

FIG. 3. — **a**, *Dynamene hispida* Guérin-Méneville, 1832, ♂ 11.6 x 9.2 mm, Somalia, Gesira, stn 12, intertidal coral (MZUF): setae on right posterolateral corner of carapace. — **b**, *Dynamene praedator* A. Milne Edwards, 1879, ♂ 9.6 x 7.8 mm, Somalia, Gesira, stn 19, intertidal coral: setae on left posterolateral corner of carapace. — **c-d**, *Dynamene pilumnoides* Alcock, 1900, ♀ 12.8 x 10.3 mm, New Caledonia, VOLSMAR, stn DW 7, 400 m: **c**, short setae from left posterolateral corner of carapace; **d**, setules on long setae from left posterolateral corner of carapace. — **e**, *Dynamene filholi* Bouvier, 1894, ♀ 10.0 x 8.7 mm, Cape Verde Id, CANCAP, stn 7.125, 85-130 m: short setae from right posterolateral corner of carapace. — **f**, *Hirsutodynamene spinosa* (Rathbun, 1911), ♂ 14.2 x 10.8 mm, Cocos Keeling Ids, 0-37 m (WAM 139-94): short setae from left posterolateral corner of carapace. (All pictures taken with scanning electron microscope.)

Compared to homolodromiids the dynomenids have a well developed and calcified carapace on which the lateral margins are well defined and grooves are often evident. In this respect their carapace is very similar to that found amongst dromiids and this overlap has led to difficulties in assigning fossil material to the correct family.

SETAE (Figs 3 a-f, 4 a-f)

All dynomenids have setae of two sizes: short and long. Most short setae are at least slightly curved near the tip, but in some species they are bent almost at right angles. The long setae can also be curved and assume various shapes, but they are never consistently bent at right angles. The short setae may be sparse or dense enough to completely obscure the body surface. In some species the long setae are arranged in clumps or tufts on the carapace and these may be associated with irregularities in the carapace surface. The shafts of both short and long setae can be divided into four regions: a bare basal region without setules, a region of small sparse setules, a region of larger dense setules, and finally a bare apical region. The percentage of the length occupied by each region varies between species. In *Dynomene hispida*, *D. praedator*, and *Metadynomene tanensis* there are no differences, between short and long setae, in the proportions of the shaft occupied by the four regions. Also the short setae are not bent at right angles and the long setae are not arranged in clumps on the carapace. Clumps of long carapace setae are found in *Dynomene filholi*, *D. pilumnoides*, *Hirsutodynomene spinosa*, *H. ursula*, and *Paradynomene tuberculata*. The short setae are bent in *D. pilumnoides*, and *H. spinosa* (but not in *H. ursula*). The setae of most dynomenids have varying arrangements and sizes of setules along their length, but very unusual setae are found on *D. filholi* and *Paradynomene tuberculata* where there is a marked difference between the structure of short and long setae. The proximal 60% of short setae in *D. filholi* have the normal radiating setules arranged around the shaft, but this is followed by a brush border of long fine setules along only one side of the shaft. In *P. tuberculata* the proximal 40% is bare but the rest of the shaft is feather-like, bearing a row of fine setules on opposite sides. None of the other dynomenids have setae which even closely resemble these aberrant forms, although DE MAN (1889) reported "Federhaar" (feather-like setae) in *D. pugnatrix*. The reasons for these differences are not clear. The setal characteristics are useful in the recognition of such genera as *Hirsutodynomene* and *Metadynomene*, but in *Dynomene* the setal differences are much greater and hence are useful in recognizing the different species. The setae of the dromiid *Dromia personata* (Linnaeus, 1758) bear a close resemblance to many of the dynomenid setae (see JACQUES, 1989, her Fig. 3. 4).

ANTENNULES, ANTENNAE AND ORBITS

The antennules are composed of three articles plus flagellae. The first article is largest, about as long as the greatest width and trapezoidal, remaining articles are much smaller, and the third article is longer than wide. Antennules are very active during feeding. First article of antenna is wider than long, usually beaked medially enclosing the urinary opening, second article is longer than wide bearing a fused exopod, third and fourth articles together are as long as exopod, terminating in a flagellum whose length can be from 23% to 60% of carapace width. The beaked first antennal article is a feature shared with members of the Homolodromiidae and Dromiidae. However, in *Acanthodromia* the first antennal article is not beak-shaped and the urinary opening is on the medial margin, concealed against the first article of the antennule.

The orbits of dynomenids are well formed and separated by the epistome which is joined to the rostrum of the carapace. In dorsal view orbits are obliquely arranged and clearly exposed dorsally. There are well developed supra- and suborbital margins, usually armed with spines or tubercles, which form a well defined cavity which can accommodate the whole of the eyestalk when it is folded away. The gap between the suborbital margin and the epistome is filled by the first article of the antennule and the first two articles of the antenna, thereby covering the base of the eye stalk. The second article of the antennule articulates at a right angle so that the rest of the appendage is folded horizontally above the eye stalk and under the supraorbital border. In a similar way, the fourth article of the antenna is angled so that the flagellum is directed laterally. However, the antennal flagellum is too long to allow the appendage to be entirely folded into the orbit.

MOUTHPARTS

During this study attention has only been paid to the third maxillipeds of dynomenids. Other authors have dealt more or less with all six appendages: see BOUVIER (1896, fig. 23) and A. MILNE EDWARDS & BOUVIER

(1900, pl. VII, figs 1-18) for mouthparts of *Dynomene filholi*, and STEBBING (1921, pl. 14) for mouthparts of *D. pilumnoides* (as *Maxillothrix actaeiformis*). Note that on STEBBING's figure of the third maxilliped the epipod is missing. The maxillae and maxillipeds of *Acanthodromia erinacea* were figured by A. MILNE EDWARDS and BOUVIER (1902, pl. III, figs 6-10). Note that their third maxilliped is also shown without an epipod. ORTMANN (1892, pl. 26, fig. 3i) figured the second maxilliped of *D. praedator* and CHEN (1979, figs 1, 4) figured the external features of the third maxilliped (as *D. sinensis*). The epipods of the maxillipeds have an important role in gill cleaning (see below).

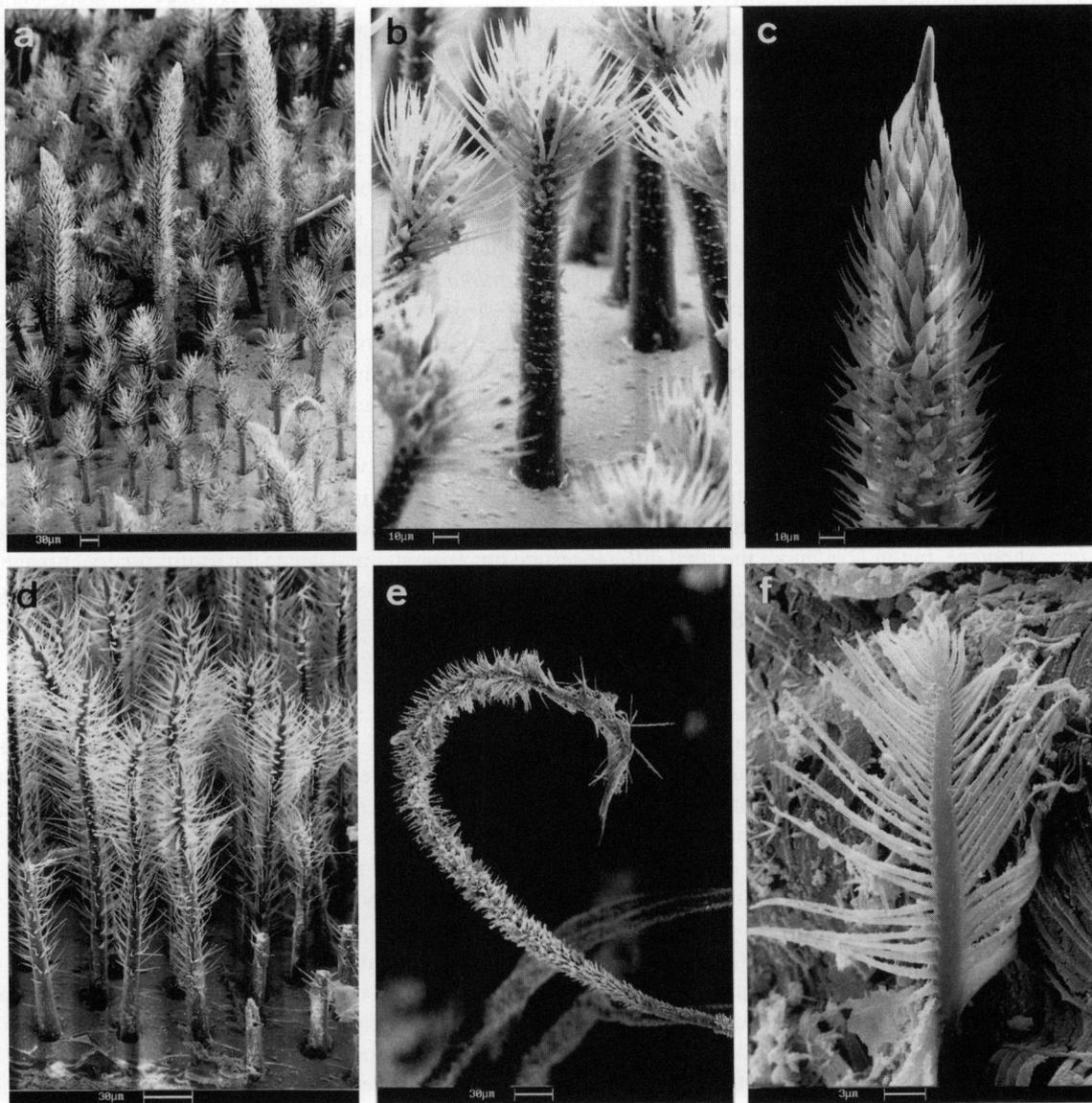


FIG. 4. — **a-c**, *Hirsutodynomene ursula* (Stimpson, 1860), ♂ 13.4 x 10.3 mm, Mexico, Espiritu Santo Id, "Velero", stn 638-37, intertidal: **a**, long and short setae from left posterolateral corner of carapace; **b**, short setae from left posterolateral corner of carapace; **c**, setules on tip of long setae from left posterolateral corner of carapace. — **d**, *Metadynomene tanensis* (Yokoya, 1933), ♂ 16.5 x 15.8 mm, New Caledonia, SMIB 3, stn DW 25, 437 m: setae from right posterolateral corner of carapace. — **e-f**, *Paradynomene tuberculata* Sakai, 1963, ♂ 22.0 x 22.8 mm, New Caledonia, SMIB 3, stn 14, 246 m: **e**, long setae from right posterolateral corner of carapace; **f**, short setae from right posterolateral corner of carapace. (All pictures taken with scanning electron microscope.)

In dynomenids the third maxillipeds are operculiform, the coxal articles are separated by tip of sternum, the basis-ischial articles are fused but with joint still visible, the medial margins of ischia are parallel (or slightly diverging) and close together, the meral article is square or oblong and smaller than the preceding article, followed by a three-articled setose palp, consisting of carpus, propodus and dactyl which is folded along medial margin of merus. The palp grasps food material from the chelipeds passing it on to other mouthparts.

Most dynomenids have a true crista dentata - a crest-like row of corneous teeth on the inner margin of the ischium of the third maxilliped. The crista dentata is found in palinurids, nephropids, astacids, thalassinids, some anomolans, and some podotremes. Working in a coordinated way with the mandibles it is used to grasp and tear food items before they enter the mouth. In dynomenids the teeth are usually of even size, but in some species they tend to increase in size distally. However, none of them have teeth such as is found in some thalassinids and astacids where the crest is curved and terminates in a large hooked tooth. The number of teeth varies from 5-8 in species of *Dynomene* and *Hirsutodynomene*, to 12-13 in *Metadynomene* and *Paradynomene*. A crista dentata is absent in *Acanthodromia*. Amongst the podotreme crabs the crista dentata is present in homolodromiids, dromiids and homolids as well as the dynomenids. The dromiids and dynomenids are the only decapods which have operculiform third maxillipeds with a crista dentata. All other decapods with a crista dentata have pediform third maxillipeds. The true crista dentata is absent from the other brachyurans.

GILLS AND EPIPODS (Figs 5 a-f, 6 a-f, 7 a-b)

In his classic work on the origin of crabs, BOUVIER (1896) compared the gills of *Dynomene filholi* and *Acanthodromia erinacea* with those of *Homarus vulgaris*. Although there were some errors made in the interpretation of the gills (see below under the treatment of these species), the branchial formula was given as 20 gills + 7 epipodites on each side. Subsequently this branchial formula has been assumed to be typical of all dynomenids. The general features of the number of gills and epipods in dynomenids are illustrated by considering the arrangement found in the type species of the family. In *Dynomene hispida* there are 19 gills and 7 epipods present on each side. There are six podobranchs, ten arthrobranchs and three pleurobranchs. The first thoracic segment has no gills and there is only the epipod of the first maxilliped extending into the anterior end of the branchial chamber. The second segment has a single arthrobranch and a podobranch on the epipod of the second maxilliped which lies anterior to the arthrobranch. The third segment has the same number of gills as the second but the epipod of the third maxilliped lies posterior to the arthrobranch. The fourth segment has two arthrobranchs and a podobranch on the epipod which lies between the two arthrobranchs. The same pattern is repeated for segments five through seven except that these segments have an additional pleurobranch. The eighth thoracic segment has no gills or epipods. The podobranchs are attached to the epipods and the hypobranchial margin of each gill is armed with long setae identical to those on the epipod itself. Thus the podobranchs themselves must also have a cleaning role since they overly the bases of the larger gills. The epipods (Fig. 6f) function as gill cleaners and are either flattened plates or elongate lobes which bear long setae. In *Paradynomene tuberculata* these setae (Fig. 7e) have the following structure: the proximal third is smooth, followed by a section covered with digital scales, which are almost identical to those on the hypobranchial setae (see below), and towards the end of the setae these scales are replaced on one side by two rows of closely spaced, short, curved pegs with a channel between them, while for a short distance, digital scales continue on the other side unchanged until they too are replaced by pegs. Near the end of the setae there are two spiralling rows of closely spaced spines on opposite sides of the setal axis. The likely function of these scales is to dislodge debris as the epipods move between the gills. Epipod size is related to the size of the associated gill(s) and all of them extend as far the dorsal limit of the branchial chamber. They have an intimate association with nearby gills with their setae often penetrating the gaps between the gill lamellae. The first epipod (on the first maxilliped) is an elongate plate with few setae, not associated with any gill, but capable of extending back over the epibranchial surface of the first three arthrobranchs. Its role is probably to keep the anterior part of the branchial chamber and the anterior arthrobranchs free of debris. The second epipod is much more setose and lies anterior to the first arthrobranch, cleaning only the anterior face of this gill. The third epipod (on the third maxilliped), which is the longest, lies between the second and third arthrobranchs and cleans the adjacent faces of these gills. Similarly with the fourth epipod which lies between the third and fourth arthrobranchs. Thus the anterior and posterior faces of the third arthrobranch (the largest gill) are cleaned by

different epipods. The fifth epipod (associated with the second pereopod) lies between the fifth and sixth arthrobranchs, cleaning the posterior and anterior faces (respectively) of these gills as well as the posterior face of the first pleurobranch. In the same way the sixth and seventh epipods clean the same faces of the remaining arthrobranchs and pleurobranchs. Apart from the third arthrobranch, all the other gills are only cleaned on one or other side: there is no cleaning limb between the first and second, fourth and fifth, sixth and seventh, eighth and ninth arthrobranchs, and the posterior face of the tenth arthrobranch cannot be cleaned by the eighth epipod because it is absent. It is unclear how these gill surfaces are kept clear of debris, but the setose margin of each podobranch may contribute to this task. The epipods can move in a vertical direction and clean the adjacent gill surfaces, right from the hypobranchial to the epibranchial margins. When they are against the body wall their setae extend under the gill and could help to clean the hypobranchial surface. The podobranchs are cleaned by long setae on the base of the epipod to which the gill is attached.

The epibranchial surface of the posterior gills is cleaned by several long flexible setae extending from the posterior border of the scaphognathite. These setae reach as far as the second pleurobranch (on the third pereopod). In *Metadynomene tanensis* the margin of the scaphognathite carries a dense fringe of short plumose setae with two very long, stout setae (Fig. 7f) inserted on the posterior border. These setae are armed with stiff, acute setules for almost their entire length. The setules project at about 45° from the setal axis, with those on the proximal half directed towards the base, while those on the distal half are directed towards the tip. The setules become denser distally. In adult dynomenids there are normally two or three such long scaphognathite setae.

Besides the epipods and long scaphognathite setae there is another gill cleaning mechanism in dynomenids. This is best developed in *Paradynomene tuberculata* where the hypobranchial wall of the posterior half of the gill chamber is covered by a dense field of long setae. These setae (Fig. 7c) have a range of lengths, are arranged in clumps and project from the body wall into the hypobranchial surface of the gills. Each seta has a complex structure: the proximal half is smooth, followed by a section where opposite sides of the seta are covered by apically-directed digital scales, separated by intervening smooth areas. At about 80% of the length of the seta the digital scales on one side are replaced by closely-spaced short, curved pegs arranged as marginal rows with a channel between them, while the digital scales on the other side continue unchanged. These scales give the setae a comb-like appearance. Comparison with the setae on the epipods (see above) shows that the digital scales are identical and it seems likely that they must also have a cleaning role. Since the setae are fixed, the gills have to move about in order to dislodge debris. It may be that the epipods produce gill movement or perhaps cause the long setae to move from side to side. Besides *Paradynomene tuberculata*, hypobranchial setae are also well developed in *Metadynomene tanensis* and *M. devaneyi*, but in *Hirsutodynomene* and all species of *Dynomene* there are only a few of these setae present. Their status in *Acanthodromia* is unknown. This kind of gill cleaning mechanism has only been reported from the dromiid *Cryptodromiopsis larraburei* (Rathbun, 1910) (BAUER, 1981, as *Dromidia larraburei*). Tufts of setae arising from the body wall beneath the gills have also been observed in some other species of the Dromiidae (McLAY, unpublished). Pereopodal epipods are greatly reduced in dromiids and it may be that these hypobranchial setae take over the role of cleaning gills in the posterior half of the branchial chamber. In *Dromia erythropus* (George Edwards, 1771) the hypobranchial setae (Fig. 7d) have a unique structure: the proximal 80% of each seta is smooth but approaching the tip there are three or four isolated, apically directed acute spines followed by a series of separate paired rows of comb-like pegs, increasing in number distally and spiralling around the setal axis. Near the tip these pegs are transformed into two closely spaced continuous rows of acute spines which continue the spiral right to the end. In profile, the distal region of the setae appear to have three or four rosettes of these acute spines. In his review of decapod grooming BAUER (1989) did not report any setae which resemble those found in *D. erythropus*. The digital scales on the hypobranchial setae of *P. tuberculata* are similar to those found on the setiferous epipods, or setobranchs, of dendrobranchiate and caridean shrimps, as well as achelate and homarid lobsters (BAUER, 1981, 1989), but they are very different from the long barbed setae found on the maxillipedal epipods of the portunid crab, *Cronius tumidulus*. Instead of bearing scales, these setae have a single row of recurved hooks (BAUER, 1989, his Fig. 12 c-d).

Dynomenids, like other Brachyura, have an epipodal gill cleaning mechanism but this is supplemented by the scaphognathite setae over the anterior epibranchial surface and by the body wall setae attending to the posterior hypobranchial gill surface. Compared to the more derived Brachyura, gill cleaning in the Dynomenidae is much