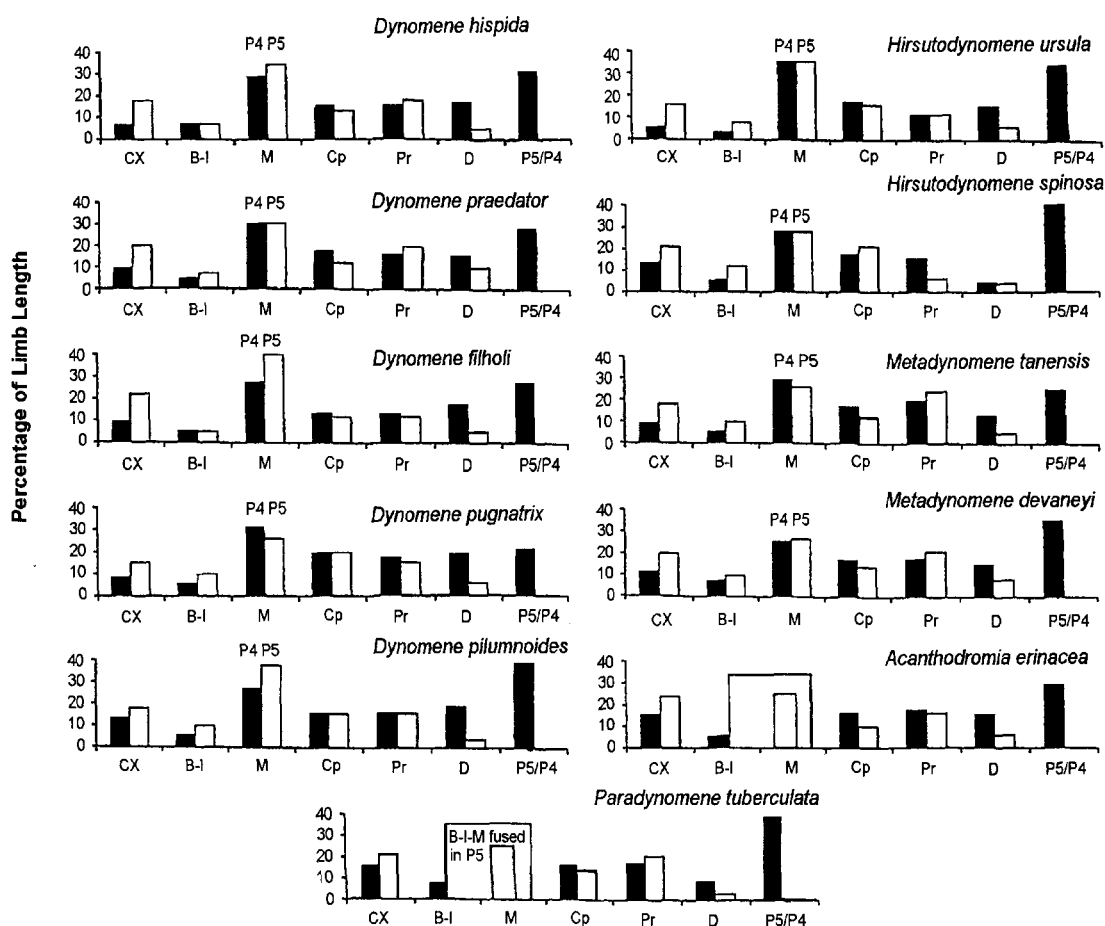
FIG. 11. — Relative size of articles of the last two pereopods of *Dynomene hispida, D. praedator, D. filholi, D. pugnatrix, D. pilumnoides, Hirsutodynomene ursula, H. spinosa, Metadynomene tanensis, M. devaneyi, Acanthodromia erinacea* and *Paradynomene tuberculata*. From left to right, the proportion of total limb length (fourth pereopod followed by fifth pereopod) is shown for coxa (Cx), basis-ischium (B-I), merus (M), carpus (Cp), propodus (Pr), dactyl (D), and the ratio of length of fifth to fourth pereopod (P5 ♀ P4). Note that in *A. erinacea* and *P. tuberculata* the basis-ischium and merus are fused. All measurements made on males except for *D. pilumnoides, D. pugnatrix,* and *A. erinacea.*

The last pereopod is subchelate. BOUVIER (1896) stated that *Acanthodromia erinacea* had a fifth pereopod of the same form as *Homolodromia paradoxa* but their resemblance is only superficial and closer examination shows that they are in fact very different. The subchelate mechanism in dynomenids involves the dactyl being opposed to a distal extension of the propodus which bears toothed or untoothed spines. The structure of the subchelate mechanism of the fifth leg is sexually dimorphic. The propodal extension is better developed in females (resembling the condition found in *Homolodromia*, thus accounting for BOUVIER's observation) than it is in males (resembling the condition found in *Dicranodromia*, see GUINOT, 1995, her fig. 3 A-H, for details). The most obvious difference is in the dactyl: in males the dactyl has the conventional claw shape but in females the dactyl is modified as a flattened plate bearing 5-16 typically untoothed spines. In females there is usually more spines on the dactyl than on the propodus. These spines are hooked and only have a few small proximal teeth or none at all. The surface of the dactyl spines is usually concave and crenulate. Other differences between male and female dynomenids are that in females of all species the propodal spines bear small teeth, but these are only found in males of *D. hispida, D. praedator* and in both species of *Hirsutodynomene*. The number of propodal spines also differs: while both sexes of *Dynomene* have a similar number (approx. 5) of spines, in *Metadynomene,*

Hirsutodynomene, and *Paradynomene* the females have a significantly larger number (8-16) of spines. In summary we find that in females there are opposable rows of usually toothed spines whereas in males the usually untoothed propodal spines are opposed by a claw-like dactyl.

In some males (*Dynomene filholi*, *Metadynomene tanensis*, and *Paradynomene tuberculata*) a dorsal or lateral spine is found on the claw-like dactyl (see Figs 7d, 8d). No dactyl spine is found in males of *Hirsutodynomene* and the condition in *Acanthodromia* is unknown. This spine resembles a similar spine found on the dactyli of the last pereopods of some primitive members of the Dromiidae (*Tunedromia* McLay, 1993, *Dromidiopsis* Borradaile, 1900, and *Lauridromia* McLay, 1993) where it helps the animal to grasp and hold its piece of sponge camouflage. Both sexes of these dromiid genera have the spine but it is only present in male dynomenids. In these dromiids the spine projects from the surface of the dactyl, but in the dynomenids the spine lies in a depression on the surface and cannot be functional. It seems to be an apomorphic vestigial structure which indicates a close relationship with the dromiids and suggests that the last pereopod of dynomenids may be derived from a camouflage-carrying limb.

What is the function of the reduced last pereopods? STIMPSON (1860) stated that ".....they fill, apparently no office in the economy of the animal, except when in place, they fill up neatly the chink between the carapax and the stouter walking feet." STIMPSON clearly believed that this limb is redundant. The small size and lack of mobility of the fifth legs suggest that the limb is vestigial. Reduction has proceeded furthest in *Acanthodromia* and *Paradynomene* where we find the greatest number of fused articles. It would seem that it only has a function in male dynomenids because it carries the gonopore in its coxal article. The subchelate tip does not appear to be functional because the dactyl is largely immovable. Therefore the subchelate tip must represent some past rather than present role. The sexual dimorphism makes it difficult to imagine what this role might have been and why it needed to be different in the two sexes. The fifth pereopod is sexually dimorphic in some of the Scyllaridae (HOLTHUIS, 1985), Thaumastochelidae (HOLTHUIS, 1974) and Palinuridae where the females have subchelate limbs which are used to clean the abdomen and brood. STEWART *et al.* (1997) suggest that the subchelate fifth pereopods in female *Ibacus peronii* are involved in the fertilization and manipulation of eggs, as they are attached to the pleopods, and subsequently used to clean and groom the egg mass. However the structure of the tip of the limb consists of a well developed dactyl opposed to a strong, simple, spine-like propodal extension. In dynomenids the structures on the dactyl and propodus are much more elaborate. Among the Homolidae, GUINOT and RICHER DE FORGES (1995: 307, 469) reported that the merus of the last pereopod is shorter in females than in males of all species of *Homologenus*.

The dynomenid female limb has a structure which resembles some kind of cleaning or grooming appendage which is typical of many anomolans but there the resemblance ends because the structure of anomolan fifth pereopods is quite different (BAUER, 1989; POHLE, 1989). Anomolan fifth pereopods have a well developed subchelate tip, not sexually dimorphic, and can be inserted into the branchial chamber to clean the gills, see for e.g. the Porcellanidae (FLEISCHER *et al.*, 1992), but dynomenids have a closely fitting carapace which would deny these limbs access to the gills. The dynomenid spine structure is somewhat similar to the propodal setae found on the fifth pereopods of carideans such as *Palaemon* and *Betaeus* which are used for body grooming (BAUER, 1989). Furthermore similar setae are found in axiid thalassinideans, astacid and cambarid crayfish, and nephropid lobsters (BAUER, 1981). In none of these cases are the limbs sexually dimorphic. BAUER (1989: 61) points out that no grooming fifth pereopod has ever been described for a brachyuran but a former body or gill grooming function seems the most likely role for the fifth pereopod in dynomenids. It should be noted that one other feature normally accompanies decapod cleaning fifth pereopods: in order for these limbs to be fully functional, and access all the areas in need of cleaning, the sternite of this limb must be mobile and not attached to the preceding sternite. Once the last sternite is attached, as it is in the Brachyura, the last pereopods can no longer perform a cleaning function.

FEMALE STERNAL SUTURES

Apart from the thoracic sternal suture 7/8 in females (see below) which is always evident, several other sutures mark the boundaries of thoracic sterna in some genera. In *Metadynomene* sutures 3/4, 4/5 (faintly), and 5/6 (very strong) are visible. *Hirsutodynomene* is the same as the previous genus except that the suture 5/6 is not apparent.

In *Paradynomene*, *Acanthodromia* and most species of *Dynomene* (suture 4/5 is faint in *D. hispida*) only the suture 3/4 is evident. Sternum 3 separates the bases of the third maxillipeds and its separation from sternum 4 is always deeply marked. The suture 4/5 is only faintly evident in a few species, while suture 5/6 is strongly marked by a semi-transparent band which only occurs in *Metadynomene*. The median line, where sutures from each side meet, is not apparent in any dynomenids. GUINOT (1979: 80) recognized four categories of thoracic sterna based on the interruption of sutures 4 to 7. Unlike sternitreme crabs, most sternal sutures are absent in dynomenids, so they do not conform to GUINOT's classification. If we regard the absence of many sternal sutures as representing the apomorphic condition, then dynomenids must be regarded as having very derived sterna. In the Homolodromiidae only the 7/8 suture and traces of 6/7 are visible (GUINOT, 1995: 174). In the Dromiidae the structure of the sternum is very much distorted by the more anterior position of the spermathecae with the result that the seventh and eighth sterna occupy much of the ventral surface of the cephalothorax. The sternum of dromiids represents the derived condition with both homolodromiids and dynomenids retaining the plesiomorphic condition where the suture is very short.

Female sternal structure 7/8: The sternal spermathecae are separate from the gonopores and lie at the boundary between the seventh and eighth sternites. The length of the sternal sutures, which mark the suture between these sternites, depends upon the proximity of the spermatheca to the gonopore. In dromiids the length of the sternal sutures 7/8 is variable: the spermatheca can lie between the bases of the first pereopod, requiring very long sternal sutures 7/8, or between the bases of the fourth pereopods, requiring only very short sternal sutures 7/8. Thus the spermathecae can be anterior or posterior to the female gonopore. Also in dromiids these sutures can end apart or together. In dynomenids the sternal sutures 7/8 are always short, usually ending just below or slightly behind the female gonopore on the third pereopod, and they always terminate apart. The sutures lie very close to the coxae of the adjacent pereopods. In *Dynomene* and *Hirsutodynomene* the sutures end on low tubercles. In *Metadynomene* the sutures lie in a shallow, V-shaped groove, below a prominent parallel medial ridge, concealed by a dense layer of long soft setae originating from the adjacent coxa of the fourth pereopod. In *Acanthodromia* the sutures end beneath a curved over-hanging lip without a setal covering. In *Paradynomene* the sutures are almost completely covered by the coxae and setae of the fourth pereopod. Close proximity of the spermathecae to the female gonopore ensures fertilization of the eggs when they are laid. In this respect dynomenids are very similar to the homolodromiids (GUINOT, 1995).

A feature of the sternal sutures 7/8 of dromiids is that in mature females they are often covered with a dark gelatinous layer which closes the spermathecae. This substance is probably produced by the male and could act as a sperm plug, preventing other males from inseminating the female. In homolodromiids GUINOT (1995) reported that many females had the broken off tips of male second pleopods blocking the entrance to the spermathecae and perhaps functioning as a different kind of sperm plug. In all the dynomenid females I have examined, I have never seen sperm plugs of either of the above kinds. This may imply that dynomenids have a mating strategy different from dromiids and homolodromiids.

ABDOMEN
Dynomenids have an abdomen of six free segments with no segments fused. Segments increase in length and breadth posteriorly with margins fringed with long setae. The telson is much wider than long, with the anterior margin angled to accommodate the uropods and the posterior margin broadly rounded. Compared to other dromiaceans, the uropods are well developed, visible externally and often completely excluding the penultimate segment from reaching the lateral margin, especially in females. The abdomen and pleopods provide a protected chamber where the eggs are incubated until they hatch. No dynomenids provide parental care for their larvae.

Unlike the Dromiidae, most of the Dynomenidae have no effective abdominal locking mechanism and the abdomen in both males and females is simply curled under the cephalothorax and held loosely in position by its own musculature. There are differences between dynomenid genera in the nature of abdomen-restricting structures. In *Dynomene* males and immature females there is a small rounded sternal tubercle at the lateral margins, below the articulation of the first walking legs, and adjacent to the uropods when the abdomen is in its natural position (see also GUINOT, 1979: 125-126). These tubercles simply restrict sideways movement of the abdomen and they

disappear in mature females where the abdomen occupies all the ventral surface. The same arrangement as in *Dynomene* is found in *Hirsutodynomene*. However *Metadynomene* has small spines (can be bifid) or ridges on the coxae of the second and third pereopods, adjacent to the margins of the telson and penultimate abdominal segments, which restrict lateral movement. In *Paradynomene* small rounded granules cover the coxal articles of the pereopods, leaving the surface of the abdominal cavity smooth. The margins of the abdomen are neatly surrounded by many granules (several on each coxa) which restrict sideways movement. In *Acanthodromia* the abdomen of mature females is confined between tuberculate coxal projections on pereopods and under projections on the coxae of the third maxillipeds. Use of the pereopod coxae to restrain the abdomen resembles the situation found amongst many dromiids and use of maxilliped spines resembles the condition found in the Poupiniidae. Clearly, the abdomen locking mechanism of *Acanthodromia* is very different from that found in the other dynomenid genera. There is a gradation from abdomen maintaining mechanisms as found in *Dynomene* + *Hirsutodynomene* where sternal tubercles are used, through *Metadynomene*, using coxal ridges or spines on the second and third pereopods, and *Paradynomene* using coxal granules, to the abdominal locking mechanism found in *Acanthodromia* which uses well developed coxal projections on the third maxillipeds and first three pereopods. (See also below under Uropods.)

Observations of live *Dynomene praedator* show that the abdomen is not always held closely against the sternum and when the crab moves, it often makes "flicking" movements similar to those seen in for e.g. porcellanids. By themselves these abdominal movements would tend to propel the crab backwards but they occur when the crab moves both forwards and backwards. Locomotion is achieved using the three pairs of walking legs. The motor pattern causing abdominal movements is probably a vestige of the past when the abdomen was involved in locomotion.

In mature females the abdomen covers the entire sternum and coxae of all pereopods with the telson covering the proximal half of the third maxillipeds. In males the abdomen is not quite so broad and the telson only extends as far as the bases of the third maxillipeds. While mature dynomenid females are clearly recognizable by their wide abdomens, immature female and male abdomens are not greatly different. Therefore abdomen width is not as reliable a method of sexing specimens as it is in eubrachyurans. The relative size of *Metadynomene tanensis* male and female abdomens is shown in Fig. 28b. In this species females seem to have a pubertal moult at a CW of around 11.0 mm and males have a pubertal moult around 15.0 mm. In both sexes the pubertal moult is not terminal.

In order to ensure sperm transfer, the female abdomen must be flexible enough to expose the posteriorly placed spermathecae. Males only need short pleopods, but because their abdomen must fit inside that of the female, it must be relatively short and/or flexible, so that it can be folded or curled to allow the pleopods to come into contact with the spermathecal openings and deposit the sperm.

PLEOPODS (Figs 12 a-f, 13 a-f, 14 a-e)

Dynomenid crabs are unusual in having five pairs of pleopods in both sexes. The first pair of female pleopods are uniramous and reduced in length, and do not carry eggs, while the remainder are normal biramous egg-bearing limbs. In males the first pair are a semi-rolled tube, with an oval apical plate surrounded by setae, while the second pair are needle-like with an exopod on the basis, and the last three pairs of pleopods are rudimentary.

Dynomenid male pleopods have been previously illustrated as follows:

Dynomene hispida : PEYROT-CLAUSADE & SERÈNE (1976, text-fig. 1, pl. 5, A-B, F), GUINOT (1979, fig. 60 e-f), DAI *et al.* (1986, fig. 11, 2-3), and DAI & YANG (1991, fig. 11, 2-3). As *D. granulobata*, DAI, YANG & LAN (1981, figs 13-14), DAI *et al.* (1986, fig. 12, 1-2), and DAI & YANG (1991, fig. 12, 1-2).

D. praedator : CHEN (1979, fig. 1, 5-6) (as *D. sinensis*). And DAI, YANG & LAN (1981, figs 8-9), DAI *et al.* (1986, fig. 12, 3-4), DAI & YANG (1991, fig. 12, 3-4) (as *D. tenuilobata*).

D. filholi : MONOD (1956, figs 84-88).

D. pilumnoides : STEBBING (1921, pl. 14) (as *Maxillothrix actaeiformis*).

Metadynomene devaneyi: TAKEDA (1977, text-fig. 1 A-C).

In *M. tanensis*, some of the sexually mature females have their first pair of pleopods developed as in males rather than being vestigial, but in all other respects they appear to be normal (see Discussion under this species).