CRUSTACEA DECAPODA:
Revision of the Family Dynomenidae

by

C.L. McLay

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With my best wishes & thanks,

Colin McLay

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Crustacea Decapoda: Revision of the Family Dynomenidae

Colin L. McLAY

Department of Zoology
University of Canterbury
Christchurch, New Zealand

ABSTRACT

The Dynomenidae are a group of small, uncommon, primitive crabs, which are often associated with corals. They inhabit depths down to around 500 m, between latitudes 40°N and 40°S. All genera and species are revised and redescribed, and the genus *Dynomene* Desmarest, 1823 is divided into two additional genera. As a result, there are thirteen known species belonging to five genera: *Dynomene* Desmarest, 1823 [*D. hispida* Guérin-Méneville, 1832, *D. praedator* A. Milne Edwards, 1879, *D. pugnatrix* de Man, 1889, *D. filholi* Bouvier, 1894, and *D. pilumnoides* Alcock, 1900], *Hirsutodynomene* gen. nov. [*H. spinosa* (Rathbun, 1911), and *H. ursula* (Stimpson, 1860)], *Metadynomene* gen. nov. [*M. devaneyi* (Takeda, 1977), *M. tanensis* (Yokoya, 1933), and *M. crosnieri* sp. nov.], *Acanthodromia* A. Milne Edwards, 1880 [*A. erinacea* A. Milne Edwards, 1880, and *A. margarita* (Alcock, 1899)], and *Paradynomene* Sakai, 1963 [*P. tuberculata* Sakai, 1963]. A key is provided to identify these species. In addition nine fossil genera, dating from the Upper Jurassic, are known: *Stephanometopon* Bosquet, 1854, *Dromiopsis* Reuss, 1859, *Palaeodromites* A. Milne Edwards, 1865, *Cyamocarcinus* Bittner, 1883, *Graptocarcinus* Roemer, 1887, *Cyclothyreus* Remes, 1895, *Gemmellarocarcinus* Checchia-Rispoli, 1905, *Glyptodynomene* Van Straelen, 1944, *Trachynotocarcinus* Wright & Collins, 1972. Some extinct species have also been placed in the genus *Dynomene*. The definition of the family Dynomenidae given by ALCOCK (1901) is updated and expanded in order to allow fossil species to be more accurately determined. Because of overlap with the Dromiidae, there has been some uncertainty about true family affinities of some fossils. Although these genera are in need of revision, this is not undertaken in this paper.

The status of *Dynomene pilumnoides* is established as a valid species, *D. pugnatrix brevimana* Rathbun, 1911 is synonymized with *D. pugnatrix* de Man, 1889, *D. granulobata* Dai, Yang & Lan, 1981 is a synonym of *D. hispida*, while *D. sinensis* Chen, 1979, *D. tenuilobata* Dai, Yang & Lan, 1981, and *D. huangluensis* Dai, Cai & Yang, 1996 are all synonyms of *D. praedator*. Dynomenids are reported from Australia for the first time in *D. pilumnoides*, and *Hirsutodynomene spinosa*. The status of *Metadynomene tanensis* (Yokoya, 1933) is established as a widespread Pacific species and shown to be part of the fauna of Japan, where it has been confused with *D. praedator*. *Paradynomene tuberculata*, previously known from Japan and New Caledonia, is now recorded from the Gulf of Aden, Indian Ocean. *P. tuberculata* as well as *D. praedator* and *H. spinosa*, are reported from Guam. The Atlantic Ocean and the Indo-Pacific share genera of dynomenids but not species. The biogeographic history of dynomenids is interpreted

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in the light of their present distribution and in relation to plate tectonics. Ancestral dynomenids are assumed to have been tethyan crabs and *D. filholi* and *Acanthodromia erinacea*, two insular Atlantic species, are shown to be tethyan relicts. By contrast, *Hirsutodynomene ursula* from the eastern Pacific, seems to be a species of quite recent origin.

In redescribing the species particular attention is paid to some new characters: setae, gills, epipods and gill cleaning mechanisms, the subchelate structure of the last pereopods and the male pleopods. This work was undertaken using a scanning electron microscope. Differences in the gross appearance of setae can be used to separate species and there are substantial differences in setal structure at the microscopic level. The standard branchial formula for dynomenids is shown to be nineteen gills plus seven epipods. There is little variation in gill numbers but substantial variation in gill shape between species. Although dynomenid gills are often said to be "transitional" they are arranged as in phyllobranchs but with the epibranchial part divided into varying numbers of lobes which gives them a trichobranch-like appearance. *Acanthodromia* has gills which are almost identical to the phyllobranchs of the Dromiidae but which retain the "dynomenid notch" on each side which, in cross section, give each gill plate a violin shape. The gill cleaning mechanism in dynomenids is complex, being carried out by no less than eight appendages (long setae on the posterior margin of the scaphognathite and the seven epipods) as well as stiff setae on the posterior hypobranchial wall of the gill chamber. In eubrachyurans only three appendages (maxillipodal epipods) are used.

In dynomenids the last pereopod is very reduced (on average less than one-third the length of the fourth pereopod) and carried in a horizontal position alongside the posterolateral carapace margin above the base of the preceding pereopod. They are not, as it has been commonly described, carried subdorsally. Using a scanning electron microscope it was revealed that this limb is sexually dimorphic: in males the dactyl has the normal shape of a tiny claw, but in females the dactyl is a flattened plate, bearing five to sixteen spines which are opposable to an extension of the propodus. In both males and females the propodal extension is armed with spines but in *Hirsutodynomene*, *Metadynomene* and *Paradynomene*, females have a significantly larger number of spines, which are armed with tiny teeth. Males of three species have an additional small spine on the outer margin of the dactyl. This is a character, previously only known amongst the Dromiidae, which suggests that the last pereopod of dynomenids may have evolved from a camouflage-carrying limb. This limb appears to be vestigial and it is difficult to know what its function may have been amongst the dynomenid ancestors. However its most likely former role appears to be as a cleaning appendage, but certainly not for carrying pieces of camouflage as it is found amongst the dromiids and homolids.

All dynomenids, except *Acanthodromia*, lack an effective abdominal locking mechanism and both sexes have five pairs of pleopods. The female has vestigial, uniramous first pleopods followed by four pairs of normal biramous pleopods, while the male has the normal first two pairs of pleopods as well as three pairs of rudimentary pleopods on segments three to five. These rudimentary pleopods can be uniramous or bifid. In *Metadynomene tanensis* 17% of females were gynandromorphs with small male first pleopods but the remaining pleopods were normal.

The diet of dynomenids seems to consist of food obtained by sieving fine sediment or perhaps coral mucus. The bunches of stiff setae on the inner margins of the cheliped fingers and third maxillipeds are probably used to separate fine organic fragments. Most of their gut contents are unidentifiable soft organic material along with small amounts of chopped chitinous fragments perhaps coming from hydroids or other crustaceans. Dynomenids appear to be deposit feeders.

Dynomenids have a broadcast reproductive strategy, with indirect development, laying small eggs (mean diameter = 0.49 mm) which probably produce planktonic larvae. Dynomenid larvae have never been reported in plankton samples. Males are on average 19% larger than females which become sexually mature at 5-8 mm CW for small species, or 9-13 mm CW for large species. Egg numbers increase logarithmically with body size. Given the sister group relationship with homolodromiids (which have very abbreviated development) it is implied that dynomenids and dromiids evolved from ancestors which had large eggs and perhaps a brooding strategy. This conclusion is contrary to accepted wisdom, but it is the most parsimonious answer. Some dromiids have retained the brooding strategy but others have independently evolved a broadcast strategy. The evolution of such a strategy in both these families is probably related to their colonization of the shallow water habitat. Both dynomenids and dromiids are mostly crabs of the continental shelf whereas homolodromiids are crabs of the continental slope.

Using morphological characters the phylogenetic relationships of the Dynomenidae are examined. Both the Dynomenidae and the Dromiidae are monophyletic, sharing significant apomorphies. The resemblance of some dynomenids and dromiids is shown to be the result of convergent evolution within these families. The Homolodromiidae are also monophyletic but are defined almost exclusively by plesiomorphies. Monophyly of the Dromiacea de Haan, 1833 is supported by morphological characters with the Dynomenidae and Dromiidae together being the sister group of the Homolodromiidae. The ancestor of these three families was probably a camouflage carrying crab, using both of the last two pairs of pereopods. A controversial aspect of the sister group relationships of the dromiaceans is the need to assume that in dynomenids the fourth pereopod has reverted to a locomotory role and the fifth pereopod became a cleaning limb. Monophyly of the Podotremata Guinot, 1977 is also supported. This analysis suggests that camouflage-carrying behaviour has evolved independently in the Dromiidae (and probably in the Homolodromiidae) and the Homolidae. Dromiids carry pieces of sponges or ascidians as well as shells, using the last two pairs of pereopods, while homolids carry sponges or anemones, using only the last pair of pereopods. The ancestor of the Dromiacea and Archaeobrachyura was probably an inhabitant of deeper waters and not a camouflage carrying crab.

RÉSUMÉ

Crustacea Decapoda: Révision de la famille Dynomenidae.

Les Dynomenidae forment un groupe de petits crabes primitifs, peu communs, souvent associés au corail. Ils habitent des profondeurs n'excédant pas les 500 m, à des latitudes comprises entre 40°N et 40°S. Tous les genres et toutes les espèces sont révisés et redécrits. Le genre *Dynomene* Desmarest, 1823, est divisé et deux nouveaux genres sont créés. Finalement, les treize espèces connues sont réparties en cinq genres : *Dynomene* Desmarest, 1823 [*D. hispida* Guérin-Méneville, 1832; *D. praedator* A. Milne Edwards, 1879; *D. pugnatrix* de Man, 1889; *D. filholi* Bouvier, 1894; *D. pilumnoides* Alcock, 1900]; *Hirsutodynomene* gen. nov. [*H. spinosa* (Rathbun, 1911) et *H. ursula* (Stimpson, 1860)]; *Metadynomene* gen. nov. [*M. devaneyi* (Takeda, 1977); *M. tanensis* (Yokoya, 1933) et *M. crosnieri* sp. nov.]; *Acanthodromia* A. Milne Edwards, 1880 [*A. erinacea* A. Milne Edwards, 1880 et *A. margarita* (Alcock, 1899)] et *Paradynomene* Sakai, 1963 [*P. tuberculata* Sakai, 1963]. Une clef permet d'identifier les diverses espèces. Neuf genres fossiles attribués aux Dynomenidae sont connus du Jurassique supérieur : *Stephanometopon* Bosquet, 1854; *Dromiopsis* Reuss, 1859; *Palaeodromites* A. Milne Edwards, 1865; *Cyamocarcinus* Bittner, 1883; *Graptocarcinus* Roemer, 1887; *Cyclothyreus* Remes, 1895; *Gemmellarocarcinus* Checchia-Rispoli, 1905; *Glyptodynomene* Van Straelen, 1944; *Trachynotocarcinus* Wright & Collins, 1972. Enfin, quelques espèces éteintes ont été rapportées au genre *Dynomene*. La définition originale de la famille des Dynomenidae, donnée par ALCOCK (1901), est mise à jour et étendue afin de pouvoir y accueillir les espèces fossiles. Les véritables affinités de certains fossiles sont incertaines et difficiles à interpréter en raison de confusions possibles avec les Dromiidae. Bien qu'une révision de ces genres fossiles s'avère nécessaire, il n'a pas été possible de l'entreprendre dans le cadre du présent travail.

Dynomene pilumnoides est établie comme une espèce valide. *D. pugnatrix brevimana* Rathbun, 1911, est mise en synonymie avec *D. pugnatrix* de Man, 1889. *D. granulobata* Dai, Yang & Lan, 1981, est synonyme de *D. hispida,* tandis que *D. sinense* Chen, 1979, *D. tenuilobata* Dai, Yang & Lan, 1981, et *D. huangluensis* Dai, Cai & Yang, 1996, sont synonymes de *D. praedator.* Pour la première fois, des Dynomenidae sont signalés d'Australie, à savoir *D. pilumnoides* et *Hirsutodynomene spinosa.* Le statut de *Metadynomene tanensis* (Yokoya, 1933) est bien établi : il s'agit d'une espèce largement répandue dans le Pacifique et qui, au Japon, avait été confondue avec *D. praedator. Paradynomene tuberculata,* auparavant connue du Japon et de Nouvelle-Calédonie, est signalée du golfe d'Aden. *P. tuberculata* ainsi que *D. praedator* et *H. spinosa* sont signalées de Guam. L'Atlantique et l'Indo-Pacifique partagent des genres mais non des espèces de Dynomenidae. L'histoire biogéographique des Dynomenidae est tracée à la lumière de leur distribution actuelle et des phénomènes liés à la tectonique des plaques. Les représentants ancestraux des Dynomenides sont supposés avoir été des formes de la Téthys. *D. filholi* ainsi qu'*Acanthodromia erinacea,* deux espèces insulaires de l'Atlantique, apparaissent comme des reliques téthysiennes. En revanche, *Hirsutodynomene ursula,* du Pacifique oriental, serait une espèce d'origine très récente.

Lors de la description des espèces, nous avons considéré de nouveaux caractères (soies, branchies, épipodites, mécanisme de nettoyage des branchies, structure subchéliforme du dernier péréiopode, pléopodes mâles) et complété nos observations par leur étude en microscopie électronique à balayage. Visibles à l'œil nu et au binoculaire, les différences dans l'apparence des soies, qui peuvent être utilisées pour séparer les espèces, se révèlent à l'échelle microscopique comme représentant des structures très variées et bien distinctes. La formule branchiale standard pour les branchies est de 19 branchies plus sept épipodites. Il y a peu de variations dans leur nombre; mais de substantielles variations dans leur forme distinguent les espèces. Bien qu'elles soient souvent qualifiées comme étant d'un type intermédiaire, les branchies dynoméniennes sont disposées comme des phyllobranchies à la différence que la partie épibranchiale est divisée en un nombre varié de lobes, ce qui leur donne une apparence de trichobranchies. *Acanthodromia* a des branchies presque identiques aux phyllobranchies des Dromiidae mais conservant l'*encoche dynoménienne* de chaque côté, ce qui, en coupe, donne à chaque branchie la forme d'un violon. Chez les Dynomenidae le mécanisme de nettoyage des branchies est complexe, étant réalisé par non moins de huit appendices (longues soies sur le bord postérieur du scaphognathite et des sept épipodites) aussi bien que par des soies raides sur la paroi hypobranchiale postérieure de la chambre branchiale. Chez les Eubrachyura, seuls trois appendices (épipodites des maxillipèdes) sont utilisés.

Chez les Dynomenidae, la dernière paire de péréiopodes est très réduite (en moyenne inférieure au tiers de la longueur du quatrième péréiopode) et disposée horizontalement le long du bord postérolatéral de la carapace, au-dessus du péréiopode précédent. L'observation en microscopie électronique a révélé que cet appendice est sexuellement dimorphique : chez le mâle, le dactyle a la forme normale d'une petite pince tandis que, chez la femelle, le dactyle est une pièce aplatie qui porte de cinq à seize épines opposables à une expansion du propode. Dans les deux sexes, l'expansion du propode est armée d'épines; mais, dans les genres *Hirsutodynomene*, *Metadynomene* et *Paradynomene*, les femelles ont un nombre plus élevé d'épines, elles-mêmes armées de très petites dents. Le mâle de trois espèces a une épine supplémentaire sur le bord externe du dactyle, ce qui était jusqu'alors un caractère connu seulement chez les Dromiidae et suggère que le dernier péréiopode des Dynomenidae pourrait provenir de l'évolution d'un appendice destiné à porter des pièces de camouflage. Le dernier péréiopode se présente bien comme un appendice vestigial, et il est difficile de savoir quelle fonction il pouvait assumer chez les Dynomenidae ancestraux. Son rôle le plus probable serait celui d'un appendice nettoyeur, et certainement pas celui d'un appendice transportant un objet pour le camouflage, comme c'est le cas chez les Dromiidae et les Homolidae.

Tous les Dynomenidae, à l'exception des *Acanthodromia*, sont dépourvus d'un appareil de maintien de l'abdomen. Les deux sexes portent cinq paires de pléopodes. La femelle possède une première paire de pléopodes uniramés, vestigiaux, suivie de quatre paires de pléopodes normalement biramés, alors que le mâle a les deux paires normales de pléopodes sexuels ainsi que trois paires de pléopodes vestigiaux sur les segments 3 à 5. Ces pléopodes vestigiaux peuvent être uniramés ou bifides. Chez *Metadynomene tanensis* 17% des femalles sont gynandromorphes, avec de petits premiers pléopodes de type mâle tandis que les autres pléopodes sont normaux.

L'alimentation des Dynomenidae paraît consister en nourriture obtenue en filtrant les sédiments fins ou peut-être le mucus des coraux. Les touffes de soies raides sur le bord interne des doigts des chélipèdes et sur les troisièmes maxillipèdes sont probablement utilisées pour séparer les fragments organiques. L'estomac contient en majorité du matériel organique mou non identifiable en même temps que de petites quantités de fragments durs de chitine provenant probablement d'hydroïdes ou de crustacés. Les Dynomenidae se présentent comme des détritivores.

Les Dynomenidae ont une reproduction avec développement non abrégé, indirect, et avec de petits œufs (diamètre moyen = 0.49 mm) qui se développent certainement en larves planctoniques. De telles larves dynoméniennes n'ont jamais été trouvées dans le plancton. Les mâles sont en moyenne 19% plus grand que les femelles; ces dernières deviennent sexuellement matures entre 5-8 mm de largeur de carapace pour les espèces de taille peu élevée, entre 9-13 mm pour les plus grandes espèces. Le nombre des œufs augmente de façon logarithmique avec les dimensions du corps. Etant donné la relation de groupe-frère avec les Homolodromiidae, il est probable que l'ensemble que constituent les Dynomenidae et les Dromiidae a évolué à partir d'ancêtres ayant eu de gros œufs. Cette conclusion est contraire à ce qui est communément accepté, mais elle est la réponse la plus parcimonieuse. Cet ensemble (Dynomenidae et Dromiidae) a peut-être eu une stratégie de protection de la ponte. Certains Dromiidae ont conservé une stratégie de protection de la ponte, mais d'autres ont, indépendamment, développé une stratégie de dissémination. L'évolution d'une telle stratégie chez ces deux familles est probablement liée à leur colonisation d'un habitat dans des eaux peu profondes. Aussi bien les Dynomenidae que les Dromiidae sont essentiellement des crabes de la plate-forme continentale, tandis que les Homolodromiidae sont des crabes du talus continental.

Sur la base des caractères morphologiques, les relations phylogénétiques des Dynomenidae sont analysées. Dynomenidae et Dromiidae sont monophylétiques, partageant des apomorphies significatives. La ressemblance de certains Dynomenidae avec les Dromiidae serait le résultat d'une évolution convergente à l'intérieur de ces familles. Les Homolodromiidae sont également monophylétiques mais ils sont presque exclusivement définis par des plésiomorphies. La monophylie des Dromiacea de Haan, 1833, est supportée par des caractères morphologiques, les Dynomenidae et Dromiidae formant, ensemble, le groupe-frère des Homolodromiidae. L'ancêtre de ces trois familles était probablement un crabe qui se camouflait en utilisant ses deux dernières paires de pattes. Les relations de groupe-frère pour les familles de Dromiacea nécessitent d'admettre une réversion pour la quatrième paire de pattes des Dynomenidae puisqu'elle a retrouvé un rôle locomoteur, tandis que la cinquième paire devenait un appendice nettoyeur. La monophylie des Podotremata Guinot, 1977, est corroborée. Cette analyse suggère que le comportement de camouflage par maintien d'un objet au-dessus du corps a évolué indépendamment chez les Dromiidae (et probablement chez les Homolodromiidae) et chez les Homolidae. Les Dromiidae portent des éponges ou des ascidies ainsi que des coquilles, en se servant de leurs deux dernières paires de péréiopodes, tandis que les Homolidae transportent des éponges et des anémones, en se servant seulement de leur dernière paire de péréiopodes. L'ancêtre des Dromiacea et des Archaeobrachyoures était probablement un habitant des eaux profondes et n'était pas un crabe se camouflant grâce au transport d'un objet au-dessus du corps.

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INTRODUCTION

Dynomenids are a small group of uncommon primitive crabs living in tropical and warm parts of the Atlantic, Indian and Pacific Oceans. The shallow water species are often associated with reef-building corals, but other species live in deeper waters of the continental shelf. The maximum depth record for a dynomenid is 540 m (for *Acanthodromia erinacea* A. Milne Edwards, 1880). The first species to be described was *Dynomene hispida* Guérin-Méneville, 1832 which was based on a specimen collected from Mauritius, in the Indian Ocean. The family name, Dynomenidae Ortmann, 1892, was not erected until much later, but the type species for the family is *D. hispida*. Until now the family has included three genera: *Dynomene* Desmarest, 1823, *Acanthodromia* A. Milne Edwards, 1880, and *Paradynomene* Sakai, 1963. By far the majority of species have been assigned to the genus *Dynomene*.

In this paper I describe one new dynomenid species, redescribe all of the previously known species, and provide a key for their identification. This work is based on the examination of almost 600 specimens. It began with the collections from New Caledonia, Philippines, Indonesia and Madagascar, held by the Muséum national d'Histoire naturelle, Paris, but also included specimens from most of the world's major museums. In the literature, dynomenids have been reported from coastal areas bordering all tropical seas except for Australia. In this paper I provide the first records of these crabs from Australian waters. Also many new records for the Pacific islands are included.

Besides the customary features used to describe these crabs, I also include some details of their structure that can only be determined using a scanning electron microscope. This has been particularly helpful in ascertaining the nature of the subchelate mechanism of the reduced fifth pereopods and has revealed that in dynomenids these limbs are sexually dimorphic. The scanning electron microscope has also been very helpful in elucidating the fine structure of setae, gills and male pleopods. Some information about the diet and reproductive strategy is also included.

Despite their occurrence in shallow tropical waters the larval stages of dynomenids have never been collected in the field. The only information comes from larvae dissected from advanced stage eggs of *Acanthodromia erinacea* (see RICE, 1981). The lack of information about larval development, which could be useful in aiding the determination of phylogenetic relationships, is a major gap in our knowledge of this family.

This work follows on from a study of the Dromiidae (McLAY, 1993) which are regarded as the sister group of the Dynomenidae. With the recent completion of a major review of the Homolodromiidae (GUINOT, 1995) the opportunity is taken to explore the phylogenetic relationships between all three families of the Dromiacea sensu DE HAAN.

HISTORY OF THE DYNOMENIDAE

The following is a chronological list of recent genera and species (where appropriate the valid name is shown in brackets):

Genus ***DYNOMENE*** Desmarest, 1823
- *D. hispida* Guérin-Méneville, 1832 (type species of the genus).
- *D. latreillii* Eydoux & Souleyet, 1842 [= *D. hispida* Guérin-Méneville, 1832].
- *D. ursula* Stimpson, 1860 [= *Hirsutodynomene ursula* (Stimpson, 1860)].
- *D. praedator* A. Milne Edwards, 1879.
- *D. pugnatrix* de Man, 1889.
- *D. filholi* Bouvier, 1894.
- *D. margarita* Alcock, 1899 [= *Acanthodromia margarita* (Alcock, 1899)].
- *D. pilumnoides* Alcock, 1900.
- *D. platyarthrodes* Stebbing, 1905 [= *Speodromia platyarthrodes* (Stebbing, 1905)].
- *D. pugnatrix brevimana* Rathbun, 1911 [= *D. pugnatrix* de Man, 1889].
- *D. spinosa* Rathbun, 1911 [= *Hirsutodynomene spinosa* (Rathbun, 1911)].
- *D. actaeiformis* (Stebbing, 1921) [= *D. pilumnoides* Alcock, 1900].
- *D. tanensis* Yokoya, 1933 [= *Metadynomene tanensis* (Yokoya, 1933)].
- *D. devaneyi* Takeda, 1977 [= *Metadynomene devaneyi* (Takeda, 1977)].
- *D. sinensis* Chen, 1979 [= *D. praedator* A. Milne Edwards, 1879].
- *D. granulobata* Dai & Yang, 1981 [= *D. hispida* Guérin-Méneville, 1832].
- *D. tenuilobata* Dai & Lan, 1981 [= *D. praedator* A. Milne Edwards, 1879].
- *D. huangluensis* Dai, Cai & Yang, 1996 [= *D. praedator* A. Milne Edwards, 1879].

Genus ***ACANTHODROMIA*** A. Milne Edwards, 1880
- *A. erinacea* A. Milne Edwards, 1880 (type species of the genus).
- *A. margarita* (Alcock, 1899).

Genus ***MAXILLOTHRIX*** Stebbing, 1921
- *Maxillothrix actaeiformis* Stebbing, 1921 (type and only species of the genus) [= *Dynomene pilumnoides* Alcock, 1900].

Genus ***PARADYNOMENE*** Sakai, 1963
- *P. tuberculata* Sakai, 1963 (type and only species of the genus).

Genus ***HIRSUTODYNOMENE*** gen. nov.
- *H. spinosa* (Rathbun, 1911) (type species of the genus).
- *H. ursula* (Stimpson, 1860).

Genus ***METADYNOMENE*** gen. nov.
- *M. devaneyi* (Takeda, 1977) (type species of the genus).
- *M. tanensis* (Yokoya, 1933).
- *M. crosnieri* sp. nov.

The following species have been described and at least initially assigned to the genus *Dynomene* Desmarest, 1823. The first dynomenid to be described was *Dynomene hispida* Guérin-Méneville, 1832 based on a specimen collected from Mauritius Id, east of Madagascar. The second species to be described was *D. latreillii* Eydoux & Souleyet, 1842 from a specimen collected from Hawaii during the voyage of the *"Bonite"*. A. MILNE EDWARDS (1879) and later PEYROT-CLAUSADE & SERÈNE (1976) showed that the preceding species was in fact a synonym of *D. hispida*. Some years later, the third species, *D. ursula* Stimpson, 1860, was collected from Cape San Lucas, Baja California, by John XANTUS. The fourth species, *D. praedator* A. Milne Edwards, 1879, was discovered at New Caledonia by M. BALANSA. The fifth species, *D. pugnatrix* de Man, 1889, also came from Mauritius. The only species of *Dynomene* known from the Atlantic, *D. filholi* Bouvier, 1894, was collected from the Cape Verde Ids during the voyages of the *"Talisman"* and *"Travailleur"*. The seventh species was *D. margarita* Alcock, 1899, collected from the Andaman Sea during deep-sea surveys by the *"Investigator"*. The eighth species, *D. pilumnoides* Alcock, 1900 was first collected from the Laccadive Archipelago, India. The next name added to *Dynomene* was the sub-species *D. pugnatrix brevimana* Rathbun, 1911, from Providence Id, followed by *D. spinosa* Rathbun, 1911 from Coetivy, Seychelles. Both of these specimens were collected during the Percy Sladen Trust Expedition to the Indian Ocean, 1905. *D. spinosa* is the last species of this genus whose type locality is in the Indian Ocean. Clearly collecting in the Indian Ocean area played an important role in the early development of knowledge about this family of crabs, contributing ten of the eleven known species.

The second phase in the development of our understanding of the dynomenids resulted from investigations in the greater Pacific Ocean. The remaining species have type localities in the Pacific Ocean: *Dynomene tanensis* Yokoya, 1933, came from Tanegasima Id, Japan, and *D. devaneyi* Takeda, 1977, was collected by the submersible, *"Star II"*, from Hawaii. The last four species have only recently been described from the coasts of China or Taiwan: *D. sinensis* Chen, 1979, *D. granulobata* Dai & Yang, 1981, *D. tenuilobata* Dai & Lan, 1981, and *D. huangluensis* Dai, Cai & Yang, 1996. Thus there have been 15 species or sub-species of dynomenid crabs assigned to the genus *Dynomene*. In addition two species of the Dromiidae have been erroneously placed in this genus: *Dynomene depressa* Brocchi, 1875 (= *Dromidia spongiosa* Stimpson, 1858), and *Dynomene platyarthrodes* Stebbing, 1905 [= *Speodromia platyarthrodes* (Stebbing, 1905)].

The second dynomenid genus to be erected was *Acanthodromia* A. Milne Edwards, 1880, for *A. erinacea* Milne Edwards, 1880, collected from Guadeloupe, Atlantic Ocean, by the United States coast survey steamer *"Blake"*. Probably through an oversight when creating the family name Dynomenidae, ORTMANN (1892) did not include this genus in his new family. A second species, *A. margarita* (Alcock, 1899), was collected from the Andaman Sea, Indian Ocean, by the *"Investigator"*, which was initially placed in the genus *Dynomene*.

The third genus *Maxillothrix* Stebbing, 1921, was initially placed in the family Xanthidae. But the only species to be assigned to this genus, *M. actaeiformis* Stebbing, 1921, based on a specimen from the Natal coast, was later found to be a synonym of *Dynomene pilumnoides* Alcock, 1900. Two authors, SERÈNE (1968) and TAKEDA (1977) used the name *Dynomene actaeiformis* (Stebbing, 1921) in faunal lists.

Finally, the monospecific *Paradynomene* Sakai, 1963 was created for *P. tuberculata* Sakai, 1963 from Sagami Bay, Japan.

Thus prior to the commencement of this work, the family Dynomenidae contained a total of 16 species belonging to 3 genera. Herein I synonymize all four of the recently described *Dynomene* species from China and

Taiwan, and create two new genera for some of the species of *Dynomene*: *Hirsutodynomene* gen. nov. for *D. spinosa* and *D. ursula*, and *Metadynomene* gen. nov. for *D. devaneyi*, *D. tanensis* and a new species, *M. crosnieri* sp. nov., from the Glorieuses Ids, north of Madagascar. In recent years new collections have extended the ranges of known species without adding greatly to the number of species. The net result of all these changes is that the family Dynomenidae now contains five genera and thirteen species.

FOSSIL DYNOMENIDAE

Dynomenids have an extensive fossil record, dating from the Upper Jurassic (GLAESSNER, 1980), and there has been much discussion about the placement of genera in this family or in other families. The fossil record does not provide a clear answer to the question about the relationships of these crabs. Some of the difficulties arise because, while it may be easy to define the essential features of extant species, which justify their inclusion in the family, it is not so easy when it comes to fossils. Here, we have only carapace shape, development of teeth, and a few grooves incised on the dorsal carapace surface. For fossils, the definition of the family has to be based on a different and very limited set of characters and it is likely that the range of fossil species included is much wider than for modern species. For the extant species most are relatively small crabs whereas many of the fossil specimens are quite large and probably do not belong in the Dynomenidae. There is no reason to think that there has been a decrease in crab size during their evolution. I have examined some of the fossils which have been assigned to this family and have attempted to include a set of carapace characters which both modern and fossil species share.

The following chronological list of fossil genera is based on BALSS (1957: 1606) and GLAESSNER (1969), but modified after WRIGHT & COLLINS (1972) and COLLINS *et al.* (1995):

DYNOMENE Desmarest, 1823 (type species *D. hispida* Guérin-Méneville, 1832, by subsequent monotypy of GUÉRIN-MÉNEVILLE, 1832).

STEPHANOMETOPON Bosquet, 1854 (type species *Stephanometopon granulatum* Bosquet, 1854 by monotypy).

DROMIOPSIS Reuss, 1859 (type species *Brachyurites rugosus* von Schlotheim, 1820, by subsequent designation of BEURLEN, 1928).

PALAEODROMITES A. Milne Edwards, 1865 (type species *P. octodentatus* A. Milne Edwards, 1865, by monotypy).

CYAMOCARCINUS Bittner, 1883 (type species *C. angustifrons* Bittner, 1883, by monotypy).

GRAPTOCARCINUS Roemer, 1887 (type species *G. texanus* Roemer, 1887, by monotypy).

CYCLOTHYREUS Remes, 1895 (type species *C. strambergensis* Remes, 1895, by subsequent designation of BEURLEN, 1928).

GEMMELLAROCARCINUS Checchia-Rispoli, 1905 (type species *G. loerentheyi* Checchia-Rispoli, 1905, by monotypy).

GLYPTODYNOMENE Van Straelen, 1944 (type species *G. alsasuensis* Van Straelen, 1944, by monotypy).

TRACHYNOTOCARCINUS Wright & Collins, 1972 (type species *Trachynotus sulcatus* Bell, 1863, by monotypy).

There are a total of nine extinct fossil genera. Only one extant genus, *Dynomene* has fossil representatives. With the revision of this genus, undertaken herein, it is likely that some of the fossil species assigned to *Dynomene* will be able to be placed in the new genera. It is beyond the scope of the present report to examine the validity of all the fossil species and until this is done the fossil record has only limited value in helping to reveal the phylogenetic relationships of the dynomenids.

MATERIAL EXAMINED

The following abbreviations are used for material examined at or borrowed from museum collections:

AMS - Australian Museum, Sydney.
ANSP - Philadelphia Academy of Natural Sciences.
BMNH - Natural History Museum, London.
BPBM - Bernice P. Bishop Museum, Honolulu.
LACM - Natural History Museum, Los Angeles County.
MCZ - Museum of Comparative Zoology, Harvard University.
MNHN - Muséum national d'Histoire naturelle, Paris.
MZUF - Museo Zoologico de "La Specola", Firenze, Italy.
NTOU - National Taiwan Ocean University, Keelung, Taiwan.
QM - Queensland Museum, Brisbane.
RMNH - Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Natuurlijke Historie).
SMF - Natur-Museum und Forschung Institut Senckenberg, Frankfurt.
UGM - University of Guam.
USNM - United States National Museum, Smithsonian Institution, Washington.
WAM - Western Australian Museum, Perth.
ZMB - Museum für Naturkunde, Humboldt Universität, Berlin.
ZMUC - Zoologisk Museum, Copenhagen.
ZRC - Zoological Reference Collection, Department of Zoology, National University of Singapore.

When in the lists of material examined, no place of deposit is mentioned, this means that the material is at the MNHN.

TERMINOLOGY AND PRESENTATION

Measurements were made, using vernier calipers under a binocular microscope, to an accuracy of 0.1 mm. Measurements of chelipeds and abdomen used for determining relative growth in *Metadynomene tanensis* were made as follows: cheliped propodus length was measured along the inferior margin from the joint with the carpus to the tip of the fixed finger; cheliped propodus depth was measured from the superior to the inferior margin at the widest point; abdomen width was measured as the greatest width of the penultimate segment. To determine the relative sizes of the articles of the last two pairs of pereopods their lengths were measured along the superior margin of each limb. The length of each article was divided by the total length and converted to a percentage.

Carapace dimensions are given as carapace width (CW) x carapace length (CL) e.g. 1 ♂ 9.8 x 8.0 mm. Carapace width includes any anterolateral teeth and was measured across the widest point. Carapace length includes any rostral teeth and was measured to the posterior margin in the mid-line.

The description of each species follows the format: carapace shape and ornamentation, tomentum, anterolateral margin, frontal margin and orbital region including antennule and antenna, subhepatic area, third maxillipeds and female sternal sutures 7/8. This is followed by the gill formula and shape of the gill plates. The cheliped is dealt with separately, followed by the first three pairs of walking legs, and then the reduced last pair of legs. Finally, the abdomen size and shape, and the five pairs of male and female pleopods.

The tomentum is an important feature of these crabs and is described in terms of the length of the setae, their density, and their distribution, especially on the surface of the carapace. Setal size is expressed either as the length ratio of long setae/short setae, or as a ratio of CW. Setal density is expressed in terms of the degree to which the carapace surface is obscured in dorsal view. Setae were investigated using a scanning electron microscope and the results are dealt with in terms of setae shape and the distribution of setules along the shaft.

The major carapace grooves are named according to GLAESSNER (1969) and are treated as follows: frontal groove, cervical groove, cardiac groove, and pleural suture.

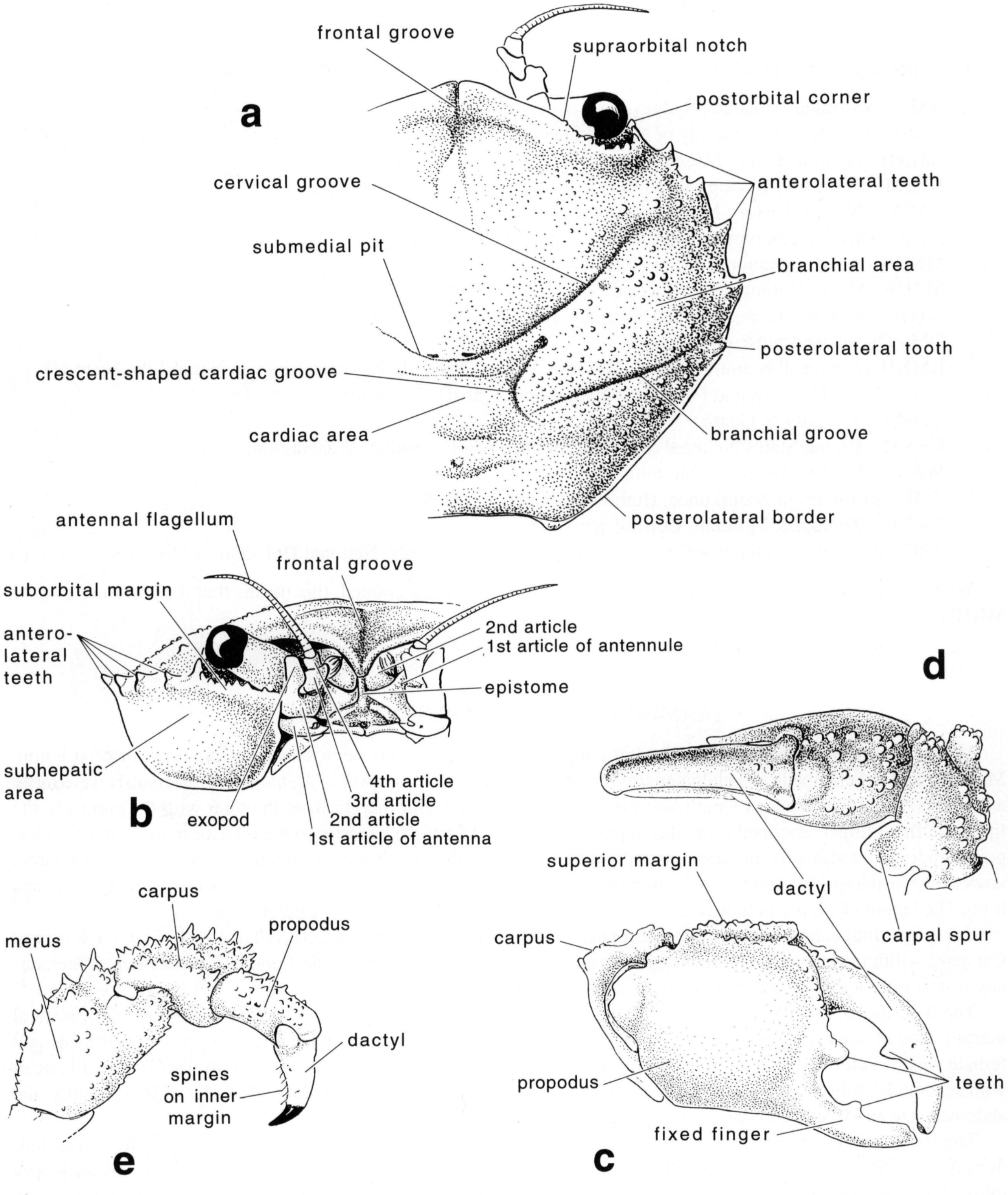

FIG. 1. — Selected figures illustrating the terminology used to describe crabs of the family Dynomenidae : a-b, e based on *Dynomene hispida*, c-d based on *D. praedator*: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod.

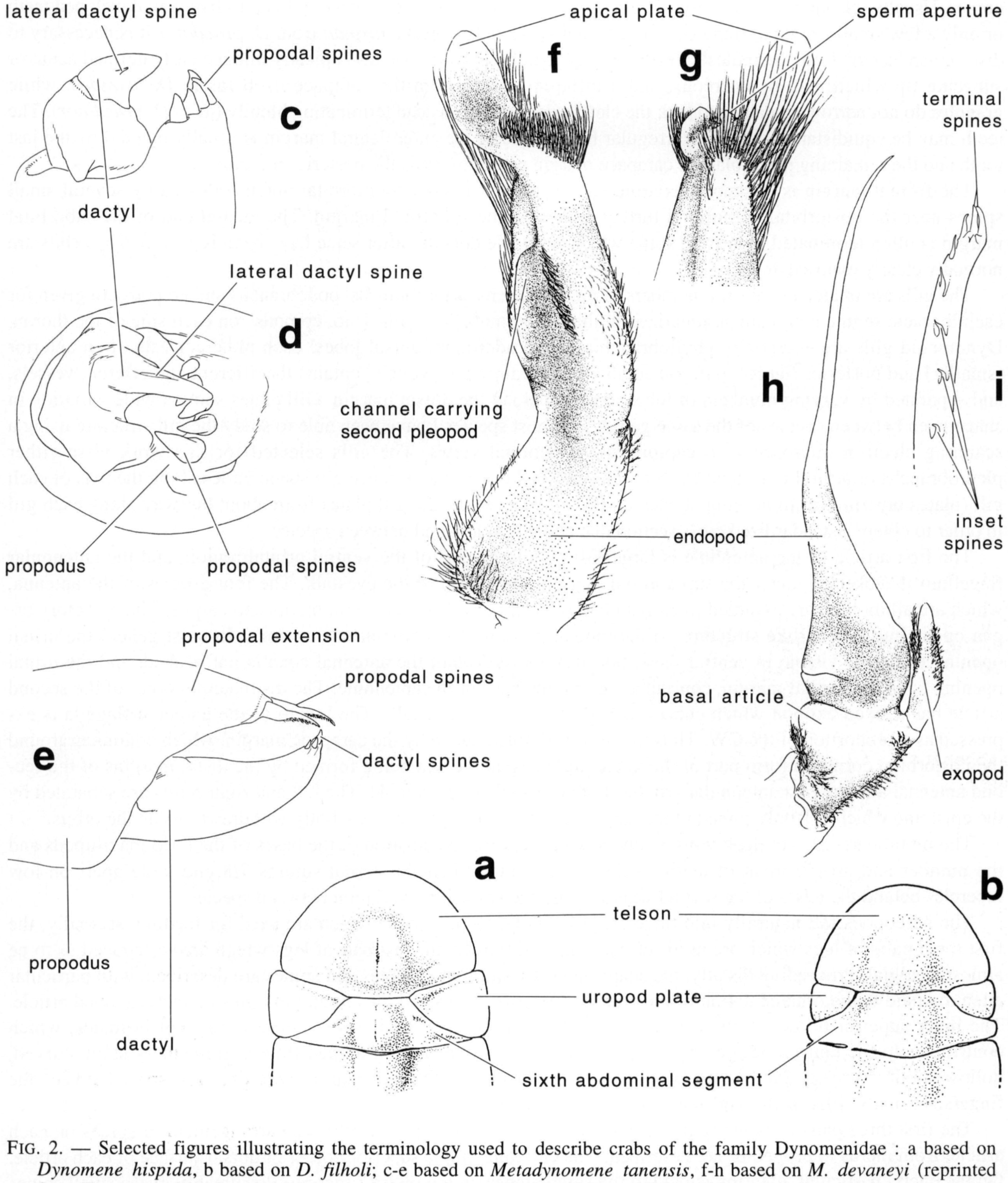

FIG. 2. — Selected figures illustrating the terminology used to describe crabs of the family Dynomenidae : a based on *Dynomene hispida*, b based on *D. filholi*; c-e based on *Metadynomene tanensis*, f-h based on *M. devaneyi* (reprinted from TAKEDA, 1977, *Pacific Science*, vol. 31 (1) by permission of the publisher); i based on *D. praedator*: **a**, ventral view of telson and terminal segments of female abdomen; **b**, ventral view of telson and terminal segments of male abdomen; **c**, lateral view of tip of male fifth pereopod; **d**, apical view of tip of male fifth pereopod; **e**, lateral view of tip of female fifth pereopod; **f**, posterior view of male left first pleopod; **g**, anterior view of tip of male left first pleopod; **h**, posterior view of male left second pleopod; **i**, tip of second pleopod.

Normally, the anterolateral margin begins in close proximity to, and at the same level as, the postorbital corner. Usually the anterolateral margin is clearly defined and it may be adorned with up to five well developed teeth or only a few small irregular granules. For the separation of *Dynomene hispida* from *D. praedator* it is necessary to distinguish "teeth" from "granules". Teeth have a broad base which narrows apically into a clearly defined acute or subacute tip which may be nacreous, and a different colour from the carapace itself (as in *D. hispida*), while granules do not narrow apically and lack the clearly defined tip, instead terminating bluntly (as in *D. praedator*). The teeth may be equidistantly spaced or irregular but the end of the anterolateral margin is usually marked by the last tooth and the remaining posterolateral carapace margin angles towards the posterior margin.

The frontal margin is V-shaped, continuous, except for a small supraorbital notch followed by several small spines near the postorbital corner and further spines on the suborbital margin. The medial end of the suborbital margin is often terminated by a stout spine which is visible dorsally after setae have been removed. The orbits are normally clearly exposed dorsally.

The gills are treated as follows: numbers of pleurobranchs, arthrobranchs, podobranchs and epipods are given for each thoracic segment and are summarized in the gill formula "no. gills + no. epipods" on each side of the thorax. Dynomenid gills are essentially phyllobranchiate with additional dorsal lobes: each plate consists of an anterior (smaller) and posterior (larger) part joined about the central axis, which contains the afferent and efferent vessels, and separated by varying numbers of lobes arranged along the dorsal margin. Gill plates show a wide variation in shape even between species of the same genus. For most species I have been able to study the gill structure using a scanning electron microscope to capture cross-sectional views. The gills selected for this work were either pleurobranchs or arthrobranchs taken from the pereopod two or three. Since gill shape varies along the axis of each gill (plates tapering off to nothing at each end), I chose to study the gill plates from about halfway along each gill in order to obtain a standardized cross section that could be compared between species.

The first article of the antennule is large, filling a large part of the ventral orbital region, and the antennular flagellum is tucked in under the supraorbital margin at the base of the eyestalk. The four articles of the antenna, which are all mobile, are assumed to correspond to coxa, fused basis-ischium, merus and carpus. The excretory organ opens into a beak-like structure on the medial margin of the first article or coxa. In most genera the urinal opening is clearly visible in ventral view, but in *Acanthodromia* the antennal coxa is not beaked, and the urinal opening is on the medial margin, concealed against the base of the antennule. The distolateral corner of the second article has a fixed exopod which curves over the base of the eyestalk. The length of the antennal flagella is expressed as a proportion of the CW. Thus the orbit is defined above by the carapace margin, which continues around the postorbital corner to form part of the suborbital margin, the rest being formed by the distal margins of the second antennal and the first antennular articles, both of which are moveable. The left and right orbits are separated by the epistome which is firmly joined to the carapace above. The eyes can be wholly withdrawn inside the orbits.

The mouthparts are not dealt with in any detail except for the position of the bases of the third maxillipeds and the number and arrangement of teeth on the crista dentata. Female sternal sutures 7/8 end wide apart on low tubercles behind the bases of the second walking legs and show little variation between species.

The pereopods fall naturally into three groups: firstly, the chelipeds which are used for feeding, secondly, the first three pairs of legs which are used for walking, and thirdly, the last pair of legs which are so reduced as to be almost vestigial. Proceeding distally, the shape and disposition of granules and spines are described, with particular attention paid to the ornamentation of the outer (or exterior) faces and the angular margins of each cheliped article. The inner superior border of the carpus usually has a well developed "spur", more prominent in males, which contributes to the unusual shape of the carpal article in dynomenids. Cheliped fingers are usually stout, curved, hollowed out internally and bearing weakly developed teeth on the outer margins and tips. The space between the fingers is usually filled with long coarse bunches of obliquely angled setae.

The first three pairs of walking legs usually decrease in length posteriorly. The arrangement of spines on each article, from merus to propodus, are described, concentrating on the superior border or dorsal surface of each article. On the dactyl particular attention is paid to the small spines on the inferior margin. Presumably, these small spines are used to provide some grip on the substrate which is often dead coral. The ratio of the length (including any spines) of the second walking leg (i.e. the third pereopod) merus to its width and to the CL are given. This character is useful for separating some species.

The size of the last pair of legs is given in terms of how far it extends along the meral article of the preceding limb (i.e. the fourth pereopod). This leg is subchelate but the mechanism appears to be obsolete because it is incapable of grasping anything. The subchelate structure is sexually dimorphic and detailed comparison of male and female limbs has been made using the scanning electron microscope.

I treat the abdomen as consisting of six segments and a telson. All abdominal segments bear appendages and are freely moveable: their shape and surface are described beginning with the most anterior segment. In dynomenids, both males and females have five pairs of pleopods on the abdomen. The first pleopod is vestigial in the female while the last three are rudimentary in the male. Uniramous uropods are inserted at the posterior border of the last abdominal segment and just in front of the telson. In dynomenids the uropod plates are large (relative to other dromiaceans), and their size is assessed in terms of what proportion of the margin of the last abdominal segment is excluded from the lateral margin. This proportion is a sexually dimorphic feature, larger in females than in males. Width of the telson is measured across the widest part at its base and the length is the maximum length measured along the mid-line.

MORPHOLOGY OF THE DYNOMENIDAE

This section includes comparison of the major morphological features of dynomenids and a discussion of them in relation to the other podotremes. Where appropriate characters are indicated to be either plesiomorphic or apomorphic.

CARAPACE

Carapace width is distinctly greater than length (ratio 1.2 to 1.3) in all species of *Dynomene* and *Hirsutodynomene*, while in *Metadynomene* width is approximately equal to length and in *Acanthodromia* and *Paradynomene* width is distinctly less (ratio 0.9 to 0.95) than length. In most species the lateral carapace margin is clearly defined and usually bears teeth. The exception is *Acanthodromia* where the anterolateral margin is poorly defined. The number of anterolateral teeth ranges from none, in *Acanthodromia*, *D. praedator* and *M. devaneyi* to six irregular teeth in *P. tuberculata*. Most dynomenids have four small anterolateral teeth.

In most dynomenids the carapace surface is smooth (or only minutely granulated) and gently undulating, but in some species there are spines or areolae. All the *Dynomene* species have a smooth carapace, species of *Hirsutodynomene* and *Acanthodromia* are spiny to varying degrees, while in *Paradynomene* the carapace is strongly areolate and granular.

The frontal margin in most dynomenids is without teeth. The margin is V-shaped, centered on the epistome, sweeping backwards and laterally above the eyes. The only exception is found in *Paradynomene tuberculata* which has a tri-dentate rostrum resembling some dromiid crabs (for further discussion see below under *P. tuberculata*).

A short frontal groove extends posteriorly from above the epistome, separating firstly, the left and right supraorbital margins, and secondly, a pair of rounded protuberances, whereupon it separates into two slightly divergent grooves which dwindle out posteriorly. Between these divergent grooves, there may be an elongate medial ridge. Further back are found two laterally-directed grooves: the first groove (cervical) arises from a small submedial pit and runs anterolaterally on to the branchial region where it may be joined by one of the divergent branches of the frontal groove. The second groove extends across the mid-line, initially running almost directly lateral but splits into an anterior branch which follows the first groove for a short distance, while the second branch curves posterolaterally bordering the anterior cardiac region. In effect the groove crossing the mid-line connects two crescent-shaped grooves with the second branch joining the branchial groove (if present) which runs towards the lateral carapace margin meeting it just in front of the last anterolateral tooth. The posterior cardiac region may or may not be well defined. The other grooves which may be evident are to be found under the anterolateral margin of the carapace: the pleural suture arises near the base of the antenna, curving around under the branchial region, giving off a short cervical groove which ascends towards the base of the first anterolateral tooth, and then running towards the base of the last anterolateral tooth where it may meet the branchial groove if it is evident.

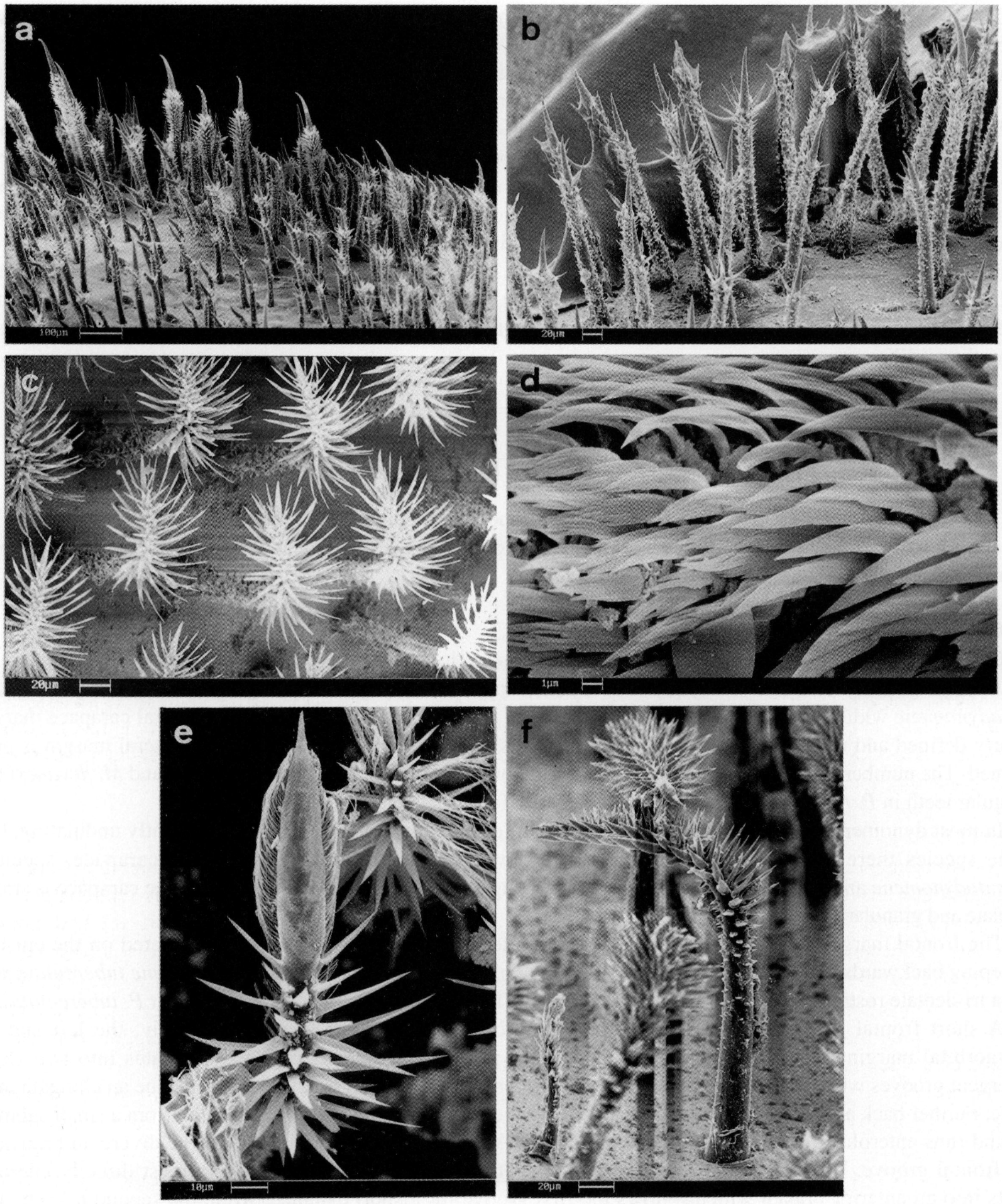

FIG. 3. — **a**, *Dynomene hispida* Guérin-Méneville, 1832, ♂ 11.6 x 9.2 mm, Somalia, Gesira, stn 12, intertidal coral (MZUF): setae on right posterolateral corner of carapace. — **b**, *Dynomene praedator* A. Milne Edwards, 1879, ♂ 9.6 x 7.8 mm, Somalia, Gesira, stn 19, intertidal coral: setae on left posterolateral corner of carapace. — **c-d**, *Dynomene 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**, *Dynomene 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**, *Hirsutodynomene 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 lead 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).

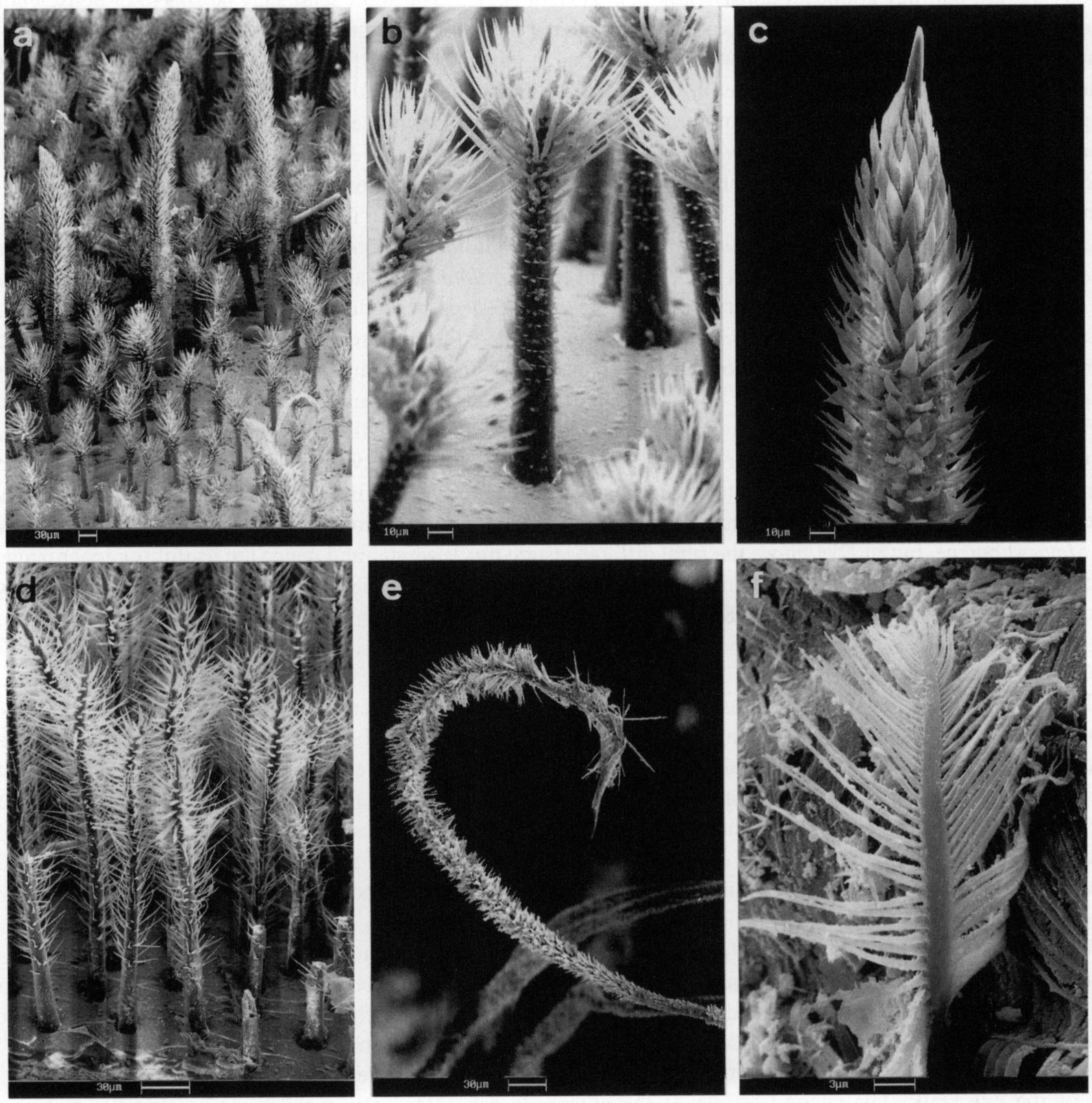

FIG. 4. — **a-c**, *Hirsutodynomene ursula* (Stimpson, 1860), ♂ 13.4 x 10.3 mm, Mexico, Espiritu Santo Id, *"Velero"*, stn 638-37, intertidal: **a**, long and short setae from left posterolateral corner of carapace; **b**, short setae from left posterolateral corner of carapace; **c**, setules on tip 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

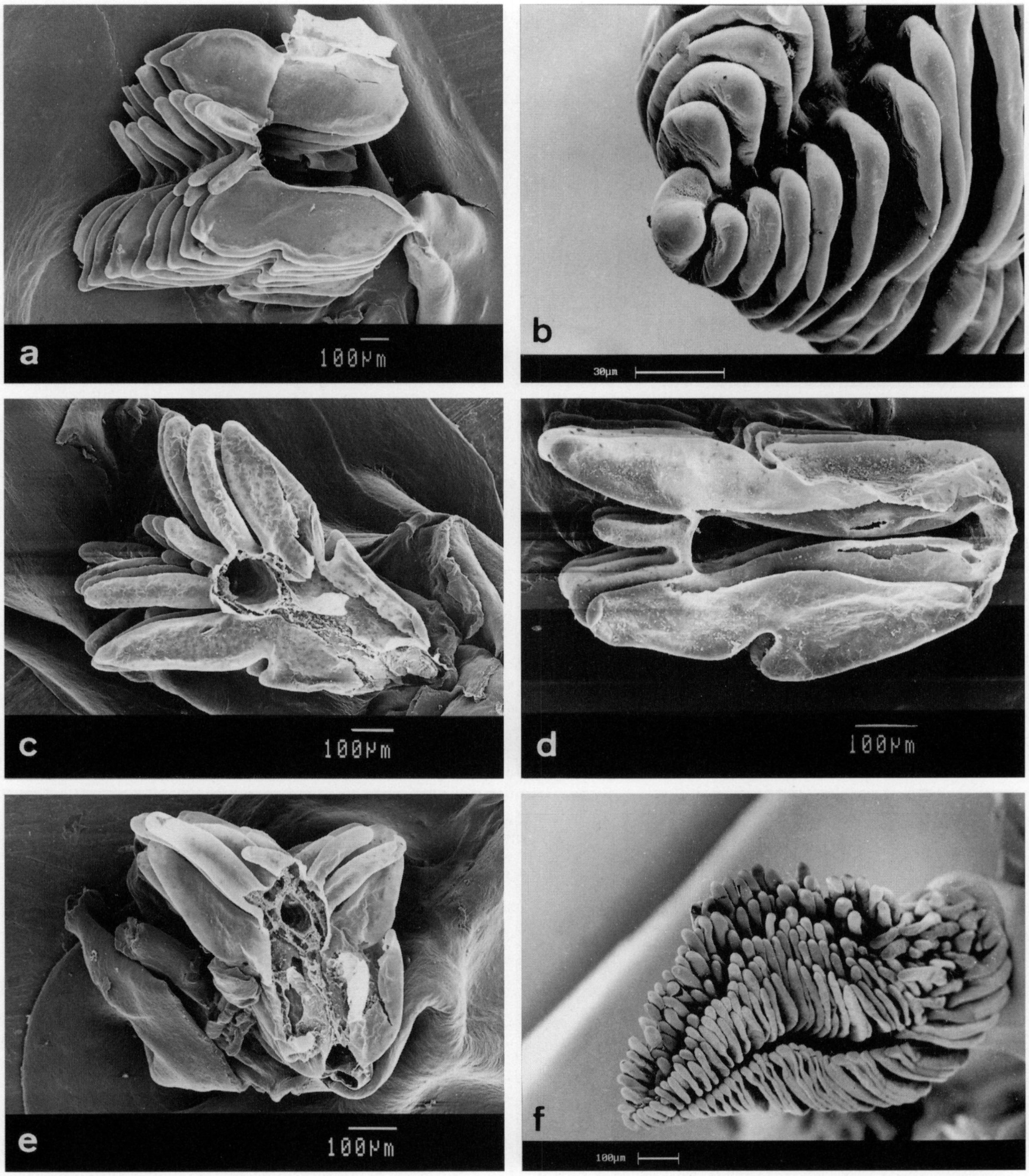

FIG. 5. — **a**, *Dynomene hispida* Guérin-Méneville, 1832, ♀ 14.0 x 10.8 mm, Hawaii, Oahu, (BPBM 658): transverse section through gill. — **b**, *Dynomene hispida* Guérin-Méneville, 1832, ♀ 10.3 x 8.9 mm, Cocos Keeling Ids. (WAM 751-89): apex of gill. — **c**, *Dynomene filholi* Bouvier, 1894, ♀ 10.0 x 8.7 mm, Cape Verde Ids, CANCAP, stn 7.125, 85-130 m: transverse section through gill. — **d**, *Dynomene pugnatrix* de Man, 1889, ♂ 9.8 x 7.2 mm, Mauritius (SMF 4857): transverse section through gill. — **e**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♀ 11.3 x 8.9 mm, Madagascar, Tuléar, stn 14-11-2, 5 m (MNHN-B 22077): transverse section through gill. — **f**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♂ 14.2 x 10.8 mm, Cocos-Keeling Ids., 0-37 m, (WAM 139-94): lateral view of whole gill. (All pictures taken with scanning electron microscope.)

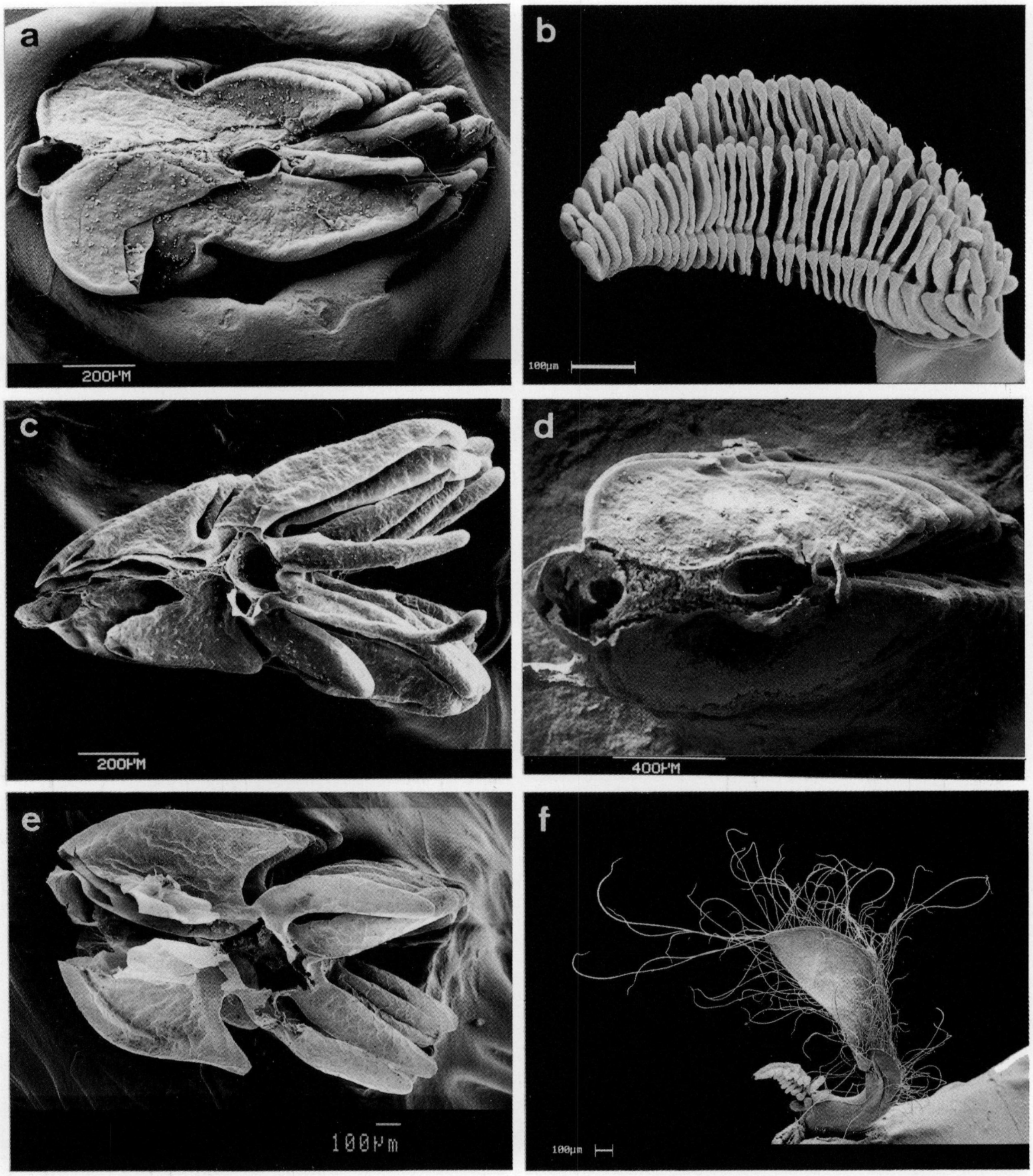

FIG. 6. — **a**, *Hirsutodynomene ursula* (Stimpson, 1860), ♀ ovig. 19.4 x 14.7 mm, ARGOSY 34 (USNM 247230): transverse section through gill. — **b**, *Hirsutodynomene ursula* (Stimpson, 1860), ♀ ovig. 15.0 x 12.2 mm, Ecuador, La Plata Id, *"Askoy"*, stn 80 (LACM): lateral view of whole gill. — **c**, *Metadynomene tanensis* (Yokoya, 1933), ♀ 19.2 x 18.9 mm, New Caledonia, MUSORSTOM 4, stn 215, 485-520 m: transverse section through gill. — **d**, *Acanthodromia erinacea* A. Milne Edwards, 1880, ♀ 16.7 x 17.7 mm, Yucatan, *"Blake"*, stn 166, 275 m (MCZ 6509): transverse section through gill. — **e**, *Paradynomene tuberculata* Sakai, 1963, ♂ 21.0 x 21.9 mm, New Caledonia, SMIB 8, stn DW 189, 400-402 m: transverse section through gill. — **f**, *Paradynomene tuberculata* Sakai, 1963, ♀ 21.5 x 21.2 mm, Loyalty Ids, MUSORSTOM 6, stn DW 406, 373 m (MNHN-B 25249): epipod and podobranch from left third pereopod. (All pictures taken with scanning electron microscope.)

more complex with the task being divided amongst eight appendages (second maxilla plus the seven epipods) as well as the body wall hypobranchial setae, compared to only three appendages (the maxillipeds). At least in part, this must be regarded as a consequence of having more gills. Besides the podobranchs, which are always small, dynomenids have thirteen large gills versus only eight or nine in other Brachyura. In order to transform the method of gill cleaning seen in dynomenids into that seen in more derived Brachyura, it is necessary to remove all the pereopodal epipods, elongate the epipod of the first maxilliped to clean the hypobranchial region, and remove the epipod of the third maxilliped from between the second and third arthrobranchs, and elongate it so that it covers the epibranchial gill surface. This is sufficient to clean the reduced number of gills and no change in the relative size of the second maxilliped epipod is necessary. Since gills are lost from the posterior part of the thorax, the field of setae on the hypobranchial wall is no longer necessary. The relationships between gill structure and gill cleaning mechanisms have been explored by SUZUKI & MCLAY (1998). Dynomenids have retained several plesiomorphic gill and gill cleaning characters.

In cross section the gills are basically violin-shaped, with afferent and efferent vessels in the 'body' of the gill and a notch on each side. Dynomenids show a great deal of variation in the shape of their gills, chiefly in the number of lobes (or filaments) on the epibranchial surface. BOUVIER (1896: 26, footnote) has already noted the variation in number of filaments along the length of each gill. Therefore in order to make comparisons between species it is necessary to standardize the point at which a cross section is taken and the gills which are used. Comparisons were made using a section across an arthrobranch or pleurobranch from the first two pereopods at approximately half the length from the point of attachment. Lobes on the gills are arranged in rows lengthwise, but they do not always lie in the same plane in cross section. This means that while the hypobranchial half of each gill is composed of a series of plates, the lobes do not always correspond exactly to each pair of plates. Furthermore, the lobes on the posterior side of the gill are usually longer than those on the anterior side.

In the type species *Dynomene hispida* and in *D. praedator* the gill cross section shows a pair of plates (or flattened lobes) on the epibranchial surface. In *D. pugnatrix* an additional short median lobe is added to make three. In *D. pilumnoides* there are four long lobes while in *D. filholi* there are six lobes decreasing in size medially. [My interpretation of the gills of *D. filholi* differs from that of BOUVIER (1896) who gave the number of filaments as being eight because he included the portion of the lateral notch as a filament, whereas I have treated them as part of the 'body' of the gill.] In both species of *Hirsutodynomene* there are six lobes decreasing in size medially. In *Metadynomene* the number of lobes increases from four (*M. tanensis*), five (*M. devaneyi*) to six (*M. crosnieri*). The gills of *Paradynomene tuberculata* have four lobes. In both species of *Acanthodromia* the epibranchial extensions consist of two flattened lobes. Thus within the Dynomenidae we have gills ranging from the multi-lobed trichobranchiate-like condition seen in *Hirsutodynomene* and *D. filholi*, through *D. hispida* and *D. praedator* in which the number of lobes is reduced to only two (which are flattened) and finally to the phyllobranchiate-like condition seen in *Acanthodromia*. But even in *Acanthodromia* the distinctive lateral notch is evident on each lamella of the gill so that they still differ from the condition found in dromiids, such as *Epigodromia*, *Hypoconcha*, and *Conchoecetes*, where the gill plates are rounded in outline, and not interrupted by notches. Dynomenid gills show little variation in numbers but great variation in shape, while gills of the Dromiidae show greater variation in numbers but almost no variation in shape.

BOUVIER (1896, figs 19, 23) compared the gill structure of *Dynomene filholi* which has several rows of "filaments" with *Acanthodromia erinacea* which has only two plates. He made comparisons with *Homarus vulgaris* as well as *Homolodromia paradoxa*, *Dicranodromia ovata*, and *D. mahieuxii*. Like the dynomenids, the latter two homolodromiid species have different numbers of epibranchial "filaments". BOUVIER regarded *D. mahieuxii* as being a little less primitive because it has fewer filaments which are more plate-like and he suggested that these gill plates might have originated by the concrescence of several short "filaments". In making the same comparison between the two dynomenids BOUVIER discussed the interesting problem of how a species such as *D. filholi* could have evolved a more advanced crab-like form and yet still retain such primitive homarid-like gills. He considered that *D. filholi*, more than any other dromiacean, showed close links with the homarids. BOUVIER argued that *D. filholi* cannot be considered as deriving from *Dicranodromia ovata* (BOUVIER used "*Acanthodromia ovata*", but this must be an error for "*Dicranodromia ovata*") which is, in many respects, more

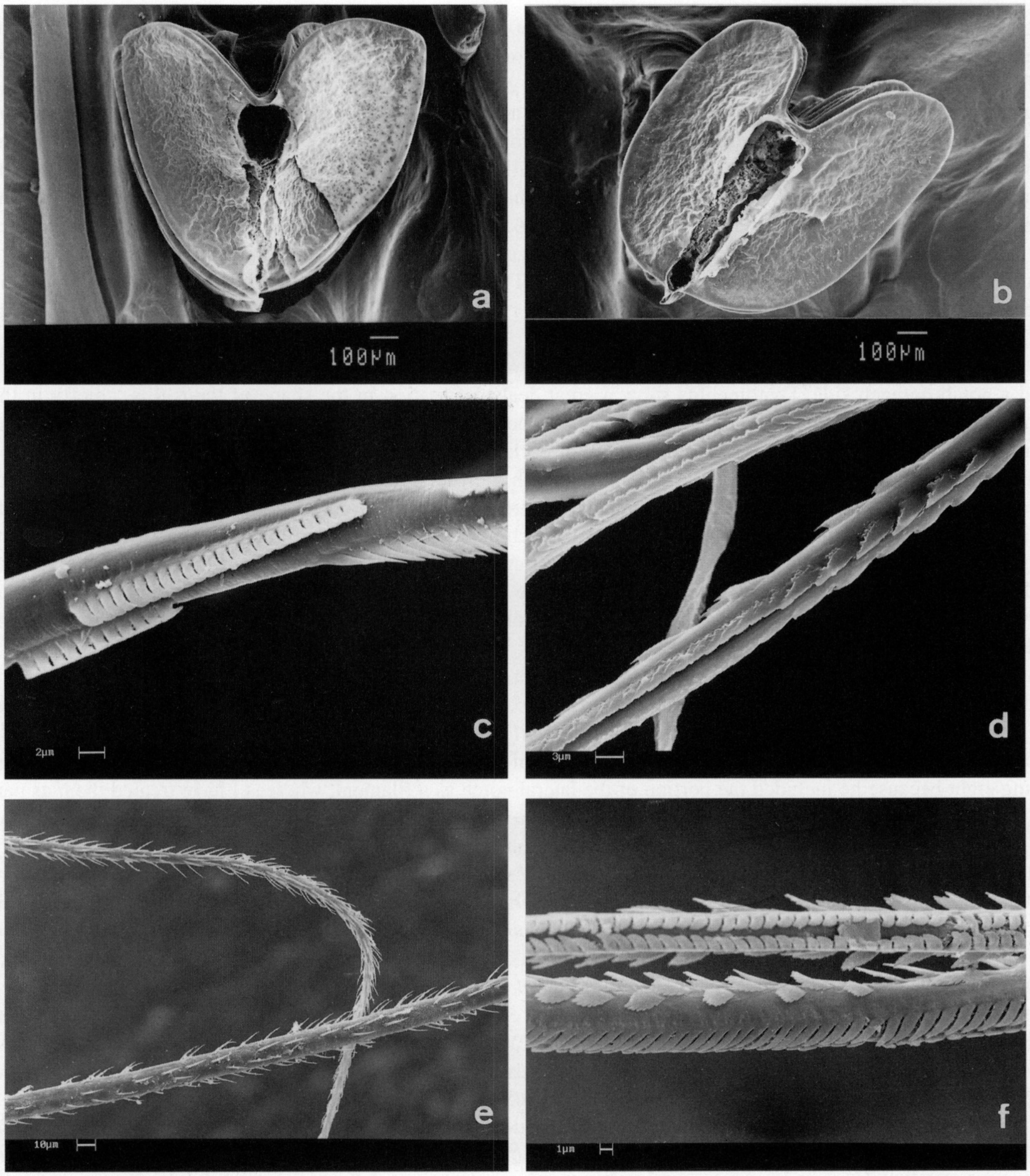

FIG. 7. — **a**, *Epigodromia areolata* (Ihle, 1913), ♂ 14.2 x 12.1 mm, New Caledonia, "*Vauban*", stn DW 1147, 210 m, 28.10.1989: transverse section through gill. (Dromiidae). — **b**, *Hypoconcha parasitica* (Linnaeus, 1763), ♂ 23.1 x 23.3 mm, Florida, off Panacea, coll. M. WICKSTEN: transverse section through gill. (Dromiidae). — **c**, *Paradynomene tuberculata* Sakai, 1963, ♂ 22.0 x 22.8 mm, New Caledonia, SMIB 3, stn 14, 246 m: cleaning setae from hypobranchial wall of right gill chamber. — **d**, *Dromia erythropus* (George Edwards, 1771), ♂ 81.5 x 62.7 mm, St. Croix, Virgin Ids (USNM 72355): cleaning setae from hypobranchial wall of right gill chamber. (Dromiidae). — **e**, *Paradynomene tuberculata* Sakai, 1963, ♀ 21.5 x 21.2 mm, Loyalty Ids, MUSORSTOM 6, stn DW 406, 373 m (MNHN-B 25249): cleaning setae on epipod from left third pereopod. — **f**, *Metadynomene tanensis* (Yokoya, 1933), ♀ 16.2 x 15.3 mm, New Caledonia, SMIB 8, stn DW 198, 414-430 m: long setae from posterior margin of the left scaphognathite. (All pictures taken with scanning electron microscope.)

primitive. He believed that other dynomenids are probably at a more advanced evolutionary state than *Dynomene praedator*, and it's possible that, as yet undiscovered species of "Acanthodromies", might be more primitive than *D. ovata*, so that it is possible to consider the genus *Acanthodromia* as being the link which connects the genus *Dynomene* to the primitive dromiaceans which originated from the homarids. This hypothesis, which now seems rather unlikely, is largely based on the resemblance of dynomenid gill structure to that found in homarids. Clearly BOUVIER considered phyllobranchiate-like gills as being derived from the trichobranchiate condition. The tendency to evolve phyllobranchiate-like gills seems to have occurred independently in the Homolodromiidae, Dynomenidae and Dromiidae since the last common ancestor of the three groups must have had multi-lobed gills.

PEREOPODS

Anterior pereopods: The first pereopods of dynomenids are longer than walking legs, chelate and sexually dimorphic, being larger in males. The meral article is long and trigonal in section, while the carpal article is distinctive in usually having a prominent sharp spur on the inner superior border. This feature is absent in *Metadynomene*, where there are three small tubercles, and in *Acanthodromia*, where the whole limb is spinous. The fixed finger is straight and is armed with from two to eight small teeth often increasing in size distally. The number of teeth on the dactyl is usually less than on the opposing finger. The tips of both fingers are usually dentate. In *Dynomene*, *Hirsutodynomene* and *Acanthodromia* the dactyl is down-curved so that the fingers gape, but in *Metadynomene* and *Paradynomene* the dactyl is essentially straight so there is little gap and the fingers touch for about half their length. Both fingers are hollowed out internally with a bunch of stiff setae inserted near the base of each finger and projecting across the gap between them. In *Dynomene* and *Hirsutodynomene* these setae are very well developed, forming a screen or sieve behind the outer dentate margins. Observations on *D. praedator* show that these setae help to sift out food particles which are passed to the third maxillipeds (see below).

The second through fourth pereopods are well developed walking legs of similar size to the first pereopods or slightly smaller. They tend to decrease in length posteriorly. Plane of movement of the sternal-coxal articulation is anterior-posterior, for the ischial-basis articulation plane of movement is dorso-ventral, the meral-ischial articulation has a small anterior-posterior plane of movement, the carpal-meral articulation is also dorso-ventral, the propodal-carpal articulation moves anterior-posterior, and finally the propodal-dactyl articulation is dorso-ventral. Dactyli are long and curved with their inner margins usually armed with two to six small spines which are probably used to grasp the substrate on which the crabs live. There is no clear pattern of variation in number of spines between the genera. The only exception is *Dynomene pugnatrix* which has ten dactyl spines. This may indicate that it lives in association with a different kind of host or habitat. At least some of the other shallow water species are known to live among corals and coral debris.

Fifth pereopod (Figs 8 a-f, 9 a-f, 10 a-d, 11): Perhaps the most distinctive feature of the Dynomenidae is the very reduced last pair of pereopods which are carried alongside the posterolateral corners of the carapace, above the base of the fourth pereopods. The reduced leg is directed anteriorly. It is commonly stated that dynomenids, like dromiids, carry their last legs in a dorsal or subdorsal position, but this is not correct. This limb cannot rise above the level of the carapace margin because it is too short and relatively immobile and so cannot be described as dorsal or subdorsal. A more accurate description would be that the limb is "horizontal". Most of the scope for movement in this limb is attributable to the coxo-basal article because the remaining joints are scarcely moveable. The basis-ischium articles are fused in all species, and in *Acanthodromia erinacea* and *Paradynomene tuberculata* the merus is also fused to the preceding articles. The inferior distal margin of the merus is hollowed out as in the previous three limbs. However, it is the anterior distal border of the propodus which is extended to form the fixed finger of the subchelate mechanism and when the limb lies in its natural position the dactyl is almost ventral, the opposite of the cheliped. Observations on live *D. praedator* show that these limbs have a very restricted scope for movement: they are only capable of moving in an anterior-posterior plane above the bases of the preceding pereopods. Most of the time they simply lie alongside the posterolateral corner of the carapace, but when the crab moves using its pereopods, they often move at the same time as though they are part of the coordinated pattern of limb movements. The last legs cannot reach above on to the posterolateral corner of the carapace or beneath the crab into the abdominal cavity. Thus they are not capable of carrying a piece of camouflage or performing a grooming role.

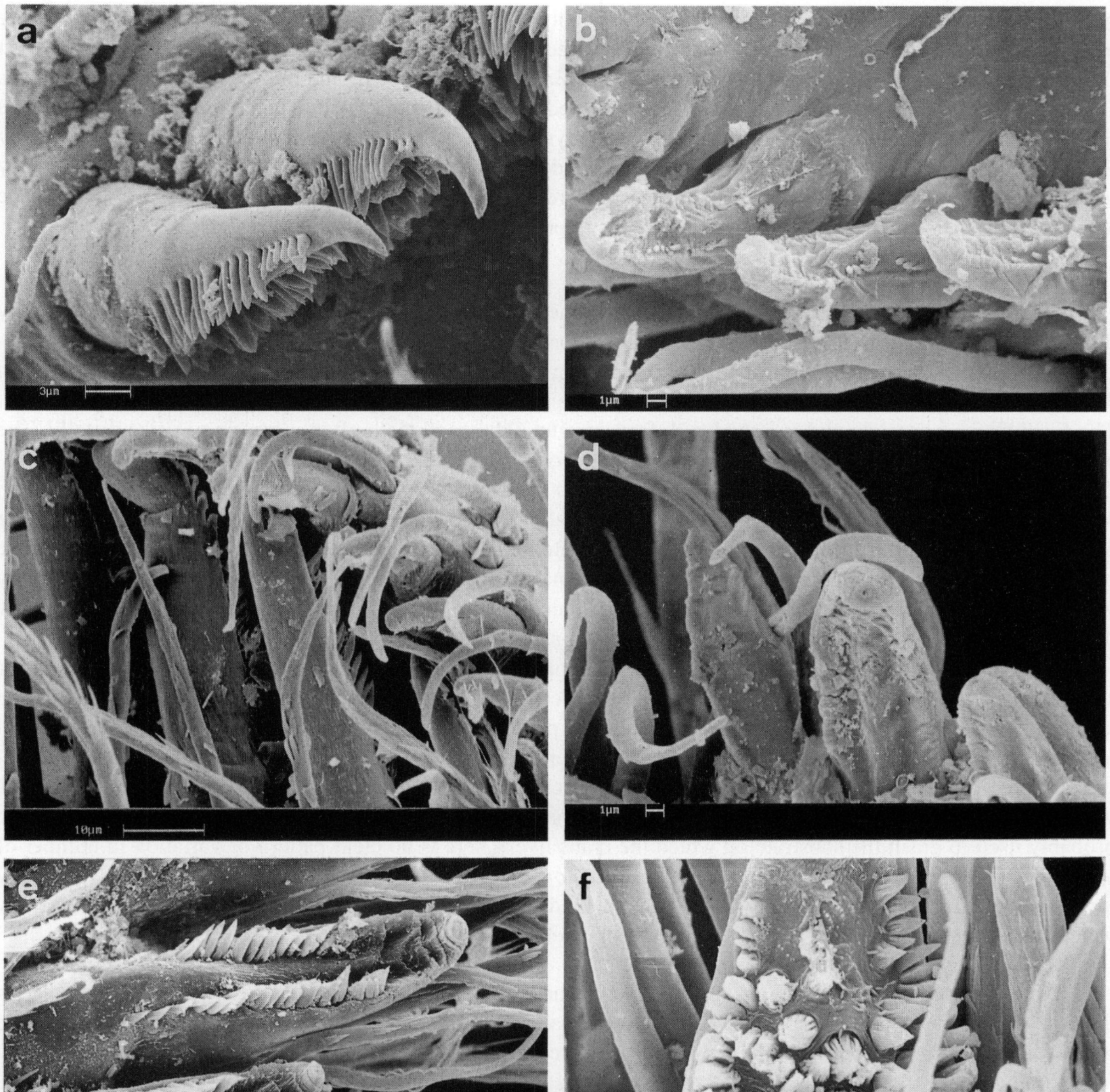

FIG. 8. — **a**, *Dynomene praedator* A. Milne Edwards, 1879, ♂ 9.6 x 7.8 mm, Somalia, Gesira, stn 19, intertidal coral (MZUF): propodal spines from left fifth pereopod. — **b**, *Dynomene praedator* A. Milne Edwards, 1879, ♀ ovig. 9.6 x 7.5 mm, Glorieuses Ids, intertidal: dactyl spines from right fifth pereopod. — **c**, *Dynomene filholi* Bouvier, 1894, ♀ 10.0 x 8.7 mm, Cape Verde Ids, CANCAP, stn 7.125, 85-130 m: dactyl and propodal spines from left fifth pereopod. — **d-e**, *Dynomene pilumnoides* Alcock, 1900, ♀ 12.8 x 10.3 mm, New Caledonia, VOLSMAR, stn DW 7, 400 m: **d**, dactyl spines from left fifth pereopod; **e**, propodal spines from left fifth pereopod. — **f**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♀ 23.8 x 17.8 mm, Cocos Keeling Ids, 0-28 m (WAM 723-89): propodal spine from left fifth pereopod. (All pictures taken with scanning electron microscope.)

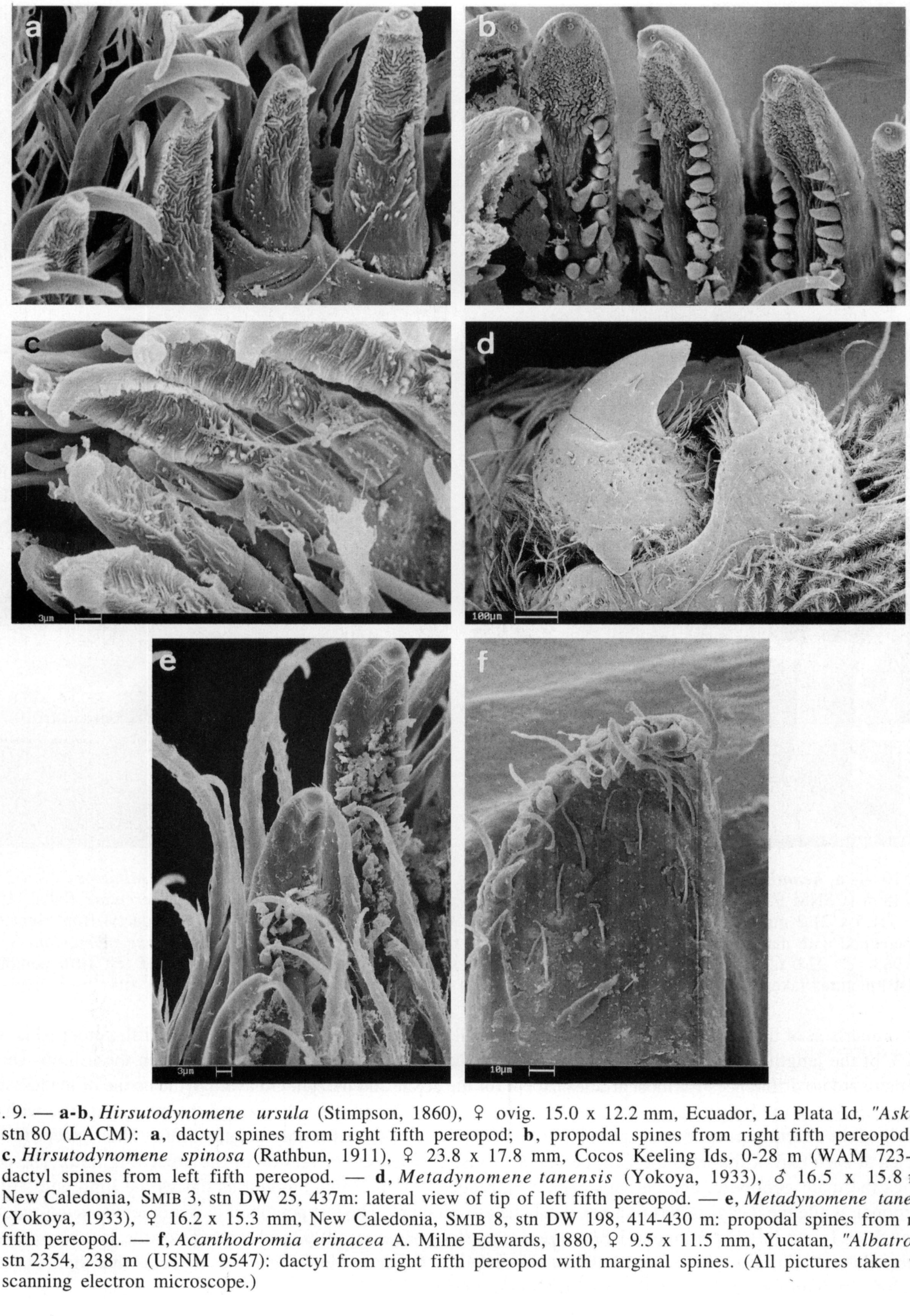

FIG. 9. — **a-b**, *Hirsutodynomene ursula* (Stimpson, 1860), ♀ ovig. 15.0 x 12.2 mm, Ecuador, La Plata Id, *"Askoy"*, stn 80 (LACM): **a**, dactyl spines from right fifth pereopod; **b**, propodal spines from right fifth pereopod. — **c**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♀ 23.8 x 17.8 mm, 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.)

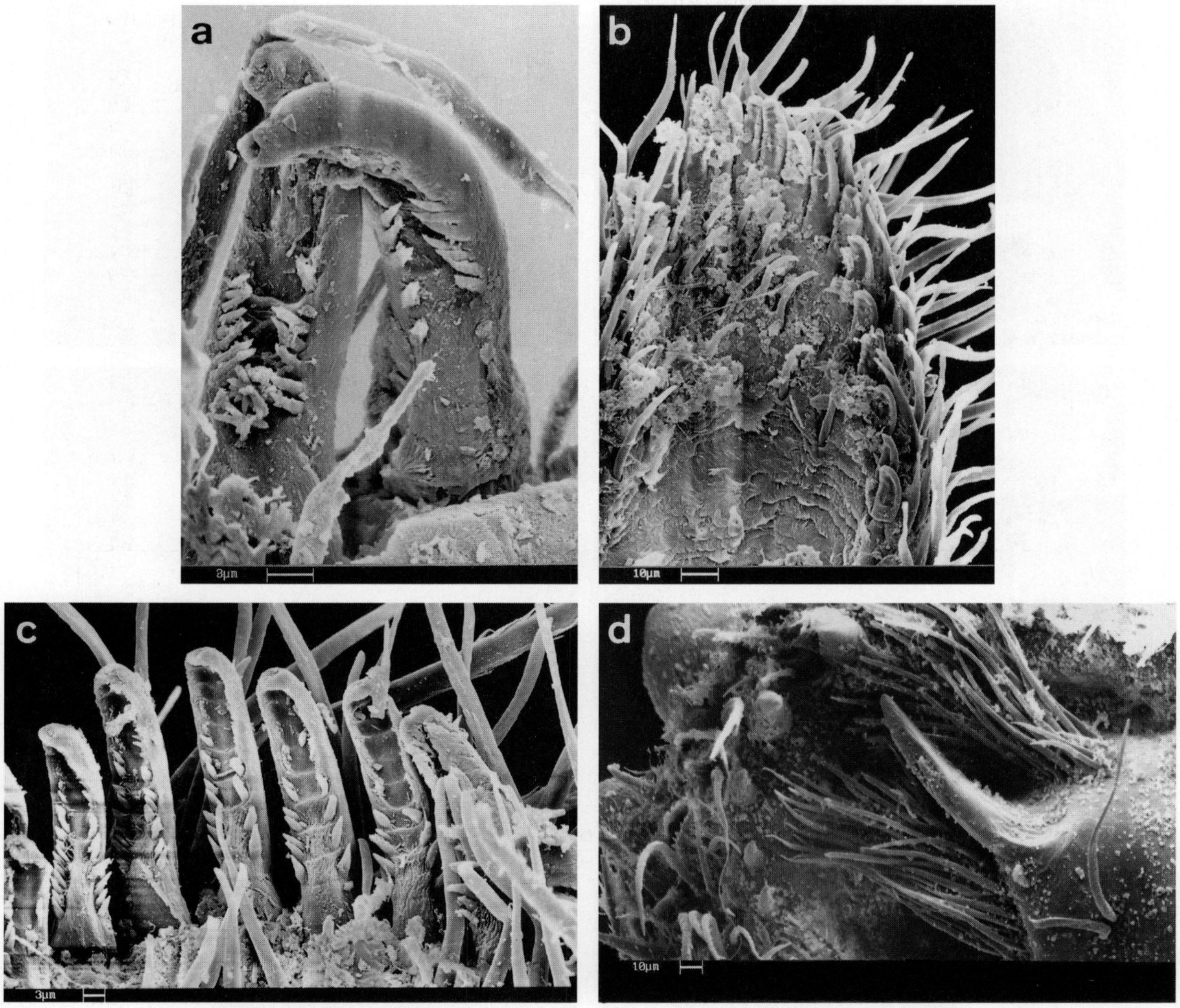

FIG. 10. — **a**, *Acanthodromia erinacea* A. Milne Edwards, 1880, ♀ 9.5 x 11.5 mm, Yucatan, *"Albatross"*, stn 2354, 238 m (USNM 9547): propodal spines from right fifth pereopod. — **b-c**, *Paradynomene tuberculata* Sakai, 1963, ♀ 21.5 x 21.2 mm, Loyalty Ids, MUSORSTOM 6, stn DW 406, 373 m (MNHN-B 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.

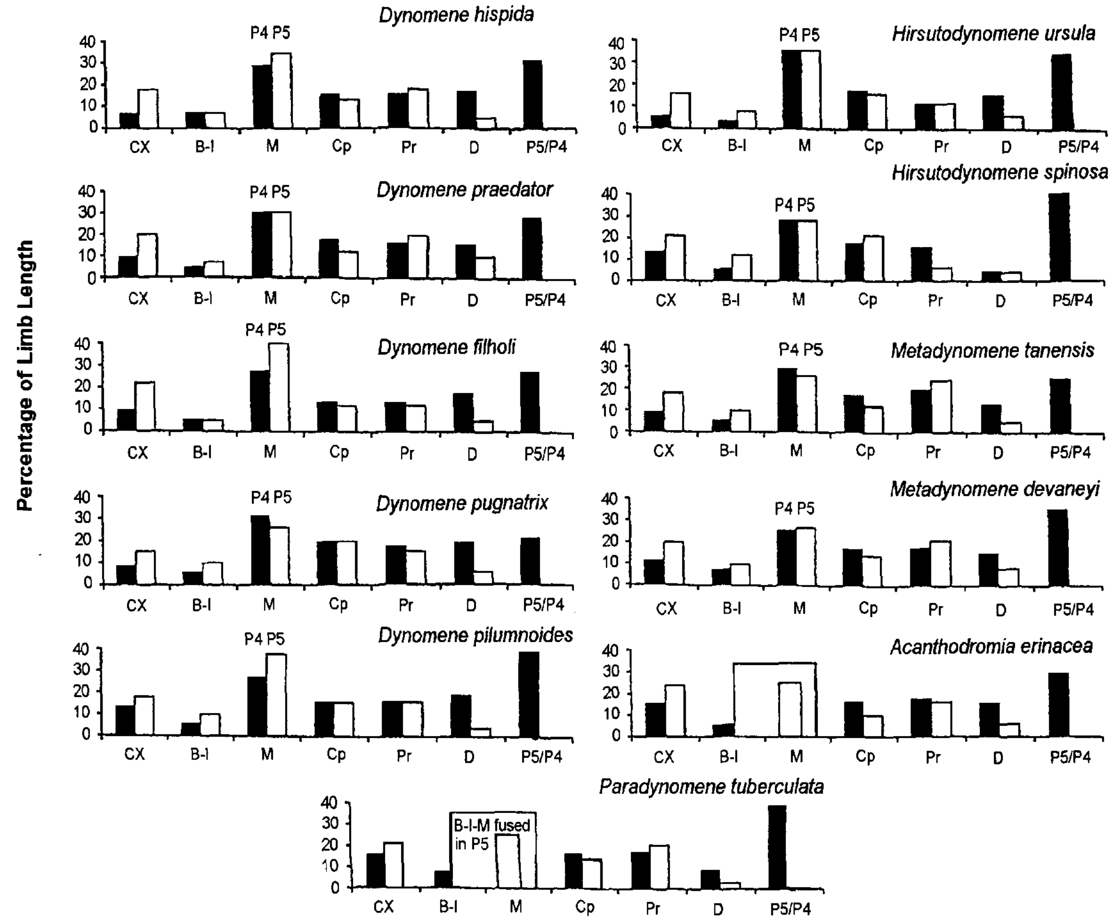

FIG. 11. — Relative size of articles of the last two pereopods of *Dynomene hispida*, *D. praedator*, *D. filholi*, *D. pugnatrix*, *D. pilumnoides*, *Hirsutodynomene ursula*, *H. spinosa*, *Metadynomene tanensis*, *M. devaneyi*, *Acanthodromia erinacea* and *Paradynomene tuberculata*. From left to right, 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).

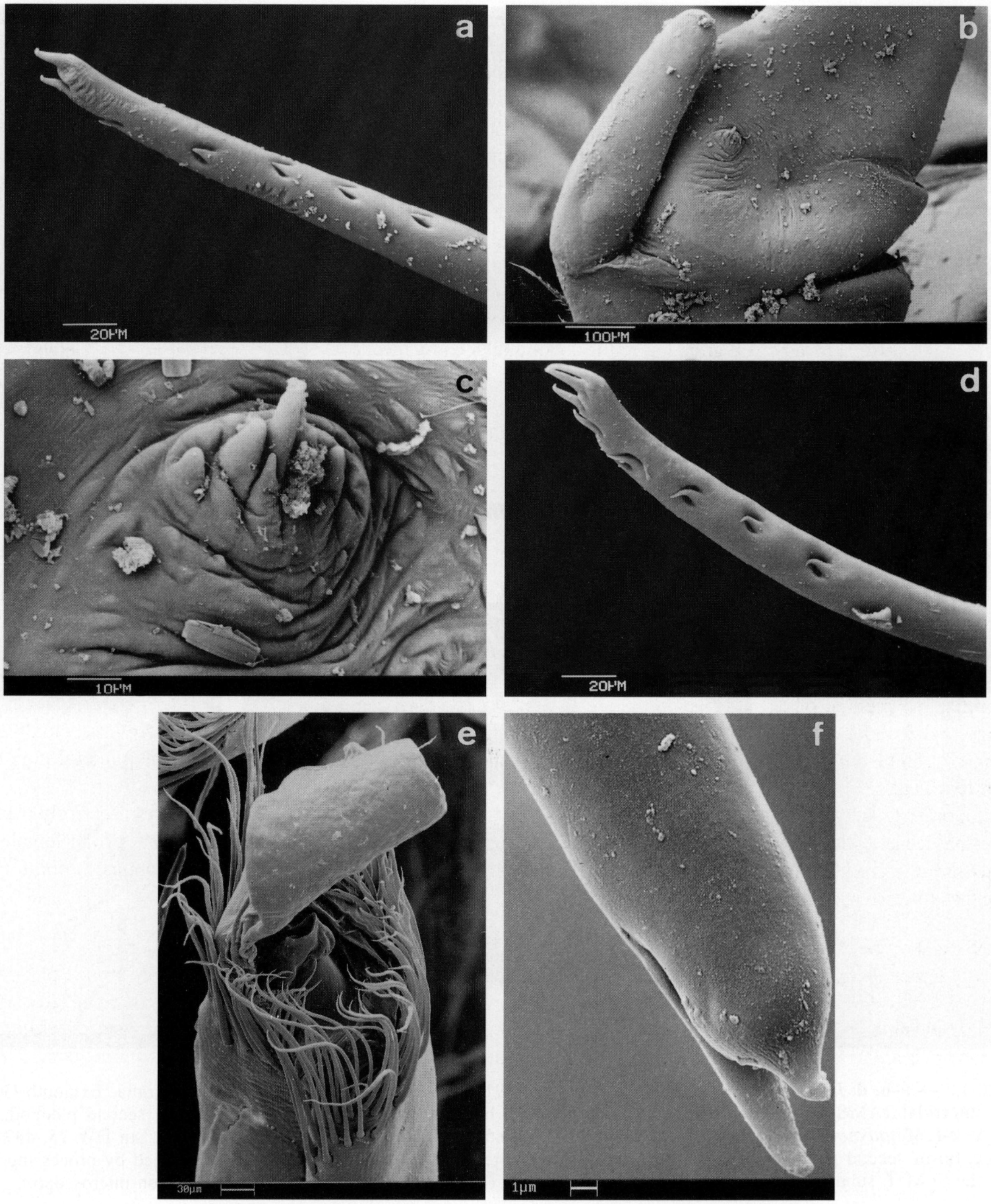

FIG. 12. — **a-c**, *Dynomene hispida* Guérin-Méneville, 1832, ♂ 11.6 x 9.2 mm, Somalia, Gesira, stn 12, intertidal coral (MZUF): **a**, tip of right second pleopod; **b**, inner surface of exopod and base of left second pleopod showing location of secretory tegumental gland; **c**, close up of secretory 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.)

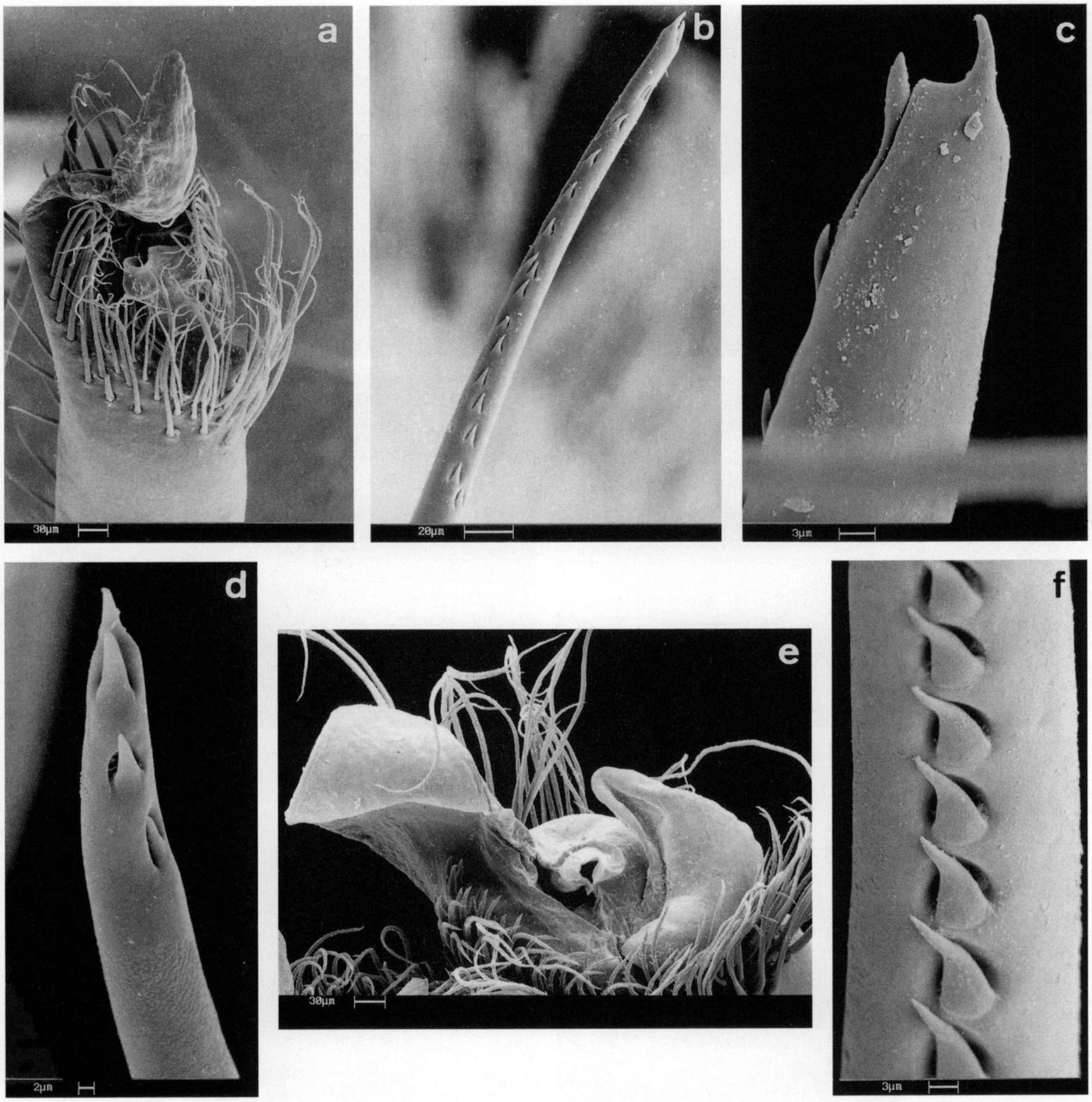

FIG. 13. — **a-b**, **d**: *Hirsutodynomene spinosa* (Rathbun, 1911), ♂ 19.6 x 14.5 mm, Western Australia, Exmouth Gulf, intertidal (AMS-P19118): **a**, tip of left first pleopod; **b**, right second pleopod; **d**, tip of left second pleopod. — **c**, **e-f**, *Metadynomene tanensis* (Yokoya, 1933), ♂ 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
Dynomene hispida	2 straight spines	5 arranged sinuously over 180°, none overlapping	Apical
Dynomene praedator	3 straight spines	5 arranged sinuously over 90°, none overlapping	Apical but with tips curved laterally
Dynomene filholi	1 straight spine	10 arranged sinuously over 90°, none overlapping	Apical
Dynomene pilumnoides	2 curved spines	15 arranged sinuously over 180°, none overlapping	Apical
Hirsutodynomene spinosa	2 straight spines	16 curving from anterior to posterior surface and back again, some overlapping	Apical
Hirsutodynomene ursula	2 curved spines	20 curving from anterior to posterior surface and back again, some overlapping	Apical
Metadynomene tanensis	2 curved spines	24 along anterior surface of pleopod, none overlapping	Apical but with tips curved laterally
Paradynomene tuberculata	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, *Stimdromia 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.

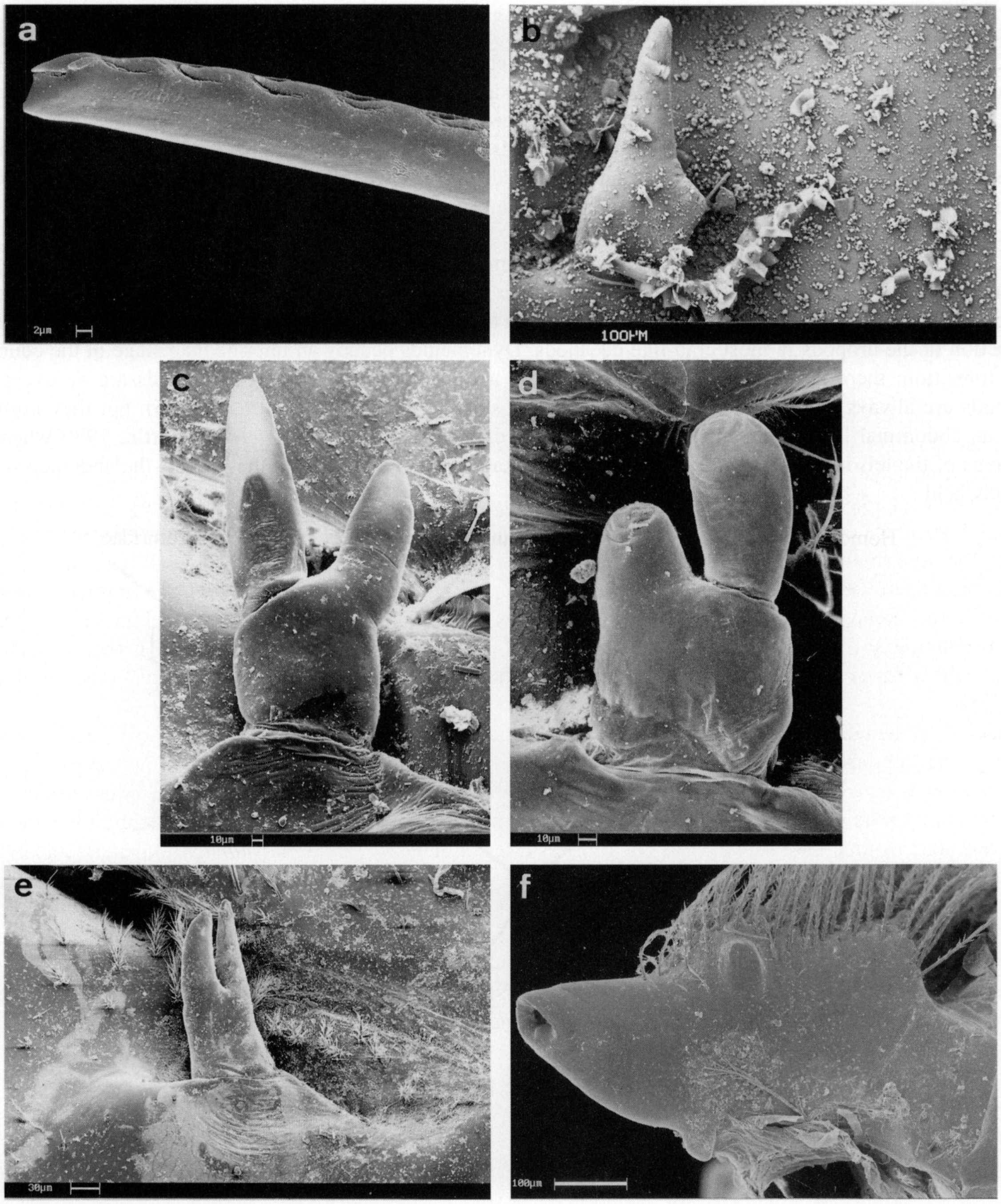

FIG. 14. — **a**, *Paradynomene tuberculata* Sakai, 1963, ♂ 22.0 x 22.8 mm, New Caledonia, SMIB 3, stn 14, 246 m: tip of second pleopod. — **b**, *Dynomene praedator* A. Milne Edwards, 1879, ♂ 10.8 x 8.5 mm, Somalia, Gesira, stn 14, intertidal coral (MZUF): male right fifth pleopod. — **c**, *Dynomene pilumnoides* Alcock, 1900, ♂ 23.5 x 19.0 mm, New Caledonia, SMIB 3, stn 18, 338 m: male left fifth pleopod. — **d**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♂ 19.6 x 14.5 mm, Western Australia, Exmouth Gulf, intertidal (AMS-P19118): male right fifth pleopod. — **e**, *Metadynomene tanensis* (Yokoya, 1933), ♂ 16.5 x 15.8 mm, New Caledonia, SMIB 3, stn DW 25, 437 m: male left fifth pleopod. — **f**, *Hirsutodynomene ursula* (Stimpson, 1860), ♂ 13.4 x 10.3 mm, Mexico, Espiritu Santo Id, *"Velero"*, stn 638-37, intertidal: coxal article of right fifth pereopod. (All pictures taken with scanning electron microscope.)

UROPODS

Compared to other dromiaceans the uropods are very well developed in dynomenids and usually sexually dimorphic. In *Dynomene* and *Hirsutodynomene* uropods are larger in females than in males. Uropods in both male and female *Metadynomene* fill the entire margin between the telson and penultimate abdominal segment and in *Paradynomene* about half the margin. In some dromiids the uropods are reduced and in some cases vestigial or absent. When present they have a role in the abdominal locking mechanism but this is not true in dynomenids because, for the most part, they do not have effective means of locking their abdomen. Compared to dromiids, dynomenid uropods are plesiomorphic.

Uropods are the uniramous remnant of a biramous limb which formed part of the tail-fan in a distant ancestor. Reduction of this appendage is associated with reduction in the size of the whole abdomen and its folding beneath the cephalothorax. There is an obvious trade off between the development of an abdominal locking mechanism and reduction of the uropods in most crab-like decapods. Dynomenids occupy an intermediate stage in the course of this transition: there is only minimal restraint of the abdomen. However homolodromiids are an exception: uropods are always rudimentary, represented by only small ventral lobes (GUINOT, 1995), but they normally lack an abdominal locking mechanism (except in the case of *Dicranodromia felderi* Martin, 1990 where the margins of the telson are held under flanges on the coxae of the chelipeds). In these crabs the abdomen is only loosely held.

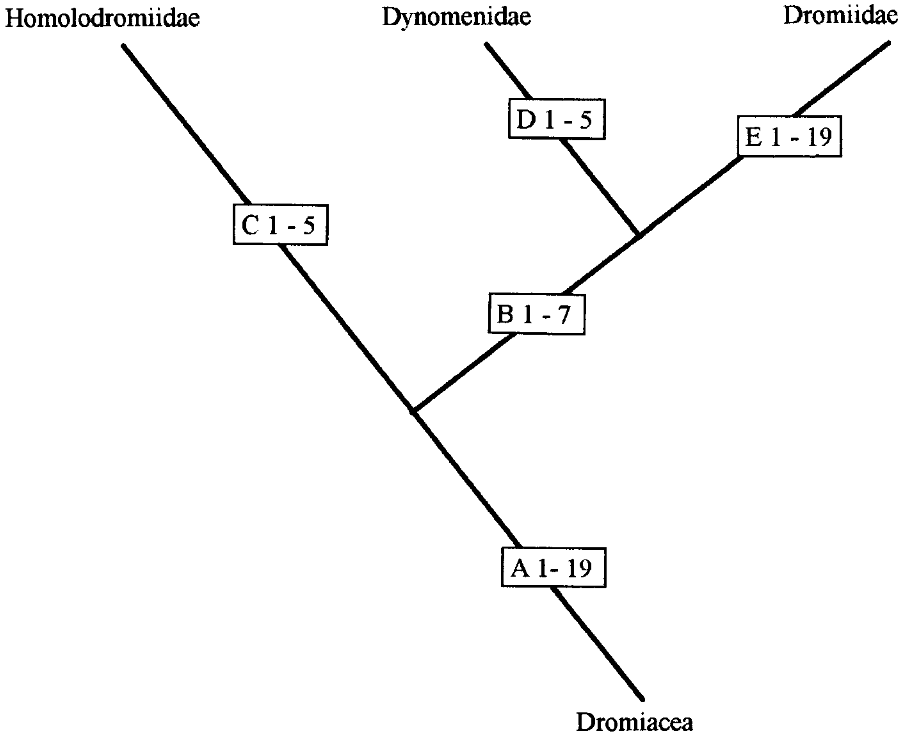

FIG. 15. — Cladogram showing the assumed relationships between the families of the Dromiacea. Numbers refer to apomorphic and plesiomorphic characters mapped on to this hypothesis (see text).

PHYLOGENETIC RELATIONSHIPS

I do not intend to closely examine the question of brachyuran monophyly. In their analysis of the relationships of reptant Decapoda, SCHOLTZ & RICHTER (1995) list the morphological apomorphies of the Brachyura as: a fossa orbito-antennularis surrounds the eyestalk and antennule, third maxilliped operculate or semi-operculate, orientation of the cheliped fingers so that the dactyl is external, all thoracic sternites fused to form the sternum, an abdomen which is reduced, ventrally flexed and sexually dimorphic, and uropods are reduced or absent. BAUER (1989) considered the use of setiferous maxillipedal epipods for gill cleaning to be a strong character confirming brachyuran monophyly. I agree with this suggestion, although the more elaborate nature of podotreme gill cleaning, with the retention of several plesiomorphic characters, does make the explanation more complex. Proposals to remove some podotreme families from the Brachyura do not seem to be worthy of serious consideration since the arguments are usually based on the occurrence of plesiomorphic larval characters and if followed would create even greater mayhem than currently exists. I accept the argument, by SCHOLTZ & RICHTER, that evolution has proceeded faster in the adult than in the larval characters so that some podotreme families show a mosaic of plesiomorphic and apomorphic characters. The morphological apomorphies listed above and spermatological apomorphies (see JAMIESON, 1994; JAMIESON *et al.*, 1995) seem to provide convincing evidence of brachyuran monophyly. The questions about the relationships within the Brachyura seem much more interesting.

GUINOT (1978) divided the Brachyura into three major groups: Podotremata, Heterotremata and Thoracotremata. The Podotremata were divided into two groups containing the following extant families: Dromiacea, including the Homolodromiidae, Dynomenidae and Dromiidae, and the Archaeobrachyura, including the Poupiniidae, Latreillidae, Homolidae, Cyclodorippidae, Cymonomidae and Raninidae. The phylogenetic relationships between some of these groups has been explored by GUINOT *et al.* (1994) using characters based on spermatozoal ultrastructure. They were able to differentiate between apomorphic and plesiomorphic characters of the Podotremata, Heterotremata + Thoracotremata as well as the Brachyura as a whole. Within the Podotremata they provide evidence of monophyly of this group. Using morphological characters I have carried out a similar exercise. I first of all map the plesiomorphic and apomorphic characters of the Dromiacea (Fig. 15) and then examine the implications of these characters for the Archaeobrachyura (Fig. 16). I assume that the most parsimonious interpretation of characters is correct. The main question here is whether or not the Podotremata are monophyletic.

If we assume that the more crab-like Dynomenidae and Dromiidae are sister groups and together are the sister group of the less crab-like Homolodromiidae, then we can display their relationships as in Fig. 15. The characters (A1 - 19) shared by the ancestor of these three families must be: 1) carapace longer than wide, 2) carapace lacking a margin, 3) branchiostegite membranous, 4) first antennal article beak-like, 5) pediform third maxillipeds, 6) crista dentata present, 7) propodus of second and third pereopods with a distal spine and a row of spines on the inner margin of the dactyl, 8) fourth and fifth pereopods reduced, subdorsal, subchelate, 9) propodal and dactyl spines on last two pairs of pereopods as found in *Dicranodromia*, 10) fifth pereopod with a spine on the outer margin of the dactyl, 11) abdomen large and only loosely folded under the body, 12) well developed uropods and no abdominal locking mechanism, 13) five pairs of pleopods in both sexes (first pair vestigial in the female and last three pairs rudimentary in the male), 14) short female sternal sutures 7/8, 15) needle-like second male pleopods without spines, 16) calcified coxal sperm tube carrying sperm to the base of the second pleopod, 17) twenty trichobranchiate-like notched gills, 18) long setae on posterior margin of scaphognathite, and 19) seven epipods.

Assumption 9) (above) implies that the dromiacean ancestor was well equipped to carry camouflage. It is assumed that the last two pairs of pereopods resembled those found in *Dicranodromia* (Homolodromiidae) but camouflage-carrying is unknown in this genus (or this family for that matter) (GUINOT *et al.*, 1995). Since the structure of these limbs is very similar to that found in *Sphaerodromia* (Dromiidae), which does carry pieces of sponge, I predict that camouflage-carrying homolodromiids will be found. Thus I assume that the dromiacean ancestor was a camouflage crab and that the particular kind of camouflage behaviour is an apomorphy of the Dromiacea.

The shared characters (B1 - 7) of the crab-like ancestor of the Dynomenidae and Dromiidae are: 1) carapace margin present, 2) carapace wider than long, 3) operculiform third maxillipeds, 4) abdomen reduced and folded more tightly under the body, 5) rudimentary abdominal locking mechanism, and 6) development of hypobranchial cleaning setae on the inner wall of the branchial chamber. An additional character (7) shared by all dynomenids and some of the primitive dromiids (e.g. *Sphaerodromia*) is the presence of an oval apical plate on the tip of the first male pleopod. The presence of this plate may be correlated with the fact that the females have posteriorly located spermathecae and consequently very short sternal sutures 7/8. The apical plate may help to ensure efficient transfer of sperm into the spermathecae.

The apomorphies (D1 - 5) of the Dynomenidae are: 1) the lack of distal propodal spines on the second to fourth pereopods, 2) development of a unique vestigial fifth pereopod carried horizontally, 3) sexually dimorphic chelate structure of the fifth pereopod, 4) reversion of the fourth pereopod to being a fully developed walking leg and 5) development of a row of spines on the second male pleopod. Perhaps the most controversial point here is the implied reversion of the fourth pereopod to being a fully functional walking leg. *Acanthodromia* lacks a beak-like first antennal article, characteristic of the Dromiacea, and a crista dentata. These must be regarded as secondary modifications.

The apomorphies (E1 - 9) of the Dromiidae are: 1) usually only two pairs of pleopods in the male (but some species of *Sphaerodromia*, *Eodromia* and *Dromia* for e.g. have retained the ancestral three pairs of rudimentary pleopods on abdominal segments 3-5), 2) soft tube-like extension of coxal article carrying sperm to the base of first pleopod, 3) spermathecae often located anterior to female genital openings and consequently the sternal sutures 7/8 are much longer, 4) gills are phyllobranchiate, 5) gill numbers reduced because there are only three or four epipods (although *Sphaerodromia* species have up to seven epipods), 6) loss of long setae on posterior margin of scaphognathite (still present in *Sphaerodromia*), 7) abdomen reduced, 8) uropods reduced (sometimes absent), and 9) a well developed locking mechanism for the abdomen involving the bases of the first two pereopods and sometimes the uropods. It is apparent that there are exceptions to several of these characters some of which have evolved within the Dromiidae. Strictly speaking, the only apomorphies, shared by all members of the family, are the possession of phyllobranch gills and a well developed abdominal locking mechanism. Since *Sphaerodromia* obviously provides several exceptions to the above list of characters, it could be proposed that this genus should shifted to the Homolodromiidae, but this would require the assumption that phyllobranchiate gills and the coxal abdominal locking mechanism had evolved independently within this family. By themselves these assumptions are not necessarily unreasonable because, after all, phyllobranch gills and an abdominal locking mechanism have evolved independently in *Acanthodromia* (Dynomenidae), so why couldn't this have also occurred in the Homolodromiidae? GUINOT (1979, p. 256) noted that the homolodromiid thoracic endophragmal skeleton is of a unique type and is different from the dromiid + dynomenid skeleton. This skeletal difference provides the strongest evidence for retaining *Sphaerodromia* in the Dromiidae (GUINOT, pers. comm.). This hypothesis is more parsimonious but it requires the assumption that the species in this genus have retained several plesiomorphic characters. Further aspects of the dromiid-homolodromiid relationship are discussed by GUINOT (1995: 168-185).

Finally, the Homolodromiidae: the only apomorphic characters (C1 - 5) which this group has are 1) reduction of uropods (GUINOT, 1993), 2) loss of the long setae from the scaphognathite, 3) presence of well developed abdominal pleurae, 4) possession of a very elongate telson, and 5) development of a spine-bearing distal propodal extension on the last two pairs of legs. However, both of the first two are shared with the Dromiidae. It is difficult to know whether the unusually elongate telson, which forms the floor of the sterno-abdominal cavity, and the abdominal pleurae are apomorphies or plesiomorphies. Along with the membranous branchiostegite, they may well have been features of the dromiacean ancestor and therefore plesiomorphies. The development of a spine-bearing distal propodal extension on the last two pairs of legs might be regarded as an apomorphy, but it only occurs in *Homolodromia* while *Dicranodromia* retains the assumed ancestral condition. The semi-crab-like Homolodromiidae can only be defined by a combination of plesiomorphic characters and synapomorphies. It is interesting to note that JAMIESON *et al* (1995) concluded that "*Homolodromia* displays a remarkable mixture of dromiid and dynomenid spermatozoal features while lacking any distinctive apomorphy.... ". Therefore the morphological and spermatological features of the Homolodromiidae are in close agreement.

The question of monophyly of the Podotremata is more difficult to decide. Are the Dromiacea the sister group of the rest of the Brachyura (see Fig. 16 b) or are they the sister group of only the Archaeobrachyura (see Fig. 16a)? If the first alternative is true then the Dromiacea and each of the major groups within the Archaeobrachyura must be independently derived from the brachyuran line and all these crab-like animals must be paraphyletic. Another possibility is that the Archaeobrachyura are monophyletic and are the sister group

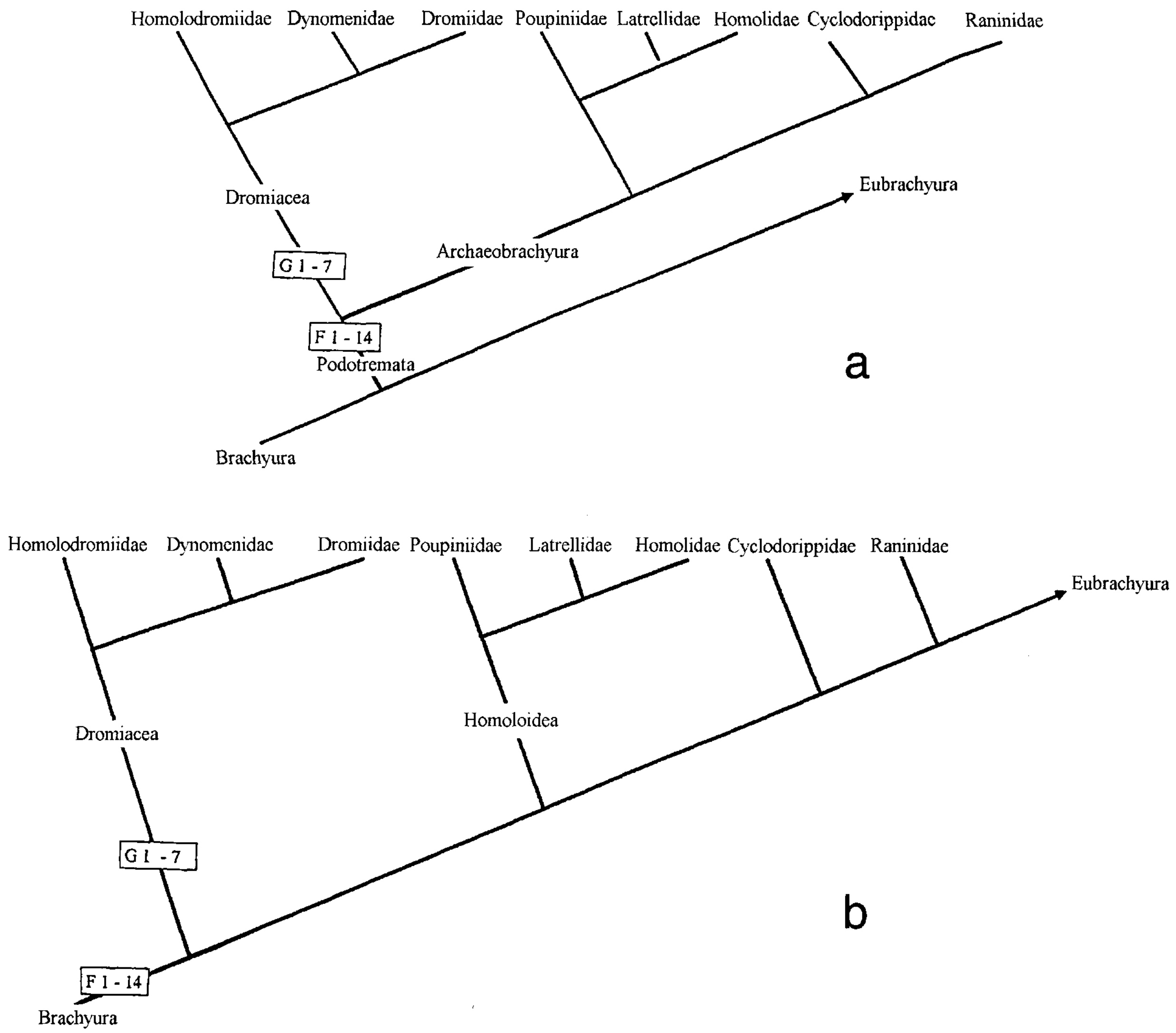

FIG. 16. — Cladogram showing two different relationships between the families of the Podotremata: **a**, the Podotremata are assumed to be monophyletic (modified after GUINOT *et al.*, 1994); **b**, the Podotremata are assumed to be paraphyletic (modified after SCHOLTZ & RICHTER, 1995). Numbers refer to apomorphic and plesiomorphic characters mapped on to these hypotheses (see text).

of the Eubrachyura. Since it is beyond the scope of this work to examine the detailed relationships within the Archaeobrachyura, I confine my attention to the case represented in Fig. 16b. JAMIESON (1994) and JAMIESON *et al.* (1995) have argued that spermatologically the Podotremata Guinot, 1977 is monophyletic and its constituent groups, the Dromiacea de Haan, 1833 and Archaeobrachyura Guinot, 1977 are also monophyletic.

The sperm data seem to support the monophyletic hypothesis depicted in Fig. 16a. If this is true then we must examine the suite of ancestral dromiacean characters to see which of them could be ancestral to all of the Podotremata and which could be apomorphies of the Dromiacea (see Fig. 16a). The ancestral characters (F1 - 14) would include: 1) carapace longer than wide, 2) carapace lacking an anterolateral margin, 3) branchiostegite membranous, 4) third maxillipeds pediform, 5) crista dentata present, 6) abdomen large and only loosely folded under the body, 7) uropods well developed, no abdominal locking mechanism, 8) five pairs of pleopods in both sexes, 9) short female sternal sutures 7/8, 10) twenty trichobranchiate-like notched gills, 11) long setae on the posterior margin of the scaphognathite, and 12) seven epipods. To these can be added 13) the coxal position of the genital apertures in both sexes and 14) separate spermathecae in the female sternum. The remaining characters (G1 - 7): 1) the beak-like first antennal article, 2) propodus of second and third pereopods with a distal spine and a row of spines on the inner margin of the dactyl, 3) fourth and fifth pereopods reduced and subdorsal with 4) propodal and dactyl spines as found in *Dicranodromia*, 5) fifth pereopod with a spine on the outer margin of the dactyl, 6) needle-like second male pleopods without spines, 7) calcified coxal sperm tube carrying sperm to the bases of the second pleopod, must be apomorphies of the Dromiacea. The assumption of monophyly implies, amongst other things, that phyllobranchiate gills, and the mechanisms for locking the abdomen have been independently evolved in the Archaeobrachyura and Dromiacea, and that the ancestor of the Podotremata had their last two pairs of legs as walking legs and not reduced. Therefore this ancestor did not carry camouflage materials. Camouflage behaviour evolved independently in the Dromiacea (e.g. Dromiidae, see McLAY, 1993) and in the Homoloidea. In the Homoloidea camouflage probably only occurs in the Homolidae (for details see GUINOT *et al.*, 1995). Furthermore the hypothesis implies that the uropods have been reduced or lost independently in the Homolodromiidae and the Dromiidae and that operculate third maxillipeds were independently evolved in the dynomenid-dromiid line and the Homoloidea.

In a tentative phylogenetic analysis, SCHOLTZ & RICHTER (1995) have argued that the dromiaceans (*sensu* Borradaile, 1907) are not a monophyletic assemblage (see Fig. 16b) and that the homolids have a closer relationship with the "higher" brachyurans. In their view the homolodromiids (with trichobranchiate gills, narrow cheliped sternite, and an elevated third maxilliped sternite) are the sister group of all other brachyurans, and the homolids (with phyllobranchiate gills, wide cheliped sternite, and non-elevated third maxilliped sternite) are the sister group of the dromiids and the "true" brachyurans. This latter group share the homolid characters as well as having truly operculiform third maxillipeds and an elongate gill-cleaning first maxilliped epipod. Thus SCHOLTZ & RICHTER (1995) tentatively propose that the Podotremata are not monophyletic but are paraphyletic. This would imply that some or all of the characters (F1-14) are plesiomorphies for the Dromiacea, Archaeobrachyura and the Eubrachyura and therefore characters of the ground pattern of the Brachyura.

The points of conflict between these two hypotheses are, amongst other things, different interpretations of the origin of phyllobranchiate gills, and operculate third maxillipeds. Given the variation in gill structure within the Dynomenidae it does not seem to be necessary to assume that phyllobranchiate gills only evolved once. Phyllobranchiate gills are found in *Acanthodromia* and all the Dromiidae but it is clear that both the dynomenids and dromiids must be derived from an ancestor with multi-lobed gills. By the same token operculate third maxillipeds could well have been independently derived from pediform appendages with a crista dentata. SCHOLTZ & RICHTER (1995) make the presence of a crista dentata the apomorphic condition of the Eureptantia Scholtz & Richter, 1995. It should be noted that there are many examples amongst the Brachyura where the crista dentata is absent. It has been lost in some Dynomenidae (e.g. *Acanthodromia*), in all Cyclodorippidae (e.g. *Tymolus*, *Xeinostoma*, and *Krangalangia*), Latreillidae (e.g. *Latreillia*), Raninidae (e.g. *Lyreidus*, *Ranina*, *Raninoides*), and all of the Eubrachyura. The polarity of this character depends upon what assumptions are made about the ancestral decapod, and whether the absence of a crista dentata in natants is ancestral or derived. SCHOLTZ & RICHTER (1995) argue that the absence of the crista dentata in some Achelata Scholtz & Richter, 1995, (e.g. *Scyllarus*), thalassinids (e.g. *Callianassa*) and anomolans should be regarded as being "secondary". Loss of the crista dentata is a synapomorphy of many groups within the Eureptantia.

The paraphyletic hypothesis also assumes that camouflage carrying was ancestral to all the Brachyura whereas the monophyletic hypothesis assumes that it is a synapomorphy of only a few of the podotrematous families. McLAY (1991: 465) put forward an hypothesis about how the camouflage-bearing limbs of dromiids might have evolved from walking legs. This hypothesis needs to be modified in the light of the hypothesis presented above that the ancestor of the Dromiacea was a camouflage-carrying crab. Thus the argument presented by McLAY (1991) should be applied to the dromiacean ancestor rather than the dromiid ancestor. Although further analysis of this complex question is required, the weight of evidence seems to favour monophyly of the Podotremata.

Which ever hypothesis is accepted, there is always going to be a problem with interpreting the evolution of the fourth pereopods. Using the characters of the last two pairs of pereopods by themselves it would be natural to group the homolodromiids and dromiids together because they have reduced fourth and fifth pereopods and to group the dynomenids and the homolids together because they have normal fourth pereopods, used for walking, and only the fifth pereopods reduced. But this grouping overlooks the fact that these modified limbs have different roles. In homolids the last pair of pereopods are subdorsal and used to carry anemones but in dynomenids they are horizontal, vestigial and probably had a cleaning function. In homolodromiids and dromiids the probable reason for having both pairs of limbs reduced is because of their camouflage carrying role (this has yet to be confirmed for homolodromiids). Given the hypothesized Homolodromiidae - Dynomenidae + Dromiidae link (see Fig. 15) it is most parsimonious to assume that their ancestor had both of the last two pairs reduced, but this requires that in the ancestral dynomenids the fourth pereopods reverted to a locomotory role and that the fifth pereopod became a cleaning limb. Provided that we derive the homolids from an ancestor with four normal walking legs, there is no great difficulty in hypothesizing that only the last pair of pereopods was modified for the specialized task of carrying anemones. Pereopodal grooming in decapods involves several different limbs and it seems reasonable to regard each different case as apomorphic.

Wherever we place the dynomenids amongst the extant groups, there is always going to be a problem with interpreting the evolution of the last two pairs of pereopods. Perhaps the reason for the apparently uncomfortable position of the dynomenids is that their closest ancestors or sister group are in fact extinct, and are to be found somewhere amongst the numerous "prosopid" species which have been described. It would be very helpful if we knew something about the limbs of the extinct dynomenid species. Unfortunately, in most cases, we only have information about their carapace and know nothing about their pereopods.

Another aspect of the phylogeny of the Dromiacea (i.e. Homolodromiidae, Dynomenidae and Dromiidae) which warrants discussion is the conflict between sperm, and 18S rRNA data, and the accepted allocation of genera to families (JAMIESON *et al.*, 1995). Briefly, in a parsimony analysis using PAUP, *Homolodromia kai* (Homolodromiidae), *Paradynomene tuberculata* and *Metadynomene tanensis* (= *Dynomene* aff. *devaneyi*) (Dynomenidae), *Stimdromia lateralis* and *Dromidiopsis edwardsi* (Dromiidae) do not show a relationship which matches their familial position (JAMIESON *et al.*, 1995). Furthermore an analysis based on 18S rRNA suggests that the dromiid *Hypoconcha arcuata* has anomuran affinities rather than being linked to another dromiid, *Cryptodromiopsis antillensis* (= *Dromidia antillensis*) (SPEARS *et al.*, 1992). The dromiids are certainly a morphologically diverse group, more so than the dynomenids, but the apomorphies listed above seem to provide convincing evidence that the Dromiidae are in fact a monophyletic group. It may well be that "the sperm never lie" (as claimed by some), but spermatological data certainly can be ambivalent and open to as many interpretations as conventional morphological characters.

Finally, it has been suggested by some decapod palaeontologists (e.g. WRIGHT & COLLINS, 1972, and GLAESSNER, 1980) that the family Xanthidae was derived from amongst the Dynomenidae. Admittedly, some extant dynomenids do resemble some xanthids (e.g. *Pilumnus* and *Panopeus*), in their chelipeds and the conformation of their carapace (see Discussion below under *Hirsutodynomene ursula*), but it should be clearly apparent from the above arguments that any resemblance of xanthids and dynomenids must be convergent and not evidence of a close relationship. It may be significant that at least some members of each of these families inhabit corals, so that their similarities may be attributable to colonization of the same habitat.

Family DYNOMENIDAE Ortmann, 1892

Dynomenidae Ortmann 1892: 541; 1898: 1155. — ALCOCK 1899: 127; 1901: 34. — STEBBING, 1905: 58. — RATHBUN, 1937: 51. — BALSS, 1957: 1605. — GLAESSNER, 1969: R487. — WRIGHT & COLLINS, 1972: 48. — TAKEDA, 1973: 80. — SAKAI, 1976: 28. — GUINOT, 1993: 1226.

Dynomeninae A. Milne Edwards & Bouvier, 1899: 9; 1902: 22.

Carapace shape usually wider than long, but can be longer than wide, generally moderately convex, commonly subcircular, ovoid or may be oblong. Surface may be smooth, spinous or areolate and is usually densely covered with setae. Lateral carapace margin usually well defined and armed with distinct teeth. Frontal groove well marked, split in two posteriorly, cervical, postcervical and branchial grooves evident. Frontal carapace margin broadly triangular, continuous, and usually without rostrum or teeth. Eyestalks short, eyes protected by well defined orbits. Sternal sutures 7/8 of female end well apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside the orbit at the base of the eyestalk. Antennal flagella shorter than carapace width. All articles of antenna moveable, first article (urinal) usually beaked medially and second article has an exopod firmly fixed. Third maxillipeds opercular, completely covering the buccal cavern, separated at their bases by a plate at the same level as the sternum; basis and ischium of endopod fused but joint always marked by a shallow groove. Pereopods include chelipeds, three pairs of walking legs, and reduced last pereopods. Chelipeds equal, stouter than walking legs, last pair of legs very reduced, dactyl rudimentary, forming an obsolete subchelate mechanism with an extension of the propodus. Gills usually 19 (including 6 podobranchs) + 7 epipods. Gill structure basically phyllobranchiate but the plates are very variable in shape with different numbers of epibranchial lobes.

Abdomen of six segments and telson, folded loosely under the thorax, uropods large, an effective abdominal locking mechanism usually absent. Both sexes have five pairs of pleopods, first pair vestigial in female, last three pairs rudimentary in the male. Male first pleopods very uniform in structure, consisting of a stout, setose semi-rolled tube with an apical plate, second pair needle-like bearing tiny inset spines, termination with two or more stouter spines.

TYPE GENUS. — *Dynomene* Desmarest, 1823 designated by ORTMANN (1892). PEYROT-CLAUSADE & SERÈNE (1976) attribute the first use of the latinized name *Dynomene* to DESMAREST (1825), but MANNING & HOLTHUIS (1981) have shown that it should be attributed to DESMAREST (1823) where a latinized version was used in the index to his article in the *"Dictionnaire des Sciences Naturelles"*.

DISCUSSION. — The above definition of the family Dynomenidae encompasses all the characters listed by ORTMANN (1892). When he defined the family, ORTMANN was chiefly interested in separating it from the Dromiidae, and Homolidae. ORTMANN regarded the following characters as being primitive: 1) incomplete connection of the pterygostomial region and the epistome, 2) margin of carapace clearly defined, 3) fifth pereopod small and simple with rudimentary dactyl, 4) uniramous uropods present, and 5) four mastigobranchs (i.e. epipods) and four pleurobranchs on the pereopods, while on all the thoracic segments there are six rudimentary podobranchs. Other characters which he regarded as important, but not necessarily primitive, were that the eyes could be completely withdrawn into the orbits, the antennule could be folded away into a groove between eyestalk and supraorbital margin, and finally the third and fourth articles of third maxillipeds are slightly widened while the fifth, sixth and seventh articles are significantly smaller. In fact all of these characters, except for the reduced fifth pereopods and presence of four epipodites, are shared with the Dromiidae De Haan, 1833. Thus it is not surprising that some dromiids have initially been described as dynomenids (see below).

Perhaps through an over-sight, ORTMANN (1892) did not include *Acanthodromia* Milne Edwards, 1880 in his new family. A. MILNE EDWARDS (1880) originally placed *Acanthodromia* in his family "Dromiens" which included *Dromia* Weber, 1795, *Dromidia* Stimpson, 1858, and *Dicranodromia* Milne Edwards, 1880. He considered that *Acanthodromia* should be placed between *Dromia* and *Dynomene*. ALCOCK (1899) placed *Acanthodromia* in the Dromiidae along with *Dromia* and *Arachnodromia*. However, ALCOCK (1901) was the first to put *Acanthodromia* in the Dynomenidae, along with *Dynomene*, and to provide a formal definition of the family. He expanded the family definition so as to include *Acanthodromia* and simply commented that it differed from *Dynomene* in that its carapace was longer than wide, convex, and closely covered with spines instead of setae. ALCOCK also noted that dynomenid gills are phyllobranchiae but sometimes showing the transition from tricho- to phyllobranchiae. A. MILNE EDWARDS & BOUVIER (1899: 10) believed the branchial formula to be the same as that of *Homarus vulgaris*. WRIGHT & COLLINS (1972) suggested that *Acanthodromia* should be placed in the fossil family Prosopidae Von Meyer, 1860. The proposal is discussed further in the section on this genus.

STEBBING (1905) added *Dynomene platyarthrodes*, from South Africa, with the idea that it was intermediate between *Dynomene* and *Acanthodromia*, believing that the characters of the front, the orbits, and the antennae were sufficiently similar to *Dynomene filholi* to justify inclusion. He did not modify or provide a definition of the family. However BALSS (1938) noted that the fourth pereopods were subchelate and the female sternal sutures 7/8 extended as far as the cheliped segment and realized that *D. platyarthrodes* in fact belonged to the Dromiidae. BARNARD (1947) erected the genus *Speodromia* Barnard, 1947, for this crab (see McLAY, 1993).

In her review RATHBUN (1937) essentially restated the family definition of ALCOCK (1901) except that she noted that the gills were phyllobranchiate, eliminating any reference to the gills being "transitional". This is true of both species of *Acanthodromia*, but the other dynomenids are different. BALSS (1957) gave the same features as ALCOCK (1901).

GLAESSNER (1969) gave a family definition which highlighted the features preserved in fossil dynomenids, concentrating on the orbits, carapace shape and incised grooves, and added the intercalated lateral platelets (i.e. the uropods) and the essential character of the reduced last pair of legs, even though these are most unlikely to ever be preserved in a fossil. The same definition was repeated by WRIGHT & COLLINS (1972). Carapace grooves have had little importance in the description of modern species but they assume more importance in fossil species.

The last genus to be added was *Paradynomene* Sakai, 1963, but SAKAI never modified the definition of the Dynomenidae to accommodate this new form, and SAKAI (1976) simply repeated the definition of RATHBUN (1937). The only substantial change that is necessary, is to include a very areolate carapace surface. TAKEDA (1973) noted that the dynomenids are distinguished from the Dromiidae by having an epipod on each of the first three pairs of walking legs and only the last pair of legs small and subdorsal.

Therefore, the modern definition of the Dynomenidae owes a lot to ALCOCK (1901). I have added the character of three rudimentary pleopods in males because it seems to be true of all dynomenids so far examined. It is interesting to note that the same condition is found in some dromiids: *Sphaerodromia* Alcock, 1899, *Eodromia* McLay, 1993, and *Exodromidia* Stebbing, 1905 (see McLAY, 1993).

CANO (1893) described a zoea larva which he assigned to ? *Dynomene* Desmarest, but WILLIAMSON (1965) stated that it was more likely that this larva belonged to *Blepharipoda* Randall or a closely allied genus of the Albuneidae. The only dynomenid larva known is a pre-zoea dissected from late stage eggs of *Acanthodromia erinacea* by RICE (1981).

The genera of the Dynomenidae have enjoyed a fairly stable existence. Only four generic names have been used to group the species in this family. *Dynomene* Desmarest, 1823 was the first to be established followed by *Acanthodromia* Milne Edwards, 1880, *Maxillothrix* Stebbing, 1921, and *Paradynomene* Sakai, 1963. Both *Acanthodromia* and *Paradynomene* are very distinctive and consequently have not caused any taxonomic problems. However species have been added to *Dynomene* in a rather haphazard way, without reference to the generic definition, and some revision is required if all three genera are to have equal status. *Maxillothrix* was shown by ODHNER (1925) to be a junior synonym of *Dynomene* (see Discussion below).

Identification keys to genera and/or species can be found in ALCOCK (1901), SAKAI (1936, 1965, 1976), RATHBUN (1937), and DAI & YANG (1991). PEYROT-CLAUSADE and SERÈNE (1976) give a key to five Indo-Pacific species of *Dynomene*. The characteristics which they used in their key were: carapace surface smooth, spinous, tuberculate or granulate, number and size of teeth on anterolateral border, tomentum length and clumping, spines on anterior border of P2-4, length/width ratio of P3 merus, presence of spines on borders of orbit, presence of a toothed lobe on the cheliped carpus. Below I present a key to all known species of extant dynomenids.

Key to the species of the family DYNOMENIDAE

1. Carapace width less than length; surface largely devoid of setae, strongly tuberculate or densely covered with long sharp spines 2

— Carapace width greater than length; surface setose to varying degrees, not strongly tuberculate and without long spines 4

2. Carapace surface densely granulated and strongly tuberculate; rostrum tridentate, median tooth on a lower level, lateral teeth at beginning of supraorbital margin; anterolateral margins with six irregular teeth .... ***Paradynomene tuberculata*** Sakai, 1963

— Carapace surface densely covered with long spines; rostrum terminated by a strong spine; anterolateral margins with numerous spines **3**

3. Supraorbital spines near corner of the orbit are long and bent posteriorly; fourth abdominal segment with a small, median, pearl-like lobe only partially divided by a short median groove; a similar smaller lobe on the fifth segment .... ***Acanthodromia erinacea*** A. Milne Edwards, 1880

— Supraorbital spines near corner of orbit are short, blunt and not bent posteriorly; fourth abdominal segment with a pair of large, smooth pearl-like median lobes separated by a groove and occupying almost the entire width of the segment; fifth segment spinous .... ***Acanthodromia margarita*** (Alcock, 1899)

4. Carapace width only slightly greater than length (ratio ≤ 1.10), densely covered with short, soft setae which give the surface an uneven, undulating appearance, with transverse troughs; no long setae on the carapace; dactyl of P1 not strongly curved; margins of fingers touching for about half their length; less than five spines on inferior margin of P2-P4 dactyli **5**

— Carapace width much greater than length (ratio > 1.10); long and short setae present on carapace; dactyl of P1 strongly curved; fingers touching only at the tips; five or six spines on inferior margin of P2-P4 dactyli **7**

5. Anterolateral carapace margin without teeth but interrupted by a faint notch mid-way between postorbital corner and where the branchial groove meets the margin .... ***Metadynomene devaneyi*** (Takeda, 1977)

— Anterolateral carapace margin with teeth **6**

6. Three well developed, unequal (posterior margin of second tooth extended and may bear two smaller denticles) and blunt anterolateral teeth; strong posterolateral tooth behind branchial groove; suborbital margin shelf-like, projecting and easily visible dorsally .... ***Metadynomene tanensis*** (Yokoya, 1933)

— Four tiny subacute anterolateral teeth, first pair separated from second pair by a blunt swelling, similar posterolateral tooth behind branchial groove; suborbital margin not projecting, scarcely visible dorsally .... ***Metadynomene crosnieri*** sp. nov.

7. Carapace surface areolate, granulate and spinous (especially near margins) under the surface tomentum **8**

— Carapace surface smooth or only minutely granulated; tomentum may be sparse or dense in which case the setae are short and bent at right angles near the tip **9**

8. Tomentum consists of a dense cover of filiform long setae, arranged in clumps associated with areolae or spines, and a dense understory of short serrated setae bent at right angles near the tip; projection on inner carpal margin of cheliped consists of a sharp spine; suborbital margin bears small acute spines... ....***Hirsutodynomene spinosa*** (Rathbun, 1911)

— Tomentum consists of a sparse cover of long and short, slightly clumped, serrate setae, which are unbent; projection on inner carpal margin of cheliped is a broad blunt lobe; suborbital margin bears small blunt granules .... ***Hirsutodynomene ursula*** (Stimpson, 1860)

9. Anterolateral teeth absent or only represented by two or three small granules not terminated by a sharp tooth .... ***Dynomene praedator*** A. Milne Edwards, 1879

— Anterolateral teeth present, well developed, and sharply pointed **10**

10. Carapace tomentum sparse, setae filiform, surface not obscured; ratio of length of antennal flagellum to CW > 0.60; carpus and propodus of P1 smooth; ratio of length of merus of P3 to CL > 0.7 .... ***Dynomene pugnatrix*** de Man, 1889

— Carapace tomentum not sparse, setae serrate, long setae may be arranged in clumps; ratio of length of antennal flagellum to CW < 0.60; carpus and propodus of P1 granulated; ratio of length of merus of P3 to CL < 0.7 .... **11**

11. Carapace tomentum consists of dense short setae, bent at right angles, obscuring the surface, and fifteen to seventeen tufts of long (> 0.2 x CW) setae; ratio of length to width of merus of P3 > 2.0 .... ***Dynomene pilumnoides*** Alcock, 1900

— Short setae not obscuring carapace surface, long setae may be arranged in clumps but length < 0.2 x CW; ratio of length to width of merus of P3 < 2.0 .... **12**

12. Carapace surface smooth, coarse serrate setae, longer setae arranged in about twenty clumps, ratio of CW to CL approx. 1.2; notch present in supraorbital margin; no spines on postorbital margin; cervical groove branching off subhepatic groove; granules on carpi of P2-P4 not arranged in rows .... ***Dynomene filholi*** Bouvier, 1894

— Carapace surface minutely granulated, coarse serrate setae, longer setae not arranged in clumps, ratio of CW to CL approx. 1.3; no notch in the supraorbital margin; five small acute spines around postorbital margin; no cervical branch from the subhepatic groove; granules on carpi of P2-P4 arranged in three rows .... ***Dynomene hispida*** Guérin-Méneville, 1832

Genus *DYNOMENE* Desmarest, 1823

Dynomene Desmarest, 1823: 252, pl. (18) fig. 2; 1825: 133, pl. 18, fig. 1. — LATREILLE, 1825: 273; 1829: 69.

Dynomene Desmarest, 1823: 422; 1825: 442. — JAROCKI, 1825: 26. — BERTHOLD, 1827: 258. — H. MILNE EDWARDS, 1837: 179. — STIMPSON, 1858: 226. — A. MILNE EDWARDS, 1879: 1; 1899: 90. — ALCOCK, 1899: 133; 1901: 35. — ORTMANN, 1898 : 1155. — STEBBING, 1905: 58. — RATHBUN, 1937: 54. — BALSS, 1938: 6. — SAKAI, 1936: 43; 1965: 12; 1976: 29. — BARNARD, 1947: 371; 1950: 336. — TAKEDA, 1973: 80; 1977: 31. — MANNING & HOLTHUIS, 1981: 23. — DAI & YANG, 1991: 31.

Dynomena Eydoux & Souleyet, 1842: 239 (err.).

Maxillothrix Stebbing, 1921: 456 (type species *Maxillothrix actaeiformis* Stebbing, 1921, a subjective junior synonym of *Dynomene pilumnoides* Alcock, 1900, by monotypy, gender feminine).

DIAGNOSIS. — Carapace shape wider than long, moderately convex, commonly subcircular. Surface may be smooth or sparsely granulate, covered with coarse setae, which may short or long, and often arranged in tufts. Lateral carapace margin always well defined and armed with distinct small teeth or granules. Frontal groove well marked, split in two posteriorly; cervical, postcervical and branchial grooves usually evident. Frontal carapace margin broadly triangular, continuous; no rostrum or teeth. Eyestalks short; eyes protected by well defined orbits. Sternal sutures 7/8 of female end well apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside orbit at base of eyestalk. Antennal flagella shorter than carapace width. All articles of antenna moveable; first article (urinal) always beaked medially and second article with an exopod firmly fixed. Third maxillipeds opercular completely covering buccal cavern, separated at their bases by a plate at same level as sternum; basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds equal, stouter than walking legs; dactyl strongly curved; fingers gaping basally. Last pair of legs very reduced; dactyl rudimentary, forming an obsolete subchelate mechanism with an extension of propodus. Gills usually 19 (including 6 podobranchs) + 7 epipods. Gills variable in shape.

Abdomen of six segments and telson folded loosely under thorax; uropods large. No effective abdominal locking mechanism. Lateral movement of abdomen restricted by small sternal tubercle, at base of each of first walking legs, which lies alongside each uropod. In both sexes, five pairs of pleopods; first pair vestigial in female; last three pairs rudimentary in male. First male pleopods very uniform in structure, consisting of a stout, setose semi-rolled tube with an apical plate; second pair simple, needle-like, with varying numbers of subterminal spines.

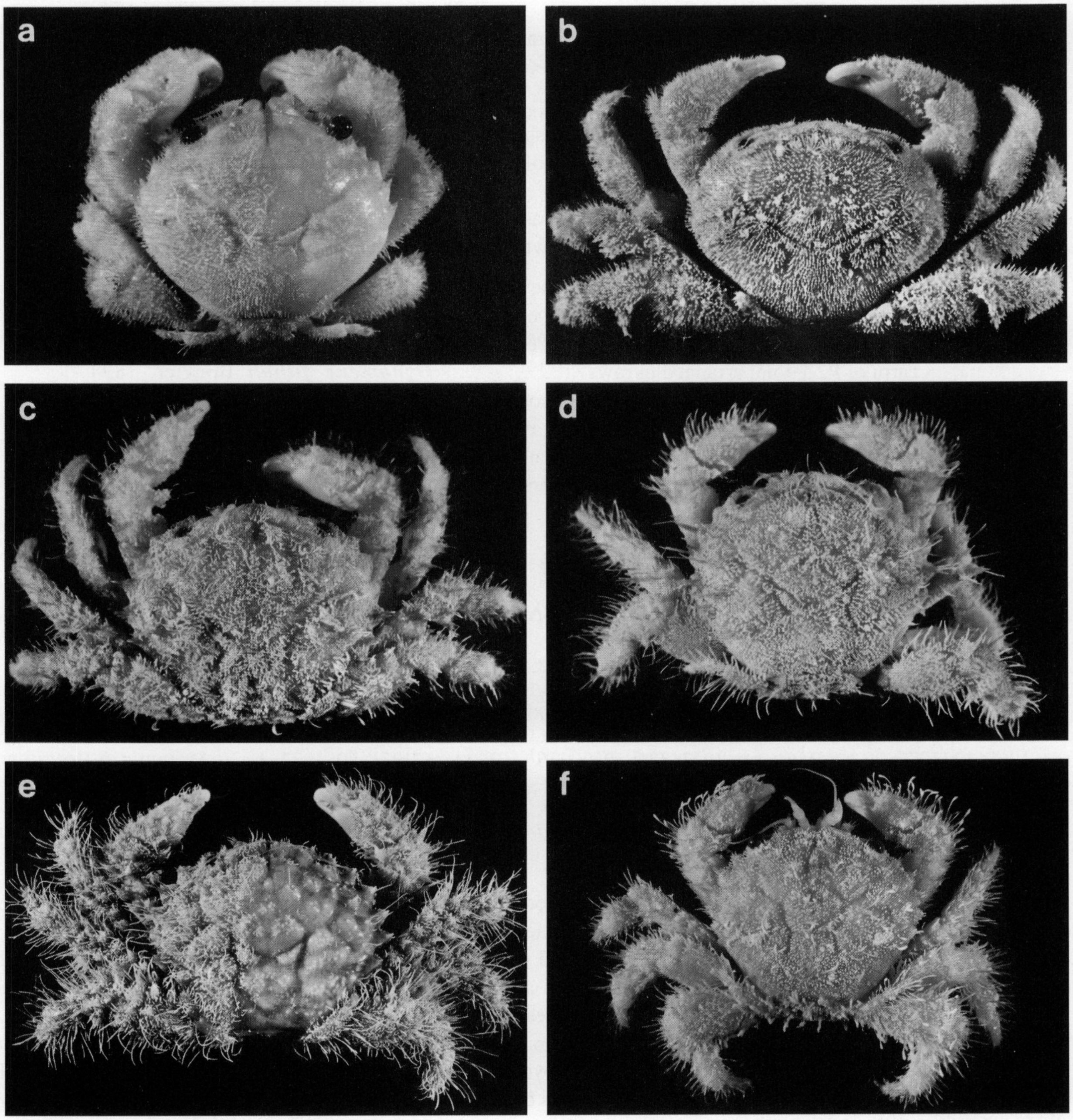

FIG. 17. — **a**, *Dynomene hispida* Guérin-Méneville, 1832, ♂ 9.2 x 7.6 mm, Madagascar, Tuléar, stn 13-3, reef flat (MNHN-B 22087): dorsal view of whole crab, setae removed from right half of carapace, right second pereopod missing. — **b**, *Dynomene praedator* A. Milne Edwards, 1879, ♂ 10.4 x 8.2 mm, New Caledonia, Île des Pins, stn 585, 43 m: dorsal view of whole crab. — **c**, *Dynomene filholi* Bouvier, 1894, ♀ ovig. 10.4 x 8.0 mm, Gulf of Guinea, Annobon Id, 35-55 m (MNHN-B 22093): dorsal view of whole crab. — **d**, *Dynomene pilumnoides* Alcock, 1900, ♀ ovig. 12.7 x 10.6 mm, Sulu Archipelago, 99-108 m, (MNHN-B 10374): dorsal view of whole crab, left fourth pereopod and right fifth pereopod are missing. — **e**, *Hirsutodynomene spinosa* (Rathbun, 1911), ♂ 17.5 x 14.0 mm, Gorong, East of Seram, RUMPHIUS II (MNHN-B 9906): dorsal view of whole crab, some setae removed from right half of carapace. — **f**, *Hirsutodynomene ursula* (Stimpson, 1860), ♀ 15.0 x 12.3 mm, Galapagos, Hood Id, HANCOCK GALAPAGOS EXPEDITION, stn 30-33 (ex USNM 68313 but gifted to MNHN, Paris): dorsal view of whole crab.

Type Species. — A genus without included nominal species; type species *Dynomene hispida* Guérin-Méneville, 1832, by subsequent monotypy, gender feminine.

Other Species. — *Dynomene filholi* Bouvier, 1894, *D. pilumnoides* Alcock, 1900, *D. praedator* A. Milne Edwards, 1879, *D. pugnatrix* de Man, 1889 (including *D. pugnatrix brevimana* Rathbun, 1911).

Discussion. — There has been considerable confusion over the authorship of the generic name *Dynomene* because at the outset it was sometimes used in the vernacular and other times in the latinized form. In Desmarest's (1823, 1825) texts (and on the plates) the name *Dynomene* is given in the vernacular (French). In the indices to these two papers (the second paper being only a new version of the first), the name, however, is given in latin. In the 1823 index the latin names are italicized and the vernacular names are in roman type, e.g. "Langouste (Voy. *Palinurus*)". This is confirmed in the 1825 index, that starts with "Nota. Les noms latins des genres sont en italiques". Other uses of the latin *Dynomene* are found in Jarocki's (1825) general zoology book and Berthold's (1827) German translation of Latreille's (1825) "Familles naturelles du Règne Animal". (I am indebted to Prof. L. B. Holthuis for the preceding information.) Thus Desmarest (1823: 422) is the author of the genus *Dynomene* which was first used in the index to this publication.

There has also been confusion about the authorship of the type species of the genus *Dynomene*. Like many authors before them, Peyrot-Clausade and Serène (1976) attributed the name *Dynomene hispida* to Desmarest (1825) but they point out that it was Guérin-Méneville who first used the full latinized form in his *"Iconographie du règne animal de G. Cuvier"*, published between 1829-1844. Manning and Holthuis (1981) state that livraison 22 of this series was published in July 1832. The latinized form was first used on pl. 14 of Guérin-Méneville (1832).

Maxillothrix Stebbing, 1921 was erected for a supposed new species of the Xanthidae, collected from the Cape Region, South Africa. But Odhner (1925: 85) established that *Maxillothrix*, type species *Maxillothrix actaeiformis* Stebbing, 1921, is not a xanthid, but in fact a dynomenid, which he recognized as being a species of *Dynomene*. Subsequently, Barnard (1947) placed *M. actaeiformis* in synonymy with *Dynomene pilumnoides* Alcock, 1900.

Dynomene hispida Guérin-Méneville, 1832

Figs 3 a, 5 a-b, 11, 12 a-c, 17 a, 18 a-g

Dynomene hispide Desmarest, 1823: pl. (18), fig. 2; 1825: 432, pl. 18, fig 2. — Latreille, 1829: 69.

Dynomene hispida Guérin-Méneville, 1832: 10, pl. 14, fig 2. — Griffith, 1833: 175, pl. 14, fig. 2. — H. Milne Edwards, 1837: 180; 1848 (in Cuvier): 180, pl. 14, fig. 2. — Lamarck, 1838: 482. — A. Milne Edwards, 1879: 5, pl. 12, figs 1-9, pl. 13, figs 10-15. — Richters, 1880: 158. — Miers, 1884: 13. — De Man, 1888: 408. — Ortmann, 1892: 543; 1894: 33. — Alcock, 1901: 74 (list). — Nobili, 1907: 378. — Rathbun, 1911: 195. — Ihle, 1913: 92 (list). — Bouvier, 1915: 38. — Balss, 1922: 105; 1938: 7. — Edmondson, 1925: 30; 1933: 265, fig. 141; 1946: 269, fig. 165. — Sakai, 1936: 43, pl. 8, fig 3; 1940: 29 (list); 1965: 660, text-fig. 1130; 1976: 29, pl. 6, fig. 4. — Buitendijk, 1939: 227. — Miyake, 1939: 198 (list); 1983: 195 (list). — Horikawa, 1940: 28. — Ward, 1942: 71. — Lin, 1949: 12. — Tweedie, 1950: 106. — Guinot, 1967: 241 (list); 1985: 448 (list). — Suzuki & Kurata, 1967: 95. — Serène, 1968: 36 (list); 1973: 119. — Takeda, 1973: 80; 1977: 35 (list). — Peyrot-Clausade & Serène, 1976: 1340, fig. 1, pl. 5 A-B,F. — Peyrot-Clausade, 1977: 212; 1981: 750; 1984: 114. — Guinot, 1979: 125, pl. 21, figs 8-9. — Chen, 1980: 118, text-fig. 1, pl. 1, fig. 3. — Highsmith, 1981: 369. — Baba, 1986: 310. — Dai, Yang, Song & Chen, 1986: 28, pl. 3-4, text-fig. 11, 1-4. — Garth, Haig, & Knudsen, 1987: 241. — Nagai & Nomurà, 1988: 92. — Nagai, 1989: 43. — Dai & Yang, 1991: 32, text-fig 11, pl. 3, fig. 2. — Poupin, 1996a: 24 (list).

Dynomena latreillii Eydoux & Souleyet, 1842: 239, pl. 3, figs 3-5. — Takeda, 1977: 35 (list).

Dynomene granulobata Dai, Yang & Lan 1981: 119, figs 10-14. — Dai, Yang, Song & Chen, 1986: 29, text-fig. 12, 1-2, pl. 3, fig. 3. — Dai & Yang, 1991: 33, text-fig. 12, 1-2, pl. 3, fig. 3.

Not *Dynomene hispida* - De Man, 1902: 689 [= *Hirsutodynomene spinosa* (Rathbun, 1911)].

Not *Dynomene hispida* - Yokoya, 1933: 95, text-fig. 37 [= *D. pilumnoides* Alcock, 1900].

Material examined. — **New Caledonia**. No locality, probably intertidal, 1873: 1 ♂ 15.2 x 11.3 mm; 1 ♀ ovig. 13.7 x 10.1 mm (MNHN-B 22086). — No locality, probably intertidal, M. Balansa coll., 1873: 7 ♂ 7.7 x

6.1 - 12.0 x 8.9 mm; 6 ♀ 8.2 x 6.6 - 10.9 x 8.5 mm; 1 ♀ ovig. 13.0 x 10.0 mm (MNHN-B 22091). — No locality, leg. A. MILNE EDWARDS, probably part of the M. BALANSA collection: 1 ♂ 13.0 x 10.4 mm; 1 ♀ 7.6 x 6.0 mm (ZMB 4324).

Mauritius. Port Louis, probably intertidal, M. THIRIOUX coll., 1913, E. BOUVIER det.: 1 ♀ ovig. 12.9 x 9.9 mm (MNHN-B 22088). — No date or locality: 1 ♀ 10.3 x 8.4 mm, dry (ANSP-CA3315, originally part of the collection of GUÉRIN-MÉNEVILLE, No. 209).

Madagascar. West coast, Tuléar, stn 13-3, external reef flat, M. PEYROT-CLAUSADE coll., 1968, R. SERÈNE det. : 1 ♂ 9.2 x 7.6 mm (MNHN-B 22087) (see PEYROT-CLAUSADE & SERÈNE, 1976 and PEYROT-CLAUSADE, 1984).

Somalia. (M. VANNINI coll.). Gesira, 18 km south of Mogadishu: stn 1, on live *Pocillopora* sp., low tide level, 1981: 1 ♀ 8.3 x 6.6 mm. — Stn 2, on live *Pocillopora* sp., low tide level, 1981: 1 ♀ 4.4 x 3.6 mm. — Stn 3, on dead *Pocillopora* sp., low tide level, 1981: 1 ♂ 6.5 x 5.2 mm. — Stn 4, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ ovig. 11.7 x 8.7 mm. — Stn 5, on dead *Pocillopora* sp., low tide level, 1981: 2 ♀ 3.6 x 3.3, 3.9 x 3.3 mm. — Stn 6, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ 5.4 x 4.7 mm. — Stn 11, on dead *Pocillopora* sp., low tide level, 1981: 2 ♂ 6.0 x 5.3, 8.5 x 6.8 mm; 1 ♀ 3.9 x 3.2 mm. — Stn 12, on dead *Pocillopora* sp., low tide level: 3 ♂ 6.7 x 5.4 - 11.6 x 9.2 mm. — Stn 13, on dead *Pocillopora* sp., low tide level: 1 ♂ 7.6 x 6.0 mm; 2 ♀ 3.9 x 3.3, 7.2 x 5.9 mm. — Stn 15, on dead *Pocillopora* sp., low tide level, 1981: 1 ♂ 9.7 x 7.9 mm; 1 ♀ 7.5 x 6.4 mm; 1 ♀ ovig. 10.0 x 7.8 mm. — Stn 16, on dead *Pocillopora* sp., low tide level, 1981: 1 ♂ 8.8 x 7.0 mm. — Stn 17, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ 8.0 x 6.6 mm. — Stn 18, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ 3.9 x 3.4 mm (all Somalia material from MZUF, see VANNINI, 1985).

Aldabra. Takora. Seaward Cove, low tide level, J. D. TAYLOR coll., 5.01.1967: 1 ♀ 11.7 x 9.0 mm (BMNH).

Cocos Keeling Islands. No locality, no depth, C. A. GIBSON-HILL coll., 1941, M. TWEEDIE det.: 1 ♀ 9.3 x 7.6 mm (ZRC 196461211). See TWEEDIE (1950). — Horsburgh Id, 0-37 m, 9.02.1989: 1 ♂ 5.7 x 4.9 mm (WAM 375-89). — Home Id, ocean side, no depth, 21.02.1989: 1 ♂ 13.8 x 10.9 mm; 1 ♀ 10.7 x 8.3 mm (WAM 751-89).

Northwest New Guinea. Salawatti Id, no depth, no date: 1 ♂ 6.0 x 5.0 mm (ZMB 5139).

Elizabeth Reef (east of Australia). Tasman Sea, 29°58'S, 159°05.1'E, no depth, 12.1987: 1 ♀ 9.0 x 7.5 mm (AMS-P 39155).

Middleton Reef (east of Australia). Tasman Sea, 29°29.5'S, 159°05.1'E, intertidal, 9.05.1987: 1 ♀ ovig. 15.6 x 12.3 mm (QM W13033).

Samoa. Pago Pago, no locality, no depth, 1924: 1 ♂ 14.0 x 11.0 mm (BPBM 2388).

French Polynesia. *Tuamotu Ids*: Marutea, Maitutaki, eastern reef, no locality, probably intertidal, M. SEURAT coll., 1905, G. NOBILI det.: 1 ♂ 8.5 x 6.7 mm (MNHN-B 22089) (see NOBILI , 1907). —*Austral Ids*. Marotiri, 27°35'S, 144°25'W, 9-5 m, D. M. DEVANEY coll., 20.02.1971: 1 ♀ ovig. 13.5 x 10.6 mm (BPBM 71.201).

Howland Island. WHIPP EXP., 0°48'N, 176°38'W, no locality, no depth, 1924: 2 ♂ 9.1 x 7.6, 13.0 x 10.0 mm; 1 ♀ ovig. 10.6 x 8.4 mm (BPBM 2353).

Johnston Island. 16°45'N, 169°30'W, no locality, no depth, C. EDMONDSON coll., 1923: 2 ♂ 8.5 x 6.8, 10.0 x 8.5 mm; 1 ♀ ovig. 11.5 x 9.6 mm (BPBM 1363).

Hawaii. No locality, no depth, 1836: 1 unknown sex. 7.9 x 6.0 mm (MNHN dry collection no. 23, type of *Dynomena latreillii* Eydoux & Souleyet, 1842). — No locality, no depth, no date: 1 ♀ ovig. 10.1 x 8.0 mm (AMS-P 5478). — Honolulu, no depth, Th MORTENSEN coll., April 1915: 2 ♂ 9.3 x 7.6 (damaged), 10.8 x 8.8 mm; 1 ♀ 15.0 x 10.5 mm (ZMUC - unregistered).

Oahu, Waikiki: no depth, 1928: 1♀ ovig. 14.1 x 10.9 mm (BPBM 1587). — No depth, 1928: 1 ♀ 11.5 x 10.2 mm (BPBM 3024). — No depth, no date: 1 ♂ 10.2 x 8.0 mm (BPBM 2883). — No depth, C. EDMONDSON coll., 1930: 1 ♀ 8.4 x 7.1 mm (BPBM 3131). — No depth, 24.04.1942: 1 ♀ ovig. 12.6 x 10.0 mm (USNM 182729). — No depth, 2.05.1942: 1 ♀ 11.7 x 9.4 mm (USNM 182729). — No depth, 29.05.1942: 1 ♀ 4.3 x 3.9 mm (USNM 182729).

Oahu, Waikiki Reef (C. EDMONDSON coll.): no depth, 1921: 3 ♂ 11.4 x 9.0 - 15.1 x 11.6 mm; 4 ♀ ovig. 9.7 x 7.7 - 10.6 x 8.6 mm (BPBM 572). — No depth, 16.02.1922: 4 ♂ 8.6 x 6.5 - 12.2 x 9.8 mm; 2 ♀ 10.0 x 7.9, 14.0 x 10.8 mm; 1 ♀ ovig. 12.5 x 9.7 mm (BPBM 658).

Oahu, Waialee: no depth, C. EDMONDSON coll., 6.07.1921: 1 ♂ 9.8 x 7.9 mm; 1 ♀ ovig. 14.3 x 11.6 mm (BPBM 510).

Oahu, Kahala Bay (C. EDMONDSON coll.): no depth, 7.03.1930: 16 ♂ 5.8 x 4.7 - 12.4 x 10.0 mm; 11 ♀ 5.2 x 4.2 - 10.8 x 8.3 mm; 4 ♀ ovig. 6.5 x 5.4 - 8.9 x 7.1 mm (BPBM 3168). — No depth, 1913: 2 ♂ 5.7 x 4.7, 10.7 x 8.6 mm (BPBM 3554). — No depth, 05.1931: 7 ♂ 9.7 x 7.8 - 12.3 x 9.7 mm (BPBM 3414). — No depth, 28.06.1934: 9 ♂ 8.3 x 6.8 - 11.5 x 9.6 mm; 2 ♀ 7.0 x 5.8, 10.8 x 8.6 mm; 7 ♀ ovig.) 9.3 x 7.5 - 10.5 x 8.6 mm (BPBM 3780).

Oahu, Pearl and Hermes Bay: no depth, 02.1928: 1 ♂ 10.0 x 8.3 mm; 1 ♀ 10.8 x 8.5 mm (BPBM 3043).

Oahu, Barbers Point: no depth, 1.09.1936: 1 ♂ 12.7 x 9.9 mm; 2 ♀ 10.7 x 8.6, 12.5 x 10.3 mm (BPBM 4234).

Oahu, Rabbit Id: no depth, 13.11.1936: 2 ♂ 10.1 x 8.2, 10.5 x 8.6 mm; 1 ♀ 12.2 x 9.5 mm (BPBM 4255).

Oahu, Kawela Bay: no depth, C. EDMONDSON coll., 15.07.1935: 4 ♂ 10.7 x 8.8 - 13.0 x 10.5 mm; 5 ♀ ovig. 9.9 x 7.7 - 13.0 x 10.3 mm, (BPBM 4038). — No depth, 10.07.1937: 5 ♂ 9.9 x 8.1 - 15.0 x 11.5 mm; 6 ♀ 9.0 x 7.2 - 13.5 x 11.1 mm (BPBM 4312).

Oahu: no locality, no depth, 10.01.1924: 2 ♂ 11.3 x 8.9, 12.6 x 10.2 mm (ZMUC). — No locality, no depth, no date: 2 ♂ 5.6 x 4.6, 13.2 x 10.1 mm; 2 ♀ 8.2 x 6.5, 11.2 x 9.1 mm; 3 ♀ ovig. 10.0 x 8.0 - 13.8 x 10.8 mm (BPBM

2186). — No locality, no depth, 1932: 5 ♂ 8.0 x 6.5 - 12.7 x 10.0 mm; 2 ♀ ovig. 8.4 x 6.6, 10.5 x 8.5 mm, C. EDMONDSON coll. (BPBM 3601). — No locality, no depth: 3 ♀ 6.4 x 5.2 -10.2 x 8.3 mm (BPBM 3683). — No locality, no depth, 1973: 4 ♂ 7.7 x 6.0 - 13.9 x 10.8 mm; 6 ♀ 5.2 x 4.3 - 12.7 x 10.0 mm; 2 ♀ ovig. 9.7 x 8.1, 11.2 x 9.1 mm (BPBM 510491). — No depth, 1973: 1 ♂ 8.0 x 6.7 mm; 1 ♀ 6.4 x 5.5 mm; 1 ♀ ovig. 11.6 x 9.3 mm. (BPBM 510492). — No locality, 12.2 m, 03.1996: 1 ♂ 6.8 x 5.2 mm (QM).

Oahu, Paile Point: no depth, 7.07.1952: 1 ♂ 11.1 x 8.5 mm; 1♀ ovig. 9.0 x 7.0 mm (BPBM 5804).

Oahu, Maili Point: no depth, 13.05.1953: 1 ♂ 10.0 x 8.6 mm; 1 ♀ 8.5 x 6.9 mm; 1 ♀ ovig. 11.0 x 9.6 mm (BPBM 6055). — No depth, 10.07.1953: 2 ♀ ovig. 9.3 x 7.6 , 10.0 x 7.8 mm (BPBM 5900).

Oahu, Kahe Point: no depth, S. COLES coll., 6-07.1977: 1 juv. 2.0 x 1.7 mm; 2 ♀ 3.6 x 3.1, 5.0 x 4.2 mm (BPBM 1977.554).

Ocean Island (= Kure Id), 80 km NW of Midway Id: no locality, no depth, 1923: 1 ♀ 4.0 x 3.3 mm (BPBM 1133).

Taiwan. Nan-Wan, Pingtung County, no locality, 6 m, from coral *Seriatopora hystrix* Dana, M. S. JENG coll., 5.12.1985: 1 ♀ 7.7 x 6.4 mm (NTOU). — Wan-li-Fong, low tide level, PING-HO-HO coll., 2.06.1992: 1 ♂ 6.6 x 5.2 mm; 1 ♀ ovig. 10.4 x 8.2 mm (NTOU).

TYPES. — *Dynomene hispida* Guérin-Méneville, 1832: according to PEYROT-CLAUSADE and SERÈNE (1976) the male 14.0 x 11.5 mm, from Mauritius was probably considered the holotype by DESMAREST. The specimen is part of the dry collection held by the Muséum national d'Histoire naturelle, Paris, registration number MP-B 245.

Dynomena latreillii Eydoux & Souleyet, 1842: holotype is a small, mounted, dry specimen 7.9 x 6.0 mm, collected from Hawaii, 1836, held by the Muséum national d'Histoire naturelle, Paris, registration number MP-B 235. As the specimen is mounted on a stub it is not possible to determine the sex.

Dynomene granulobata Dai, Yang & Lan, 1981: holotype is a male 6.2 x 5.4 mm, collected from Dongdao, Xisha Ids, South China Sea, 04.1965, held by the Beijing Natural History Museum, registration number 65079.

DESCRIPTION. — Carapace wider than long (CW/CL = 1.3 approx.), broadly rounded in outline but frontal and posterior margins truncated, surface minutely granulated and quite convex. Carapace surface and pereopods covered with coarse, plumose setae of two lengths: short setae clothing surface, but interspersed with slightly longer (0.08 x CW) setae which also fringe limbs. Setae not arranged in clumps. Density of setae not sufficient to completely obscure body surface. Structure of setae identical for both sizes: proximal 20% mostly smooth, followed by a region occupying about 40% with very short setules arranged in closely spaced bands, then a region occupying about 25% where setules increase rapidly in size distally forming a dense bunch, and finally the distal 15% is smooth, slightly curved or angled, and narrows to an acute tip.

A shallow frontal carapace groove separates a pair of low rounded protuberances, and then divides into separate grooves which gradually become more faint. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately from small pits curving anteriorly on to branchial region, while second groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally, bordering anterior cardiac region. In effect groove crossing mid-line, connects two crescent-shaped grooves. Mid-way along cardiac groove begins a faint branchial groove which runs towards base of last tooth on lateral margin. Posterior cardiac area outlined by a faint groove. Anterolateral carapace margin begins at level of postorbital corner, is evenly convex and bears four distinct, sharply pointed, equidistant teeth, first two of which are directed anteriorly and last two directed more laterally. Near beginning of posterolateral border there is another smaller tooth which lacks a sharp spine. Thus lateral margin has five teeth in total. Posterior carapace margin recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin continuous without orbital notch, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits; towards postorbital corner are about five small acute spines and another five spines continued on suborbital margin, which is essentially straight. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral region; distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth above opening of antennal gland is scarcely produced. Second article wider than long, distal margin widest, to which exopod is fixed, curving over base of eyestalk and becoming broader but terminating as a sharp point.

Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and together with small fourth article just matches length of exopod. Remaining antennal articles directed laterally, extending about as far as postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.24. Eyestalk can be completely folded into orbit, and the cornea is well developed, occupying all of tip. Epistome broadly triangular, surface concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace marked by a suture which can be clearly seen on inner surface of orbit.

Subhepatic area slightly convex. A groove begins near base of antenna, curving round under branchial region without a cervical branch and meeting lateral carapace margin just anterior to tooth on posterolateral border and connecting with branchial groove. Third maxillipeds operculiform; bases widely separated by tip of sternum. Crista dentata has only five or six small, distally placed teeth on each side. Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

The branchial formula is 19 gills and 7 epipodites on each side:

Somite	VII (Mxp1)	VIII (Mxp2)	IX (Mxp3)	X (P1)	XI (P2)	XII (P3)	XIII (P4)	XIV (P5)
Pleurobranchiae	-	-	-	-	1	1	1	-
Arthrobranchiae	-	1	1	2	2	2	2	-
Podobranchiae	-	1	1	1	1	1	1	-
Epipods	1	1	1	1	1	1	1	-

Gills are unequal (anterior half larger) violin-shaped plates, marginally notched, and joined together along central axis which carries afferent and efferent blood channels. Epibranchial corners thickened and bluntly pointed. Towards base of each arthrobranch and pleurobranch there are pairs of elongate epibranchial lobes which increase in length proximally. A transverse section near base shows two plates separated, on epibranchial surface, by two lobes, while a section mid-way shows only two plates. Hypobranchial setae at posterior end of branchial chamber poorly developed. Posterior margin of scaphognathite with two long setae. Hypobranchial margin of podobranchs bears same setae as on epipod.

Cheliped only slightly longer than first leg. Merus trigonal; inner face smooth and fitting closely against pterygostomial region of carapace; borders with small granules; outer face with a subterminal groove separating a thickened ridge on which there are three larger granules. Outer face of carpus convex with several small granules, two more prominent distal tubercles; inner superior border with a flattened, distomedially directed, granulated spur which abuts against distal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin is produced as a smooth obtuse flange fitting against merus when limb is withdrawn. These two structures give carpal article an unusual shape. Transverse section of propodus decreases in area distally; outer and superior faces with 6-7 rows of small granules, inner and inferior faces smooth. Fixed finger almost straight with two large teeth; moveable finger curved with a single, large tooth opposite first tooth on fixed finger; both fingers, thick, hollowed out internally, touching only at tips which are without interlocking teeth. Just below teeth on fixed finger is a distinct pit in which several long setae are inserted with a similar group of setae on inner margin. Larger groups of long stiff setae, inserted near base of dactyl and fixed finger, are directed across space between the two fingers. On dorsal surface of dactyl there are several small distal granules.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with a row of four or five small teeth and scattered granules, and a shallow subterminal restriction; length of merus of second leg about 1.5 times its width and equal to about a third of CL. Carpi inflated, dorsal surface bearing three longitudinal rows of granules, and produced distally to overhang base of propodi. Dorsal surface of propodi granulated. Dactyli curved, inferior margin armed with 5-6 small spines, tip brown and subacute.

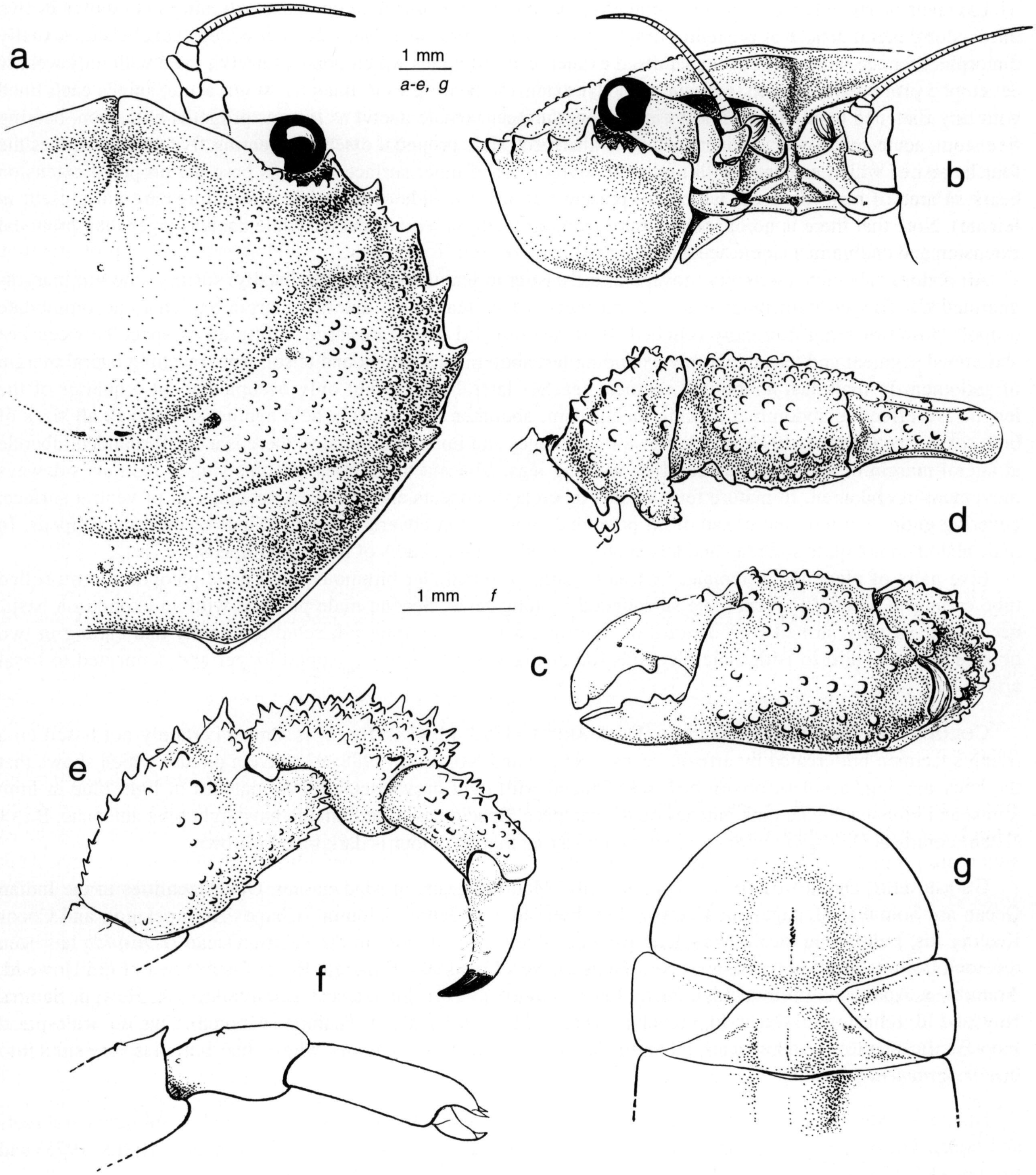

FIG. 18. — *Dynomene hispida* Guérin-Méneville, 1832: **a-g**, ♀ ovig. 12.9 x 9.9 mm, Port Louis, Mauritius, M. THIRIOUX coll. (MNHN-B 22088): **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of left cheliped; **d**, dorsal view of left cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of female abdomen.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching only as far as two thirds along meral article of preceding limb; borders of articles unarmed. Last pair of legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing four, unequal, stout, acute, spines each lined with tiny flattened teeth along almost entire inner surface. Female dactyl as long as propodal extension, bearing five stout, acute spines whose inner surface is unarmed. Male propodal extension bearing five unequal spines the four largest of which are lined with tiny teeth along most of inner surface. Near its base the propodal extension bears an area of rasp-like teeth which are present on only one side of limb (these structures are not present in female). Note that there is no opposing area of similar teeth on base of dactyl. Male dactyl longer than propodal extension and ending in a single acute claw.

All abdominal segments freely moveable, increasing in length and breadth distally; surface smooth; margins unarmed but fringed with long setae. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In female uropod plates are large, filling all of space between last abdominal segment and telson, entirely excluding last abdominal segment and telson from reaching lateral margin of abdomen. In male last abdominal segment reaches lateral margin but only occupies about a quarter of the length. No effective abdominal locking mechanism: abdomen only loosely held against sternum in all sizes of both sexes (see GUINOT, 1979, pl. 21, figs 8-9). In males and immature females, there is a small rounded tubercle at lateral margin of sternum, between first walking legs, adjacent to uropods, but this simply restricts sideways movement of abdomen. In mature females this tubercle disappears and abdomen occupies all of ventral surface, covering entire sternum and coxae of all pereopods with telson covering proximal half of third maxillipeds. In male abdomen not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. First male pleopod a semi-rolled tube ending in a curved apical plate surrounded by long setae. Second male pleopod with an exopod on basis, needle-like distally, armed with a series of five tiny, acute, inset spines directed terminally and ending in two hooked spines. Third to fifth male pleopods rudimentary and biramous; exopod longer and connected to basal article by a joint.

COLOUR. — The coloured figure by DESMAREST [1823, pl. (18), fig. 2] is almost certainly not based on a living specimen but created by artistic license. NAGAI and NOMURA (1988: 92) have a picture which shows that the body and legs are dark brown or black, fringed with light brown setae. Some patches of light blue in limb joints, and bluish and pale pink patches on the carapace. Specimens from Somalia have light blue antennae. BABA (1986) contrasts *D. hispida* with *D. pilumnoides* saying that its colour is dark blue or brown.

GEOGRAPHIC DISTRIBUTION. — Type locality: Mauritius, east of Madagascar. Other localities in the Indian Ocean are Somalia, Madagascar, Coetivy (Seychelle Ids), Aldabra, Salomon (Chagos Archipelago), and Cocos Keeling Ids. Indonesian localities include Kupang, Timor and Ambon. In the Pacific Ocean *D. hispida* has been recorded from Salawati Id (north west New Guinea), New Caledonia, Elizabeth Reef (Tasman Sea), Lord Howe Id, Aranuka & Apamama (Gilbert Ids), Xisha Ids (Taiwan), Ryukyu Ids (Japan), Enewetak Atoll, Hawaii, Samoa, Howland Id, Johnston Id, Ocean Id, French Polynesia (Marutea-Vaitutaki, Tuamotu, Moorea). This is a widespread Indo-Pacific, shallow water species, inhabiting coral reefs and rocky bottoms, whose distribution is very similar to that of *Dynomene praedator*.

DEPTH. — Most of the recorded specimens of *D. hispida* come from intertidal and shallow subtidal coral reefs and rocks. The deepest reliable depth records are from *Acropora humilis* at 30 m, La Réunion (RIBES, 1978) and from dead *Acropora* sp. at 24 m, Tuléar Reef, Madagascar (PEYROT-CLAUSADE, 1981).

SIZE. — The maximum size for males is greater than for females: 19.0 x 14.0 mm (SAKAI, 1976) and 15.6 x 12.3 mm (this study). The smallest ovigerous female is 6.5 x 5.4 mm recorded from Oahu, Hawaii (this study). Records of ovigerous females (mostly from Hawaii) extend from January to July. Despite living in tropical waters *D. hispida* seems to be a seasonal breeder. Newly laid eggs were found on females throughout the period January to July, suggesting that the egg bearing season extends beyond July. The only females with eggs ready to hatch were recorded in May and June. The smallest ovigerous females (CW = 8 mm) carried around 70 eggs and the largest ovigerous females (CW = 14 mm) carried around 900 eggs. The average egg diameter was 0.44 mm, indicating that there is a planktotrophic larvae (larval stages have not been described). This is to be expected from the very wide distribution of *D. hispida* which occurs throughout the Indo-Pacific area.

DISCUSSION. — Different authors have attributed the name of this species to LATREILLE (e.g. WARD, 1942), DESMAREST (e.g. PEYROT-CLAUSADE & SERÈNE, 1976), or H. MILNE EDWARDS (e.g. GUINOT, 1979). However, MANNING and HOLTHUIS (1981) point out that while the first latinized use of the generic name *Dynomene* was by DESMAREST (1823), the first latinized use of the specific name *hispida* was by GUÉRIN-MÉNEVILLE (1832). Thus this species should be known as *Dynomene hispida* Guérin-Méneville, 1832.

The above description is based upon the same material (MNHN-B 22086) used by A. MILNE EDWARDS (1879) who gave the first detailed description of *D. hispida.* The specimens examined are of very similar size to the original dimensions given by A. MILNE EDWARDS (1879, pls 12-13) who illustrated some of the features of a male specimen, but his figs 14 and 15 clearly show a fifth leg which must belong to a female and not a male as is implied by the plate caption.

A. MILNE EDWARDS (1879) was the first to treat *Dynomena latreillii* Eydoux & Souleyet, 1842 as a synonym of *D. hispida* Guérin-Méneville, 1832, stating that the supposed differences were due to the fact that it was based on a juvenile specimen. The type specimen of *D. latreillii* is not in fact a juvenile (7.9 x 6.0 mm, although it is not possible to determine the sex because the ventral surface has been glued to a stub) and was collected from Hawaii in 1836 by EYDOUX and SOULEYET, two doctors on the corvette *"La Bonite"*. In their original description of *D. latreillii* they list the differences between this species and *D. hispida.* Among these differences are: ".. les bords latéro-antérieurs sont courbes, entiers, sans aucune trace de dents,... Les orbites, ovalaires, n'ont pas de dents à l'angle externe et sont ouverts à l'angle interne." I have examined this specimen and there are in fact four anterolateral teeth and small spines around the supra- and suborbital margins. Thus it agrees well with *D. hispida* where the anterolateral carapace margins have small well defined, acute teeth and there are small acute spines on the orbital margin. The characters highlighted by EYDOUX & SOULEYET are in fact typical of *Dynomene praedator* A. Milne Edwards, 1879 and both these species are known from Hawaii. Therefore it was essential to check the type of *D. latreillii.* In treating it as a synonym of *D. hispida*, A. MILNE EDWARDS (1879) pointed out that the type specimen was small and stated that in *D. hispida* anterolateral teeth "..les bords antérieurs ne sont pas aussi nettement découpés qu'ils le deviennent par les progrès de l'âge." (i.e. become more distinct with age). I have examined a large series of *D. hispida* specimens from Hawaii and even when small the anterolateral teeth are distinct and easily seen, provided that the setae are cleared away. Therefore, I agree with PEYROT-CLAUSADE and SERÈNE (1976) who supported the synonymy of A. MILNE EDWARDS. It is important to clarify these differences between *D. hispida* and *D. praedator* so as to avoid confusion and the erection of unnecessary new names.

After examining material from Hawaii and Mauritius (the type locality of *D. hispida*) WARD (1942) disputed the synonymy of *D. latreillii* and *D. hispida.* He argued that the Hawaiian species should remain distinct but it is possible that his specimens from Hawaii were in fact *D. praedator.* I have examined many of the collections made by EDMONDSON and deposited in the Bishop Museum, Hawaii, and found that they contain both *D. hispida* and *D. praedator*, sometimes mixed together and sometimes mis-identified. Thus the records of EDMONDSON (1925, 1933, 1946) may well be for either *D. hispida* or *D. praedator* but it is clear that both species occur in Hawaiian waters.

Dynomene granulobata Dai *et al.* (1981) was described for a small male specimen from the Xisha Ids, Taiwan. The illustrations of this animal closely resemble *D. hispida.* The distinctive features alluded to by the authors relate to the cheliped and second pleopod. However the cheliped features are allometric, changing with size, while the distal characters of the second pleopod (see DAI *et al.*, 1981, figs 13-14, DAI *et al.*, 1986, fig. 12, 1-2, and DAI & YANG, 1991, fig. 12, 1-2) are the same as found in *D. hispida.* The habitat of *D. granulobata*, "coral reefs in shallow waters", is the same as that of *D. hispida.* For these reasons I think that *D. granulobata* is a synonym of *D. hispida.*

A detailed discussion of the gills and epipods of *Dynomene hispida* is given above (see Morphology of the Dynomenidae). The branchial formula is 19 gills + 7 epipods. The gill structure of *D. hispida* is especially interesting since they show both phyllobranchiate and "trichobranchiate" shapes. A section mid-way along an arthrobranch or pleurobranch shows a pair of plates surrounding the afferent and efferent blood vessels as seen in the phyllobranchiate Brachyura. The only differences are that the plates are bluntly pointed, as well as being thickened, at their epibranchial corners and mid-way along each side is a notch. The thickening probably helps to keep the lamellae separated. However, a section near the base of the gill shows the same two plates separated by a pair of elongate epibranchial lobes thus giving the gill a "trichobranchiate-like" appearance. The podobranchs bear only elongate lobes and their hypobranchial margins bear the same cleaning setae as found on the epipods to which the gills are attached. Thus within one species and one gill we have both kinds of gill structure present. As in all dynomenids, *D. hispida* has an epipodal gill cleaning mechanism aided by two long setae extending from the posterior end of the scaphognathite. The field of hypobranchial setae on the posterior body wall of the branchial chamber seen in some other dynomenids, e.g. *Paradynomene tuberculata*, is scarcely developed in *D. hispida*.

Previous work by PEYROT-CLAUSADE and SERÈNE (1976, text-fig. 1, pl. 5, A-B, F) showed the general features of the male pleopods including light microscope photo-micrographs. Further details were provided by DAI *et al.*, (1986, fig. 11, 2-3) and DAI and YANG (1991, fig. 11, 2-3). This study presents the first scanning electron microscope pictures of the male pleopods of *D. hispida* and these confirm the observations of DAI and YANG (1991): there is a well developed curved apical plate on the tip of the first pleopod and there are five subterminal and two terminal spines on the second pleopod. The subterminal spines are arranged in a series which curves around to the inferior margin of the pleopod. Each spine is apically directed and lies in a triangular depression. The terminal spines are larger than the others, unequal and curved sharply upwards at their tips. Near the base of this article, beside the exopod, is the opening of a secretory gland which may provide additional seminal fluid to aid sperm transfer. MINIGAWA (1993) has reported similar tegumental glands in the first and second pleopods of *Ranina ranina*. The last three pairs of pleopods in *D. hispida* are rudimentary and biramous with the exopod being longer. The endopod lacks a joint and appears to be an extension of the basal article. This condition is found in most of the other dynomenids.

A. MILNE EDWARDS (1879) illustrated examples of the long and short plumose setae found on the carapace. His figures (pl. 12, figs 8-9) show the fine setules forming the dense distal band on the long setae as being similar to more proximal setules, while those forming the dense band on the short setae are shown as being much stouter. Furthermore, the tip of the short setae is shown as being angled while that of the long setae is shown as being straight. Examination with a scanning electron microscope confirms most of the features illustrated by A. MILNE EDWARDS but shows that stout distal setules are found on both setal types and the tips of the both setae can be angled. There is a great deal of variation in setule development between setae.

In both females and males the tip of the last leg is fashioned into an obsolete subchelate mechanism but there are significant differences between the sexes. The female has a dactyl which bears several unarmed spines while the male has only a simple dactyl. The female propodal extension has four toothed spines while the male has five spines on which the teeth are fewer and smaller, and there is an area of rasp-like teeth near the base of the propodal extension. Perhaps these structures are a vestige of what was a grasping or cleaning limb and perhaps the female has lost the rasp-like teeth but still has better developed remnants of the claws. It does not seem sensible to hypothesize that formerly these limbs had different roles in males and females. What their exact role was is still a matter for speculation.

Marco VANNINI kindly supplied the *D. hispida* specimens from the coast of Somalia and data about their habitat. Whole coral heads (n=119) of *Pocillopora* sp. were enclosed in plastic bags, removed and the fauna extracted. A total of 36 dynomenid specimens were collected: 22 *D. hispida* and 14 *D. praedator*. Of the 19 corals inhabited by dynomenids only 2 were alive, the others being encrusted and more or less dead. Despite being relatively common, the dynomenids did not co-occur with the typical decapod inhabitants of live *Pocillopora* sp. such as *Trapezia* spp., *Cymo* spp., *Alpheus lottini* and *Synalpheus charon*. Perhaps these data indicate that more recently evolved brachyurans have replaced the ancient dynomenids from the more productive live-coral habitat. Furthermore, *D. hispida* occurred in 13 corals and *D. praedator* in 7 corals so that in only one case did the two species occur together, suggesting that there may be some competitive exclusion between these two species.

EDMONDSON (1946) found that Hawaiian *D. hispida* are very abundant in crevices of porous rocks. Gut contents of two specimens (CW = 13.5 and 15.0 mm) from Hawaii included mostly fine organic particles, sand grains, a few cut lengths of tubular hydroid(?) and a chitinous fragment that may have come a decapod leg. The groups of stiff setae on the cheliped fingers may act as a sieving device for collecting food particles.

Massive corals from Enewetak Atoll contained relatively few dynomenids: *Goniastrea retiformis*, only one *D. hispida* among 36 decapods from 18 coral heads; *Porites lutea*, no dynomenids amongst 77 decapods from 43 coral heads (HIGHSMITH, 1981). Of 2722 Brachyura and Anomura (except pagurids), collected from seven stations on the barrier reef of Moorea, PEYROT-CLAUSADE (1977) found only three specimens of *D. hispida* (approx. 0.11%). The fauna was dominated by xanthid crabs (approx. 70%), and galatheids (approx. 17%). PEYROT-CLAUSADE (1981) recorded *D. hispida* from clumps of dead *Acropora* from 1.5-24 m, Tuléar Reef, Madagascar, and RIBES (1978) found only single specimens in *Pocillopora damicornis*, *Favia stelligera*, *Acropora clathra*, *A. humilis*, *A. variabilis*, and *Oulophyllia crispa* from La Réunion. Above is also listed a Taiwan specimen collected from *Seriatopora hystrix*. These data suggest that *D. hispida* inhabits a variety of corals but is comparatively rare in some reef communities.

Dynomene praedator A. Milne Edwards, 1879

Figs 3 b, 8 a-b, 11, 12 d, 14 b, 17 b, 19 a-g

Dynomene praedator A. Milne Edwards, 1879: 8, pl. 14, figs 20-26. — MIERS, 1884: 13. — DE MAN, 1888: 409. — ORTMANN, 1892: 543, pl. 26, fig. 3. — ALCOCK, 1901: 75 (list). — RATHBUN, 1911: 196. — IHLE, 1913: 92 (list). — BALSS, 1938: 7. — MIYAKE, 1938: 194, text-fig. 4, 2; 1939: 198 (list); 1983: 195 (list). — BUITENDIJK, 1939: 227, pl. 7, fig. 4. — TWEEDIE, 1947: 30; 1950: 106. — LIN, 1949: 12. — GUINOT, 1967: 241 (list). — SERÈNE, 1968: 36 (list). — TAKEDA, 1973: 81; 1977: 35 (list). — MONOD & SERÈNE, 1976: 25 (list). — MIYAKE, 1983: 195 (list). — GUINOT, 1985: 448 (list). — GARTH, HAIG & KNUDSEN, 1987: 241. — RODGERS & OLEROD, 1988: 302. — POUPIN, 1996a: 24 (list).

Dynomene sinense Chen, 1979: 9, fig. 1; 1980: 119, pl. 1, fig. 1. — DAI & YANG, 1991: 31 (key).

Dynomene sinensis - ODINETZ, 1983: 208. — GUINOT, 1985: 448 (list).

Dynomene sp. - NAIM, 1980: 55.

Dynomene tenuilobata Dai, Yang & Lan, 1981: 118, figs 5-9. — DAI, YANG, SONG & CHEN, 1986: 29, text-fig. 12, 3-4, pl. 3, fig. 4. — DAI & YANG, 1991: 33, text-fig. 12, 3-4, pl. 3, fig. 4.

Dynomene huangluensis Dai, Cai & Yang, 1996: 234, fig. 1.

Dynomene hungluensis - DAI, CAI & YANG, 1996: 251 (err.).

?*Dynomene* sp. - CALMAN, 1909: 703.

Not *Dynomene praedator* - SAKAI, 1976: text-fig. 17. — NAGAI & TSUCHIDA, 1995: 108, pl. 1, fig. 2 [= *Metadynomene tanensis* (Yokoya, 1933)].

MATERIAL EXAMINED. — **Somalia**. Gesira, 18 km south of Mogadishu: stn 20, habitat unknown, low tide level, G. CHELAZZI coll., 1980: 1 ♀ ovig. 9.0 x 7.0 mm (MZUF).

M. VANNINI coll.: stn 7, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ 6.0 x 5.0 mm. — Stn 8, on dead *Pocillopora* sp., low tide level, 1981: 1 ♂ 9.5 x 7.2 mm (bopyrid isopod in right gill chamber, *Gigantione* sp. nov.). — Stn 9, on dead *Pocillopora* sp., 1981: 1 ♂ 6.7 x 6.1 mm. — Stn 10, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ 8.7 x 6.7 mm. — Stn 14, on dead *Pocillopora* sp., low tide level, 1981: 1 ♂ 10.8 x 8.5 mm. — Stn 15, on dead *Pocillopora* sp., low tide level, 1981: 1 ♀ 10.0 x 8.0 mm. — Stn 19, reef locality, low tide level, 1981: 3 ♂ 5.9 x 5.1 - 9.6 x 7.8 mm; 4 ♀ 5.1 x 4.2 - 8.0 x 6.4 mm. (All Somalia material from MZUF, see VANNINI, 1985).

Glorieuses Islands. Intertidal zone, low tide level, A. CROSNIER coll., 29.01.1971: 1 ♂ 8.7 x 6.7 mm; 1 ♀ ovig. 9.6 x 7.5 mm.

Madagascar. *Nosy Be*: stn 899, no location, low intertidal, 02.1962: 1 ♂ 12.0 x 9.6 mm (MNHN-B 6863). — Stn 961, no location, low intertidal, 02.1962: 3 ♂ 5.1 x 4.4 - 12.4 x 9.5 mm; 2 ♀ 8.7 x 7.2, 11.0 x 8.0 mm; 1 ♀ ovig. 9.0 x 7.5 mm (MNHN-B 6864). — Intertidal zone, 03.1971: 2 ♀ 9.1 x 7.3, 9.5 x 7.7 mm (MNHN-B 6903). — Madirokely, intertidal zone, no date: 1 ♂ 13.5 x 10.7 mm.

Seychelles (Aldabra). Reef West, A. J. BRUCE coll., no date: 1 ♂ 9.8 x 8.0 mm; 1 ♀ 7.8 x 6.5 mm; 1 ♀ ovig. 8.2 x 6.6 mm.

Reunion. On *Acropora* sp., no locality, 10 m, no date: 1 ♂ 6.8 x 6.0 mm. — On coral, no locality, 20 m, no date: 1 ♂ 5.0 x 4.2 mm. — On *Pocillopora* sp., no locality, 10 m, S. RIBES coll., no date: 1 ♀ 5.0 x 4.1 mm.

Cocos Keeling Islands. No locality, no depth, C.A. GIBSON-HILL coll., 1941, M. W. F. TWEEDIE det.: 1 ♂ 8.0 x 6.4 mm; 1 ♀ 6.2 x 5.1 mm. (ZRC 19646129-10). See TWEEDIE (1950). — NW end of N. Keeling Id, 0-28 m, 23.02.1989: 1 ♂ 5.9 x 4.8 mm; 2 ♀ 6.7 x 5.4, 7.0 x 5.7 mm; 1 ♀ ovig. 6.9 x 5.5 mm (WAM 137-94).

Christmas Island. No locality, no depth, C.A. GIBSON-HILL coll., 1940, M. W. F. TWEEDIE det.: 5 ♂ 6.1 x 5.0 - 7.9 x 6.4 mm; 1 ♀ 6.7 x 5.3 mm; 2 ♀ ovig. 6.5 x 5.0, 7.0 x 5.8 mm (ZRC 19646121-8). — No locality, no depth, C.A. GIBSON-HILL coll., 1947, M. W. F. TWEEDIE det.: 2 ♂ 7.3 x 6.1, 7.5 x 6.1 mm; 1 ♀ ovig. 10.0 x 7.9 mm (ZRC 1970.1.20.51-54). See TWEEDIE (1947).

Indonesia. *Moluccas*. RUMPHIUS 2: stn 902 (26), Gorong, east of Seram, on *Porites*, 1975: 1 ♂ 5.4 x 4.3 mm. — *Amboina*. No details (see DE MAN, 1888), J. BROCK coll., 7.09.1885: 1 ♂ 9.8 x 7.9 mm (SMF 163). — *North Celebes*. Lembek Strait, no depth, no date: 1 ♀ 9.8 x 7.9 mm (USNM 122953).

Mariana Islands (coll. H. T. CONLEY). Guam, Piti Reef, 13°27'N, 144°47'E, among rocks, 1.5 m, 22.07.1993: 2 ♂ 8.5 x 6.5, 13.0 x 10.3 mm (UGM). — *Ibidem*, among rocks, 1 m, 1.08.1993: 1 ♀ 7.8 x 7.0 mm (UGM).

Solomon Islands. Bougainville, Tiop, no depth, coll. H. SCHOEDE, 4.11.1909: 10 ♂ 4.1 x 3.6 - 9.3 x 7.6 mm, 14 ♀ 4.3 x 3.6 - 7.5 x 6.2 mm (ZMB 14407).

New Caledonia. Exact locality unknown, probably intertidal, M. BALANSA coll., 1873: 1 ♀ (probably the ♀ paratype) 10.2 x 8.1 mm (MNHN-B 7029). — Exact locality unknown, probably intertidal, M. BALANSA coll., 1873: 6 ♂ 6.5 x 5.4 - 9.6 x 7.5 mm; 2 ♀ 6.5 x 5.5, 9.8 x 7.3 mm (MNHN-B 22075).

LAGON: stn 585, île des Pins, 22°46.0'S, 167°32.0'E, 43 m, B. RICHER DE FORGES coll., 18.07.1985: 1 ♂ 10.4 x 8.2 mm; 1 ♀ 5.7 x 4.2 mm.

Récif Mbéré: 22°19.9'S, 166°13.2'E, 10 m, P. BOUCHET coll., 5.05.1993: 2 ♂ 6.2 x 5.1, 8.7 x 6.8 mm; 4 ♀ 5.0 x 4.1 - 10.4 x 8.1 mm.

OPÉRATION MONTROUZIER. Koumac, récif Infernet, B. RICHER DE FORGES coll., 7.10.1993: 1 ♂ 8.7 x 7.1 mm.

French Polynesia. *Society Ids*. Tahiti. No details, 2 ♂ 9.8 x 8.1, 11.2 x 9.3 mm; 2 ♀ ovig. 10.2 x 8.3, 11.6 x 9.1 mm. (SMF 4855). ORTMANN (1892) reported 2 ♂ from Tahiti, but under *Dynomene hispida* he also reported 2 ♂ and 2 ♀ from Oshima, Japan, so it is possible that he confused the material of these two species. — *Moorea*. On algae (*Amphiroa foliacea*), O. NAIM coll., 1978, : 1 ♀ ovig. 11.6 x 8.9 mm (MNHN-B 20203) (see NAIM, 1980). — Associated with *Pocillopora damicornis* and *P. elegans*, O. ODINETZ coll., 1981, D. GUINOT det. in 1982 as *Dynomene sinensis*. : 1 ♂ 11.2 x 9.1 mm (MNHN-B 17090) (see ODINETZ, 1983).

McDonald Volcano. 28°58'S, 140°16'W, approx. 50 m, B. RICHER DE FORGES coll., 19.05.1979: 3 ♀ 4.3 x 3.9 - 4.4 x 4.0 mm.

Line Islands. WHIPP EXPEDITION: *Washington Id*, 4°43'N, 160°21'W, no depth, 1924: 1 ♂ 5.0 x 4.3 mm (BPBM 2359). — *Christmas Id*, 1°51'N, 157°23'W, no depth, 1924: 1 ♂ 11.1 x 8.2 mm (BPBM 2313).

Johnston Island. 16°45'N, 169°30'W, northwest side of outer reef, F. M. BAYER coll., 28.08.1947: 3 ♀ 4.8 x 4.0 - 5.7 x 4.5 mm (USNM 176603).

Hawaii. *Oahu Id*, Kawela Bay: no depth, C. EDMONDSON coll., 17.07.1935: 2 ♂ 8.0 x 6.6, 9.0 x 7.0 mm (BPBM 4038). — No depth, 03.1936: 3 ♂ 7.0 x 5.7 - 10.0 x 8.1 mm, 1 ♀ 10.0 x 8.0 mm (BPBM 4212). — No depth, 10.07.1937: 2 ♂ 8.6 x 7.2, 10.7 x 8.4 mm; 3 ♀ 7.6 x 6.4 - 10.4 x 8.4 mm (BPBM 4312).

Oahu Id, Black Point: no depth, C. EDMONDSON coll., 12.07.1937: 1 ♂ 9.2 x 7.3 mm (BPBM 3844). — No depth, L. R. WOODWARD coll., 1937: 1 ♂ 5.6 x 4.5 mm (USNM 175882).

Oahu Id, Waikiki Reef: no depth, C. EDMONDSON coll., 1921: 1 ♂ 10.6 x 8.8 mm, 1 ♀ ovig. 12.0 x 9.6 mm (BPBM 572). — No depth, C. EDMONDSON coll., 1922: 1 ♂ 12.0 x 10.2 mm (BPBM 739). — Off Waikiki, 5 m, 1.01.1945: 2 ♂ 6.0 x 5.0, 6.6 x 5.7 mm; 2 ♀ 5.2 x 4.0, 7.7 x 6.6 mm; 1 ♀ ovig. 9.7 x 7.3 mm (BPBM 5096).

Oahu Id, Kahala Bay: no depth, C. EDMONDSON coll., 7.03.1930: 10 ♂ 6.2 x 5.5 - 10.3 x 8.4 mm; 8 ♀ 6.4 x 5.2 - 9.8 x 7.4 mm; 3 ♀ ovig. 9.4 x 7.4 - 9.5 x 7.7 mm (BPBM 3168). — No depth, C. EDMONDSON coll., 05.1931: 1 ♀ ovig. 10.3 x 8.1 mm (BPBM 3414). — No depth, C. EDMONDSON coll., 28.06.1934: 5 ♂ 7.0 x 5.7 - 12.0 x 9.8 mm; 1 ♀ 8.6 x 7.3 mm; 2 ♀ ovig. 8.2 x 6.8, 8.6 x 7.2 mm (BPBM 3780).

Oahu Id, Kahe Point: no depth, S. COLES coll., 06-07.1977: 2 ♂ 4.6 x 4.0, 4.8 x 4.0 mm; 7 ♀ 4.5 x 3.8 (parasitic isopod attached to pleopods) - 7.0 x 5.6 mm (BPBM 1977.554).

Oahu Id, no locality, no depth, C. EDMONDSON coll., 1932: 1 ♂ 9.2 x 7.4 mm; 1 ♀ ovig. 9.4 x 7.5 mm (BPBM 3601). — No locality, no depth, W.A. BRYAN coll., no date: 1 ♂ 11.0 x 9.3 mm (BPBM 184). — No depth, 1973: 1 ♂ 9.0 x 7.2 mm (BPBM 510492).

Kauai, Anahola Bay, 15 m, 7.09.1959: 1 ♂ 7.6 x 6.1 mm; 1 ♀ 8.8 x 7.1 mm (BPBM 6819).

Hawaii, no locality, no depth, B. DEGENER coll., 21.09.1929: 1 ♀ 5.6 x 4.4 mm (USNM 108395).

Japan. Kuroshima Ids. In dead coral branches, inner reef, 1992: 1 ♀ 10.3 x 8.0 mm; 1 ♀ ovig. 9.1 x 7.3 mm. — No locality, coll. M. OSAWA, 1993, 1 ♀ 10.1 x 7.8 mm (collection of C. McLAY).

TYPES. — *Dynomene praedator* A. Milne Edwards, 1879: holotype is a male 13.0 x 10.0 mm, collected by M. BALANSA from the intertidal, New Caledonia, 1873, but it probably no longer exists (see Discussion below under this species). However there is a paratype female 10.2 x 8.1 mm, from the same collection, and held at the Muséum national d'Histoire naturelle, Paris, registration number MNHN-B 7029.

Dynomene sinense Chen, 1979: holotype is a female 9.2 x 7.5 mm, collected from Shenhang Dao, Xisha Ids, South China Sea, 13.04.1958, held by the Beijing Natural History Museum, registration number IOAS-C00801. A paratype male collected from Shi Dao, Xisha Ids, 6.04.1958, is held at the same institution, registration number IOAS-C00802.

Dynomene tenuilobata Dai, Yang & Lan, 1981: holotype is a male 6.4 x 5.6 mm, collected from Jinyindao, Xisha Ids, South China Sea, 5.12.1974, held by the Beijing Natural History Museum, under number 74073.

Dynomene huangluensis Dai, Cai & Yang, 1996: holotype not designated from among the five specimens (4 males and 1 female) collected from three different reefs of the Nansha Ids, South China Sea (6°56'N, 113°35'E - 10°50'N, 114°10'E). Specimens deposited in the Bejing Natural History Museum.

DESCRIPTION. — Carapace wider than long (CW/CL = 1.25 approx.), broadly rounded in outline but frontal and posterior margin truncated, surface minutely granulated and evenly convex. Carapace surface and pereopods covered with coarse, plumose setae of two lengths: short setae clothing surface, but interspersed with longer setae (0.08 x CW) which also fringe limbs. Setae not arranged in clumps. The setae give this crab a yellowish colour but their density is not sufficient to completely obscure body surface. Structure of setae identical in both sizes: proximal 65% of shaft with many short setules, then a region occupying about 10% where there are approximately a dozen long setules projecting almost at right angles to setal axis, and finally the distal 25% which is smooth, slightly curved, and narrows to an acute tip.

A shallow frontal carapace groove separates a pair of low rounded protuberances, and then divides into separate grooves which gradually become more faint. Just in front of cardiac region two laterally-directed grooves originate: the first groove (cervical) arises separately from small pits curving anteriorly on to branchial region, while second groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally bordering the anterior cardiac region. In effect the groove crossing the mid-line, connects two crescent-shaped grooves. No branchial groove is evident. Anterolateral carapace margin begins at level of postorbital corner, evenly convex and usually adorned with small granules, although there are two (sometimes three) larger blunt granules interrupting margin at equidistant intervals and near beginning of posterolateral border there is a small group of similarly prominent granules. Development of granules on anterolateral margin is quite variable among individuals collected from the same site and often differs between the left and right sides of the carapace of individual crabs. But there are never well defined, acute teeth as found in *D. hispida*. Posterior carapace margin is recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits without a notch, towards postorbital corner are a few minute granules which are continued on suborbital margin, which is bluntly produced as a small lobe, making the border sinuous. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral region; distal margin almost adjacent to distal margin of second antennal article, the two of them continuing the line of the suborbital margin. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth above opening of antennal gland is scarcely produced. Second article wider than long; distal margin longest, to which is fixed exopod curving over base of eyestalk and becoming broader. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in beside exopod, and together with small fourth article just matches length of exopod. Remaining antennal articles directed laterally, extending about as far as postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.23. Eyestalk can be completely folded into orbit, and cornea well developed, occupying all of tip. Epistome broadly triangular, surface concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker.

Subhepatic area slightly convex with a few minute granules. A groove begins near ventromedial corner of carapace, curving round, without a cervical branch, under branchial region and meeting lateral carapace margin just anterior to tubercle on posterolateral border. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has only five or six small, distally placed teeth on each side. Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

There are 19 gills and 7 epipodites on each side. Distribution of gills and epipods as for *D. hispida*. Gills are unequal (anterior half larger) violin-shaped plates, marginally notched, and joined together along central axis which carries afferent and efferent blood channels. Epibranchial corners thickened and bluntly pointed. Towards base of each arthrobranch and pleurobranch there are pairs of elongate epibranchial lobes which increase in length proximally. A transverse section near base shows two plates separated, on epibranchial surface, by two lobes, while a section mid-way shows only two plates. Setae on inner posterior wall of branchial chamber poorly developed. Posterior margin of scaphognathite with two long setae. Hypobranchial margin of podobranchs bear same setae as on epipod.

Cheliped only slightly longer than first leg, merus trigonal, inner face smooth and fitting closely against pteryogostomial region of carapace; borders with small granules; outer face has a subterminal groove separating a thickened ridge without granules. Outer face of carpus convex with several small granules, two more prominent distal tubercles; inner superior border with a flattened, distomedially directed, unornamented spur which abuts against distal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin produced as a smooth obtuse flange fitting against merus when limb is withdrawn. These two structures give carpal article an unusual shape. Transverse section of propodus decreases in area distally; outer and superior faces covered in small granules; inner and inferior faces smooth. Fixed finger of female almost straight with two small teeth; moveable finger curved with a single, larger tooth opposite first tooth on fixed finger; both fingers hollowed out internally, touching only at tips which may be faintly divided into three or four blunt, interlocking teeth. In mature male (CW = 12.0 mm) chelipeds more massive and teeth are similar to female except that near point of articulation with dactyl there is a tooth-like projection directed distally. This projection seems to occur in males with CW > 10.0 mm. Left and right chelipeds are sometimes different in number of teeth. Just below teeth on fixed finger is a distinct pit in which several long setae are inserted with a similar group of setae on inner margin. Small groups of long stiff setae, inserted mid-way along dactyl and fixed finger, are directed across space between the two fingers.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate; both faces of meri of first two legs and anterior face third leg merus smooth and nacreous; inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with several minute granules, a shallow subterminal restriction; length of merus of second leg about three times its width and equal to about half CL. Carpi inflated and produced distally to overhang base of propodi. Dactyli curved, inferior margin armed with 5-6 small spines, tip brown and subacute. Borders of all leg articles minutely granulated.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching only as far as mid-way along meral article of preceding limb; borders of articles unarmed. Last pair of legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing four, unequal, stout, acute, spines each lined with tiny flattened teeth along almost entire inner surface. Female dactyl as long as propodal extension, bearing fourteen unequal, stout, hooked spines (arranged asymmetrically around perimeter of the dactyl) whose inner surface is wrinkled and mostly devoid of tiny teeth. Male propodal extension bearing five unequal hooked spines the four largest of which are lined with many tiny flattened teeth along most of inner surface. Male dactyl longer than propodal extension and ending in a single acute claw.

All segments of abdomen freely moveable, increasing in length and breadth distally, surface smooth, margins unarmed but fringed with long setae. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In female uropod plates large, filling almost all space between last abdominal segment and telson, excluding most of last abdominal segment and telson from reaching lateral margin of abdomen. In male last abdominal segment reaches lateral margin but only occupies about a quarter of the space. No effective abdominal locking mechanism: abdomen only loosely held against sternum in all sizes of both sexes. In males and immature females, there is a small rounded sternal tubercle between first walking legs, adjacent to uropods, but this simply restricts sideways movement of abdomen. In mature females this tubercle disappears and abdomen occupies all of ventral surface, covering entire sternum and coxae of all pereopods with telson covering proximal half of third maxillipeds. In male, abdomen not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. First male pleopod a semi-rolled tube with a very small apical plate surrounded by long setae. Second male pleopod with an exopod on basis, needle-like distally, armed with a series of five tiny, curved, acute, inset spines and ending in three larger spines. Terminal spines slightly curved at their tips and last two form a cheliped-like structure. Third to fifth male pleopods uniramous and rudimentary.

COLOUR. — Light yellowish-brown body and limbs, fingers white. Antennae same colour as the body, not light blue as in *Dynomene hispida*.

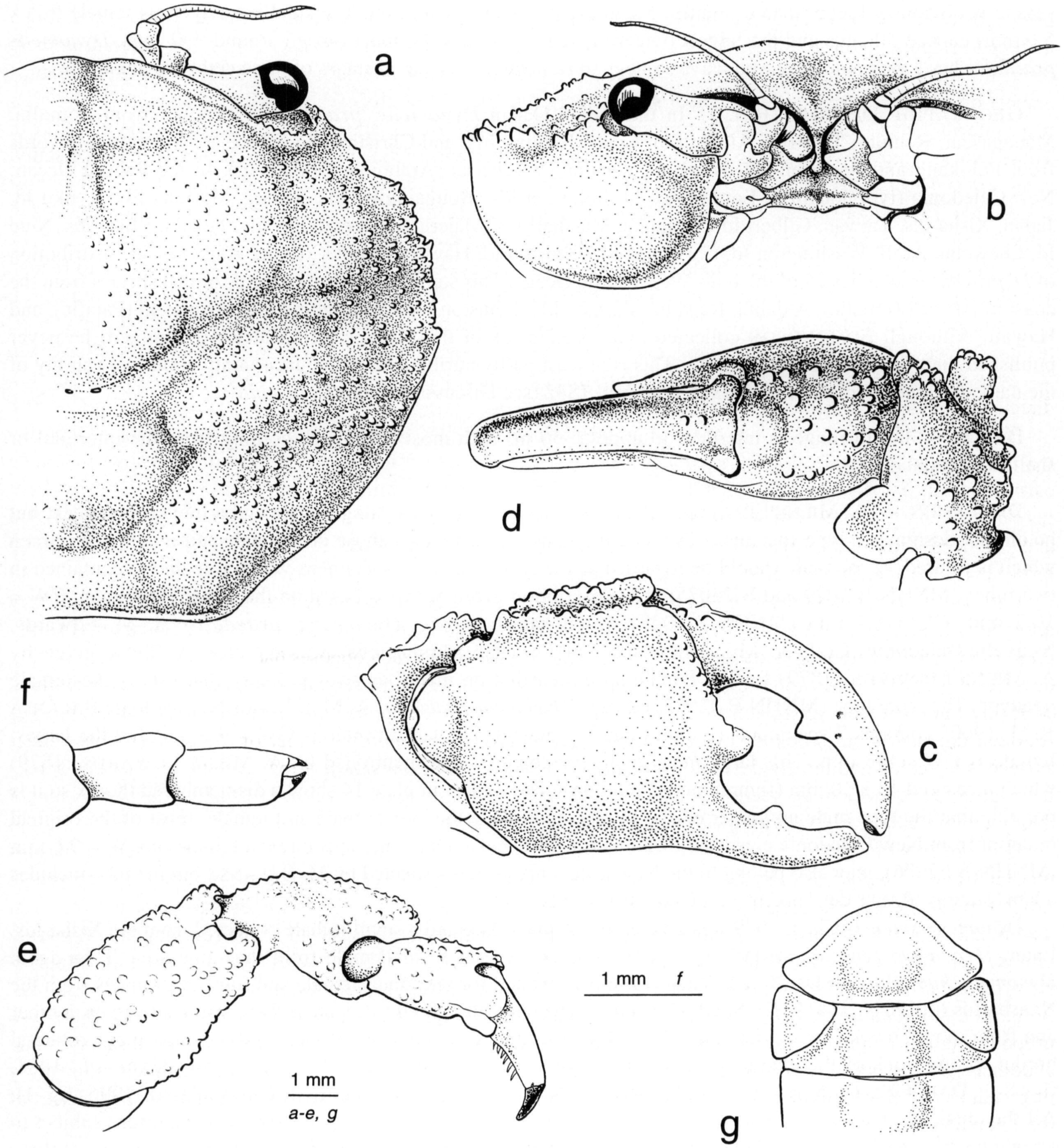

FIG. 19. — *Dynomene praedator* A. Milne Edwards, 1879: **a-g**, ♂ 13.5 x 10.7 mm, Nosy Be, Madagascar, A. CROSNIER coll.: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of male abdomen.

SIZE. — The maximum size for males is 13.5 x 10.7 mm, for females 12.0 x 9.6 mm, while the smallest ovigerous female is 6.5 x 5.0 mm. SAKAI (1976) gives the maximum size for males as 16.0 x 13.0 mm, but this is probably based on the misidentification of *Metadynomene tanensis* (Yokoya, 1933). Ovigerous females have been recorded from January to June with eggs ready to hatch in January and new eggs in June so the breeding season is obviously longer than 6 months. Mean egg diameter = 0.46 mm. The smallest ovigerous female (6.5 x 5.0 mm) carried 50 eggs and the largest ovigerous female (12.3 x 9.6 mm) carried around 900 eggs. *Dynomene praedator* has a very similar reproductive strategy to *D. hispida*. The larval stages of these crabs are unknown.

GEOGRAPHIC DISTRIBUTION. — In the Indian Ocean *Dynomene praedator* is known from Somalia, Madagascar, Reunion, Coetivy, Aldabra Id, Cocos Keeling Ids, and Christmas Id. There are Indonesian records from Pelokang and Postiljon Ids, North Celebes and Moluccas (Amboina, Obilatu Id). In the Pacific Ocean: New Caledonia (type locality), Lord Howe Id, Solomon Ids (Bougainville Id), Samoa, Mariana Ids, Ryuku Id, Japan, Xisha Ids, Taiwan, Gilbert Ids, Aranuka, Marshall Ids, Majeru, Viti Levu, Fiji Ids, Tuvalu, Ellice Ids, Niue Id, Enewetak Atoll, Washington Id, Christmas Id, Johnston Id, Hawaii, Moorea, Tahiti, Rapa Id. The distribution of *D. praedator* includes all of the Indo-West Pacific Ocean. This study reports new records of this species from the coast of Africa (Somalia), Aldabra, Rapa Id, Mariana Ids, Johnston Id, Washington Id, Christmas Id (Pacific), and Hawaii. Although EDMONDSON collected many specimens of this species (see Material Examined) he never published their occurrence from Hawaii. This is at least partly attributable to the uncertainty about the validity of the name *Dynomene latreillii* Eydoux & Souleyet, 1842 (see Discussion under *D. hispida*).

DEPTH. — Depth range is intertidal to approx. 50 m, with most specimens coming from the intertidal or shallow subtidal depths.

DISCUSSION. — A. MILNE EDWARDS (1879) described this species using a male and a female specimen, but he did not designate a type specimen. The measurements given first are those of the male and it is this specimen which is figured, so the male should be regarded as the type. The eight specimens which remain are contained in two tubes (MNHN-B 7029 and B 22075). The description given above is based on the female specimen, CW = 10.2 mm, CL = 8.1 mm (MNHN-B.7029) which has the label "*Dynomene praedator* A. M. Edwards, Nouvelle Caledonie. Coll. A. Milne Edwards, 1903". These dimensions are very close to those given by A. MILNE EDWARDS (1879) for the female specimen that he mentions so it is likely that this is the female paratype. The other tube (MNHN-B 22075) labeled "*Dynomene praedator* A. M. Edwards N. Caledonie BALANSA 1873. 1900" contains 7 specimens (5 males and 2 females). The largest male is CW = 9.6 mm and the largest female is CW = 9.8 mm. This large male is smaller than the one mentioned by A. MILNE EDWARDS (1879) which measured 13 x 10 mm (figured on his plate 14). The figures in plate 14 show a dismembered thorax so it is possible that the type male no longer exists. In fact, apart from the largest male and female, most of the original material from New Caledonia consisted of immature specimens. One other specimen, a female of CW = 9.6 mm (MNHN-B 22076), may also belong to the New Caledonian series collected by M. BALANSA but the tube includes a label stating "BALSS det." and there are no other details available.

Dynomene sinensis Chen, 1979 was erected for a small male and a small female collected from the Xisha Ids. Later, *Dynomene tenuilobata* Dai *et al.*, 1981 was erected for a small male from the same area. Then again *Dynomene huangluensis* Dai, Cai & Yang, 1996 was created for one small female and four small males from the Nansha Ids (10°50'N, 114°10'E), South China Sea. The characters used to separate these species from each other and from other *Dynomene* species, especially *D. praedator*, were number of lobes on the carapace anterolateral border, proportions of the cheliped manus and male pleopods (see CHEN, 1979, fig. 1, 5-6; DAI *et al.*, 1981, figs 8-9; DAI *et al.*, 1986, fig. 12, 3-4; DAI & YANG, 1991, fig. 12, 3-4 and DAI, CAI & YANG, 1996, fig. 1). All the cheliped characters are sexually dimorphic and allometric, changing with size, and therefore subject to variation within each species and therefore clearly unsuitable for species definition. The overall appearance of these three species is very close to that of *D. praedator* and the male pleopods of *D. tenuilobata* and *D. huangluensis* are identical to those described above. Furthermore, the development of lobes or granules on the anterolateral margin of *D. praedator* is variable and, as noted above, it is the absence of distinct teeth on the anterolateral margin that separates this species from *D. hispida.* All three species from the Xisha and Nansha Ids must be regarded as synonyms of *D. praedator.*

When studying the dynomenids from the Palau Ids, TAKEDA (1973) recorded both *Dynomene hispida* and *D. praedator.* He noted that in *D. hispida* ".. the anterolateral teeth are more prominent, regular and equidistant,..." than in *D. praedator*, where "..the anterolateral border is provided with five obtuse teeth...". Furthermore, he mentions that "In the smaller specimens from the Ryukyu Ids those teeth are spine-tipped". It is likely that these small specimens may be *D. hispida* rather than *D. praedator.*

In identifying *Dynomene praedator* it is important to realize that the tomentum does not completely obscure the body surface. SAKAI (1976) synonymized *Metadynomene tanensis* (Yokoya, 1933) with *D. praedator* but this was based on a misinterpretation of the nature of the tomentum. Further problems have arisen because of the somewhat inaccurate description and figures given by A. MILNE EDWARDS. This led CHEN (1979) to describe a new species, *Dynomene sinensis*, from the Xisha Ids, China. CHEN recognized the similarity of her specimens to *D. praedator* but believed that there were differences in the anterolateral margin, merus of the third walking leg, and dentition of the cheliped fingers. A close examination of a series of eight specimens from the type locality of *D. praedator* shows that the arrangement of tubercles on the anterolateral carapace margin is variable on the two sides of the carapace and also between specimens. It is not easy to ascertain the supposed differences in respect of the merus of the third walking leg, but cheliped dentition is variable: in the female, the dactyl typically has two teeth and the fixed finger only one, but these may be located proximally or distally; in males, the dactyl usually has one tooth, but the fixed finger can have either one or two teeth (these can be different between left and right limbs) and these may be located proximally or distally. The basal tooth on the fixed finger (well illustrated by A. MILNE EDWARDS, 1879, pl. 14, fig. 3) only occurs in males and does not develop until the size reaches about CW = 10.0 mm. The redescription given above, based on the same material as used by A. MILNE EDWARDS (1879), shows that there are in fact no significant differences between the Chinese and the original specimens from New Caledonia. The cheliped dentition characters are variable and in some cases attributable to ontogenetic variation. Therefore *D. sinensis* must be regarded as a synonym of *D. praedator.*

The branchial formula is the same and the gill structure of *Dynomene praedator* is very similar to that of *D. hispida* with most of each arthrobranch and pleurobranch consisting of violin-shaped plates on each side of the gill axis but with epibranchial lobes separating the plates proximally. For other features of *D. praedator* not illustrated here, see ORTMANN (1892, pl. 26, fig. 3i) for the second maxilliped and CHEN (1979, fig. 1, 4) and DAI, CAI & YANG (1996, fig. 1,1) for the third maxilliped (as *D. sinensis* and *D. huangluensis* respectively). As in *D. hispida*, the posterior margin of the scaphognathite bears two long setae which extend back over the epibranchial surface of the gills, and the hypobranchial margin of each podobranch is setose.

The original description of *Dynomene praedator* by A. MILNE EDWARDS (1879) did not include a comparison with the setae of *D. hispida.* The setae of *D. praedator* differ in several ways: there is no proximal smooth region at the base of the setae and the distal "dense band" consists of only a dozen or so long stout setules directed almost at right angles. In other respects the two species are similar.

There are some differences in the male pleopods between *Dynomene praedator* and *D. hispida*: both species have five inset subterminal spines on the second pleopod but in *D. praedator* these spines are curved instead of straight; there are three larger curved, terminal spines in *D. praedator*, with the last two forming a "pince-like" structure, but in *D. hispida* there are only two hooked spines which do not form a "pince"; finally, the rudimentary last three pairs of pleopods are uniramous in *D. praedator* but biramous in *D. hispida.*

Detailed illustrations of sexual dimorphism of the last leg of *Dynomene praedator* have not previously been published. In most respects the structure of the obsolete subchelate mechanism in *D. praedator* is similar to that of *D. hispida* except that the female has a much larger number of spines on the dactyl while in the male the teeth on the propodal spines are better developed and the area of rasp-like teeth near the base of the propodal extension is absent. Observations of living *D. praedator* from Hawaii (see below) suggest that the last leg is carried horizontally above the bases of the preceding legs and is only capable of a very restricted range of movements. The limb cannot be placed in a subdorsal position over the posterolateral corner of the carapace and cannot reach under the legs or under the abdomen. When the other legs move the last legs also move in an anterior-posterior direction to a very limited extent. There is no evidence that the last legs are capable of carrying pieces of camouflage or that they could be used for grooming or cleaning.

Dynomene praedator has been collected from reefs on corals such as *Pocillopora damicornis*, *P. elegans*, *Pocillopora* sp., *Acropora* sp., *Porites* sp., and from the crustose alga *Amphiroa foliacea*. The specimens collected by B. RICHER DE FORGES from the McDonald volcanic seamount came from near the top of this active volcano where there are no corals and only fresh volcanic rocks and gravels. For discussion of the co-occurrence of *D. praedator* and *D. hispida* in *Pocillopora* corals see Discussion under the latter species.

A male specimen from Somalia contained a bopyrid parasite which is a new species of *Gigantione* (Daniel ADKISON, pers. comm.). It is similar to the bopyrid specimens from *Petalomera pulchra* Miers, 1884 (from the Chesterfield Ids, see McLAY, 1993: 166) which are being described by John MARKHAM as a new species of the same genus. Both these new species are similar to *G. mortenseni* Adkison, 1984 which is known from *Cryptodromiopsis antillensis*, *Hypoconcha sabulosa*, and *H. spinosissima*.

With the help of Ron HOLCOM, who video-taped *Dynomene praedator* in its natural habitat and in an aquarium in Hawaii, I have been able to study the feeding behaviour of this dynomenid. During feeding the antennules are especially active and are periodically cleaned by the third maxillipeds. There are two modes of feeding: firstly, grazing algal covered rocks using the chelipeds to pick up food items, and secondly sifting through sand to remove organic material. The latter feeding method is performed while the crab hangs upside-down from a rock or coral with its third maxillipeds very close to the sand. One cheliped is used to shovel sand to the outer maxillipeds which pick it up and sift out organic material using the setose palps and inner margins. Then the sand is pushed aside using the other cheliped. In this way sand is moved across the mouth-field and the food extracted from it. Examination of the stomach contents of four *Dynomene praedator* from Hawaii, ranging in size from 8.6 x 7.3 to 12.0 x 9.8 mm (two males and two females, BPBM 3780 and 4312), revealed unidentifiable soft organic material and sand grains. The stomach contents of crabs, caught at a different time, confirm the observed feeding behaviour and suggest that separation of organic material from sand (deposit feeding) is the main mode of feeding.

Dynomene filholi Bouvier, 1894

Figs 3 e, 5 c, 8 c, 11, 17 c, 20 a-g

Dynomene filholi Bouvier, 1894: 6; 1896: 57, figs 22-23. — A. MILNE EDWARDS & BOUVIER, 1900: 5, pl. 3 (col.), fig. 3, pl. 8, figs 1-18. — ALCOCK, 1901: 75 (list). — ORTMANN, 1899, pl. 119, fig. 11. — IHLE, 1913: 92 (list). — BALSS, 1921: 47. — BOUVIER, 1922: 50. — MONOD, 1956: 76, figs 84-88, 873. — FOREST & GUINOT, 1966: 48. — MANNING & HOLTHUIS, 1981: 23. — FRANSEN, 1991: 93.

MATERIAL EXAMINED. — **Cape Verde Islands**. *"Talisman"*: no stn number, îlot Branco, 60 m, July 1883: 1 ♂ 14.6 x 12.0 mm (used as the basis for the description and illustrated by A. MILNE EDWARDS and BOUVIER, 1900, see Discussion below); 2 ♀ 6.3 x 5.1, 7.2 x 5.9 mm (one of these specimens was listed as a male by A. MILNE EDWARDS and BOUVIER, 1900) (MNHN-B 22080); 1 ♀ 4.0 x 3.6 mm (ZMUC). — Stn 103, near la Praya, red coral banks, 275-150 m, 23.07.1883: 1 ♀ 8.7 x 7.0 mm (used for describing the color) (MNHN-B 22087). — Stn 107, about 16°56'N, channel between Saint Vincent and Saint Antoine, 75 m, 29.07.1883: 6 ♂ 3.6 x 3.3 - 9.4 x 7.8 mm; 1 ♀ 4.9 x 4.0 mm; 1 ♀ ovig. 5.8 x 4.9 mm (MNHN-B 22081); 2 ♂ 5.4 x 4.8, 6.8 x 5.0 mm (MNHN-B 22083); 1 ♀ 6.4 x 5.2 mm (ZMUC).

IFAN (Institut Français d'Afrique Noire): N Maio Id, 42 m, J. CADENAT coll., 11.06.1955: 1 ♀ 3.8 x 3.6 mm. (MNHN-B 22079).

CANCAP: stn 6.069, 15°52'N, 13°00'W, 76-90 m, 13.06.1982: 1 ♂ 7.5 x 5.8 mm. — Stn 7.125, 16°36'N, 24°36'W, 85-130 m, 1.09.1986: 1 ♀ 10.0 x 8.7 mm (RMNH) (see FRANSEN, 1991).

Guinea Bissau. *"Gazelle"*: 10°60'N, 17°16'W, 274 m, 1.08.1874: 1 ♂ 8.5 x 7.0 mm (ZMB 16722).

Gulf of Guinea, Annobon Island. *"Calypso"*: stn 52, 1°27.5'S, 5°36.5'E, 35 m, 13-06-1956: 1 ♂ 6.8 x 5.9 mm (MNHN-B 22085) (reported as a female by FOREST & GUINOT, 1966). — Stn 107, 1°26.15'S, 5°35.40'E, 60 m, 4.07.1956: 1 ♀ 5.6 x 4.5 mm (MNHN-B 22082) (see FOREST & GUINOT, 1966: 48).

ANNOBON 3: Drague 2, 1°28.40'S, 5°35.50'E, 40 m, A. CROSNIER coll., 11.12.1965: 1 megalopa 3.2 x 3.2 mm (MNHN-B 22090). — Drague 3, 1°25.30'S, 5°39.00'E, 52 m, A. CROSNIER coll., 11.12.1965: 2 ♂ 8.4 x 7.0, 8.6 x 6.8 mm; 2 ♀ 8.0 x 6.6, 9.2 x 7.6 mm; 1 ♀ ovig. 10.5 x 8.2 mm. (MNHN-B 22092).

ANNOBON 5: chalutage au sud de l'île Annobon, 1°28.50'S, 5°37.50'E, 35-55 m, F. POINSARD coll., 16.06.1967: 3 ♂ 6.0 x 5.0 - 10.2 x 7.7 mm; 1 ♀ 8.0 x 6.5 mm; 1 ♀ ovig. 10.4 x 8.0 mm. (MNHN-B 22093)

Gulf of Guinea, Principe Island. *"Calypso"*: stn 86, 1°35'N, 7°28'E, 45 m, 26-06-1956: 2 ♂ 9.4 x 7.3, 10.9 x 8.6 mm; 3 ♀ 6.9 x 5.4 - 9.2 x 7.0 mm (MNHN-B 7028). — Stn 95, 1°38.35'S, 7°21.35'E, 35 m, 1956: 1 ♂ 12.3 x 9.9 mm (MNHN-B.22084) (see FOREST & GUINOT, 1966: 48).

TYPES. — The specimen dissected by BOUVIER in 1894 for describing the gills cannot be found and very likely has disappeared. So I designate as neotype the male 14.6 x 12.0 mm collected near îlot Branco, Cape Verde Islands, 60 m, in July 1883, registered at the Paris Museum under MNHN-B 22080, which was chosen by A. MILNE EDWARDS and BOUVIER amongst the 28 specimens collected by the *"Talisman"* at the Cape Verde Islands, as the basis of the first complete description of the species.

DESCRIPTION. — Carapace wider than long (CW/CL = 1.2 approx.), broadly rounded in outline but frontal and posterior margins truncated, surface smooth and quite convex. Carapace surface and pereopods covered with coarse, plumose setae of two lengths: short setae clothing surface, but interspersed with slightly longer setae (0.07 x CW) which also fringe limbs and tend to be arranged in clumps, especially on carapace where there are about twenty distinct tufts. Density of setae is not sufficient to completely obscure body surface. Structure of short and long setae is different. In short setae the proximal 35% of shaft has very short setules, then a region occupying about 25% where long, stout setules are directed almost at right angles to shaft, forming a dense bunch, then the next 30% which bears a brush of long fine setules on only one side, and finally the distal 10% which is smooth, slightly curved, and narrows to an acute tip. In long setae the proximal 25% is sparsely setose, 70% is covered with small setules which distally increase in density, but not in size, and last 5% is smooth, slightly curved and narrows to an acute tip.

A shallow frontal carapace groove separates a pair of low rounded protuberances, and then divides into separate grooves which gradually become more faint. Just in front of cardiac region two laterally-directed grooves originate: the first groove (cervical) arises separately from small pits curving (slightly sinuously) anteriorly on to branchial region, while the second groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally, bordering anterior cardiac region. In effect the groove crossing the mid-line, connects two crescent-shaped grooves. Mid-way along cardiac groove begins a faint branchial groove which runs towards base of last tooth on lateral margin. Posterior cardiac area is outlined by a faint groove. Anterolateral carapace margin begins at level of postorbital corner, evenly convex and bears four distinct, broad-based, equidistant teeth, each ending in a short spine; first two teeth directed anteriorly and last two directed more laterally. Near beginning of posterolateral border there is another smaller tooth without a terminal spine. Posterior carapace margin is recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates the orbits). Supraorbital margin not projecting, continuous above orbits with a small notch closer to postorbital corner, without granules; suborbital margin essentially straight, but terminating as a subacute tooth. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral region; distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth above opening of antennal gland is smaller. Second article wider than long; distal margin widest, to which is fixed the exopod curving over base of eyestalk and becoming broader and terminating bluntly. Third antennal article is longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and together with small fourth article just matches length of the exopod. Remaining antennal articles are directed laterally, extending well beyond postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.45. Eyestalk can be completely folded into orbit, and cornea is well developed, occupying all of tip. Epistome broadly triangular, surface concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace marked by a narrow suture.

Subhepatic area slightly convex. A groove begins near base of the antenna, curving round under branchial region, giving off a cervical groove which passes under base of second anterolateral tooth, and meeting lateral carapace margin just anterior to tooth on posterolateral border and connecting with branchial groove. Third maxillipeds operculiform; bases widely separated by tip of sternum. Crista dentata has six or seven well developed, distally placed teeth on each side. [BOUVIER (1896, fig. 23) and A. MILNE EDWARDS and BOUVIER (1902, pl. 8, figs 1-18) figure some of mouthparts.] Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

Branchial formula 19 gills + 7 epipods on each side. There is no podobranch on fifth pereopod. In cross section gills have the lateral margin deeply notched, dividing gill into a hypobranchial plate (containing efferent vessel) and an epibranchial lobe (anterior lobe longer). Between these marginal lobes are two pairs of lobes, first similar and second much shorter than marginal lobes. Thus the epibranchial surface shows six rows of blunt lobes, decreasing in size medially, which are arranged above the afferent blood vessel.

Cheliped stout (especially in male) only slightly longer than first leg; merus trigonal, inner face smooth and fitting closely against pterygostomial region of carapace, borders with a few small granules, outer face has a subterminal broad, restriction which separates a thickened ridge on which there are three small blunt granules. Outer face of carpus convex with three small granules, two more prominent tubercles on distal margin, inner superior border with a flattened, distomedially directed, spur which abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, the inferior carpal margin is produced as a smooth obtuse flange fitting against merus when limb is withdrawn. These two structures give the carpal article an unusual and distinctive shape. Transverse section of propodus decreases in area distally; outer and superior faces with very small granules which tend to be arranged in two or three longitudinal rows; inner and inferior faces smooth. Fixed finger almost straight with six teeth increasing in size distally; moveable finger curved with four teeth, first mid-way and separated from the remainder which are on tip; both fingers, thick, hollowed out internally, touching only at tips where teeth interlock. Just below proximal teeth on fixed finger are two distinct pits in which several long setae are inserted with a group of similar setae on inner margin. Groups of long stiff setae, inserted near base of dactyl and fixed finger, are directed across space between the two fingers. Collectively, these setae form a sieving screen.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with two or three small granules, length of merus of second leg about 1.7 times its width and equal to almost a half of CL. Dorsal surface of carpi bearing three small granules on anterior margin and two on posterior margin, and produced distally to overhang base of propodi. Dorsal surface of propodi smooth. Dactyli curved, inferior margin armed with 5-6 small spines, tip brown and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching only as far as two-thirds along meral article of preceding limb; borders of articles unarmed. Last pair of legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing four, unequal, stout, acute, spines each lined with tiny flattened teeth along almost the entire inner surface. Female dactyl as long as propodal extension, bearing eight unequal, stout, hooked spines (arranged asymmetrically around perimeter of dactyl) whose inner surface is concave, wrinkled and devoid of teeth. Male propodal extension bearing two unequal hooked spines without teeth. Male dactyl longer than propodal extension, bearing a single spine on lateral margin and ending in an acute claw.

All segments of abdomen freely moveable, increasing in length and breadth distally; surface smooth; margins unarmed but fringed with long setae. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In female uropod plates are large, filling about two thirds of space between last abdominal segment and telson, excluding most of last abdominal segment and telson from reaching lateral margin of abdomen. In male last abdominal segment occupies about a half of length. No effective abdominal locking mechanism: abdomen only loosely held against sternum in all sizes of both sexes. In mature female it occupies all the ventral surface, covering coxae of all pereopods with telson covering proximal half of third maxillipeds. In male the abdomen is not quite so broad and telson only extends as far as bases of third maxillipeds.

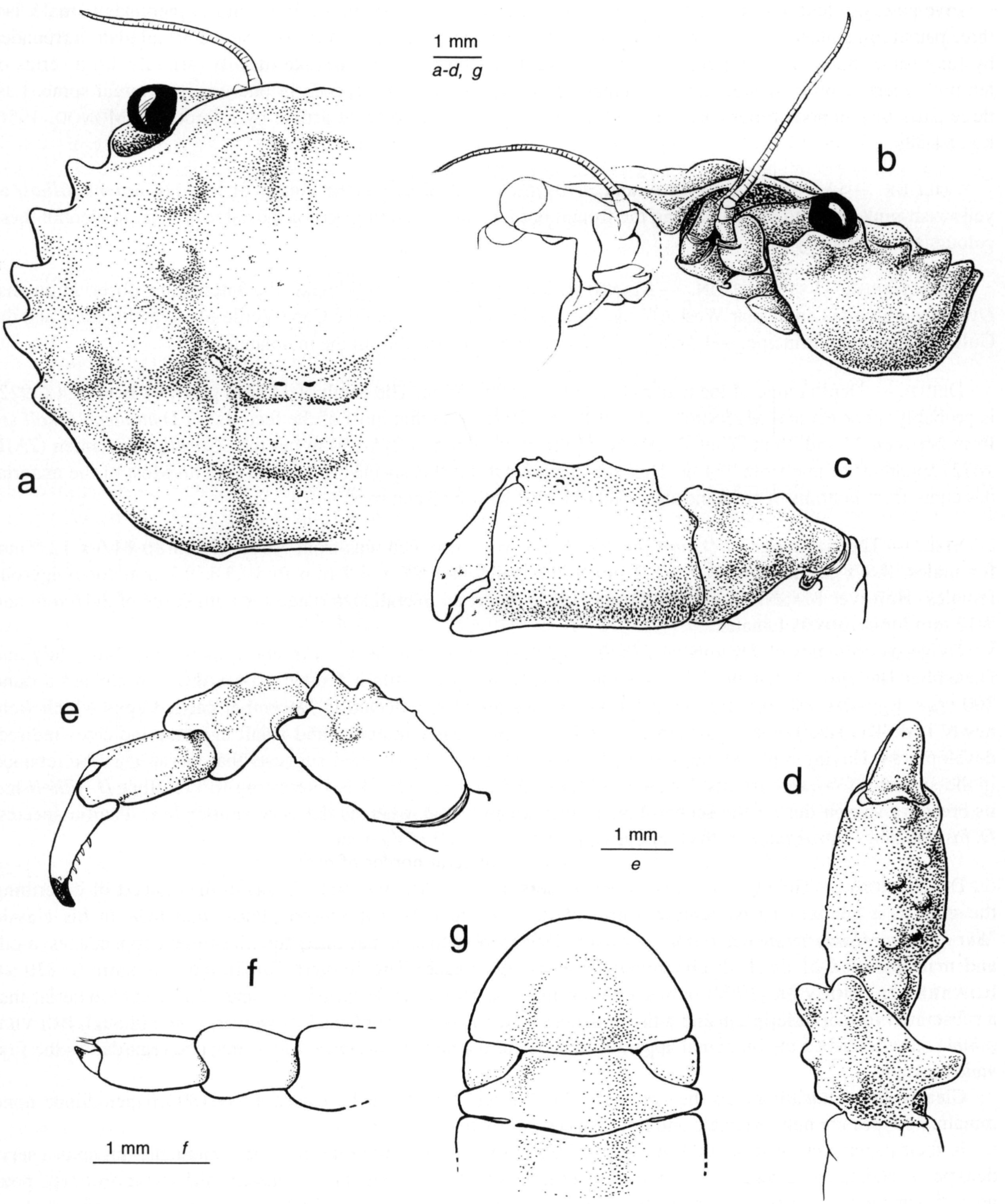

FIG. 20. — *Dynomene filholi* Bouvier, 1894: **a-g**, ♂ 12.3 x 9.9 mm, Principe Island, Gulf of Guinea, *"Calypso"* (MNHN-B 22084): **a**, dorsal view of left half of carapace; **b**, ventral view of left orbital area; **c**, outer face of left cheliped; **d**, dorsal view of left cheliped; **e**, posterior view of terminal articles of left fourth pereopod; **f**, posterior view of terminal articles of left fifth pereopod; **g**, ventral view of telson and terminal segments of male abdomen.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. Five pairs of pleopods in male, last three pairs rudimentary. First pleopod a semi-rolled tube ending in a well developed, curved apical plate surrounded by long setae. Second male pleopod with an exopod on the basis, needle-like distally, armed with a series of ten tiny, acute, closely spaced spines decreasing in size distally, and ending in one larger terminal spine. Last three pairs of pleopods biramous, exopod longer and connected to basal article by a joint (see MONOD, 1956, figs 84-88).

COLOUR. — A. MILNE EDWARDS and BOUVIER (1900) describe the colour of live *Dynomene filholi* as yellowish-pink with red, notably along the frontal border and on certain parts of the anterior legs. In alcohol these colours are completely lost.

GEOGRAPHIC DISTRIBUTION. — MANNING and HOLTHUIS (1981) make the interesting observation that *Dynomene filholi* is an insular West African species, known so far from the Cape Verde Ids (type locality) and the Gulf of Guinea Ids, Principe, and Annobon. It has not been recorded from the mainland.

DEPTH. — Depth range of the material examined is 35-275 m. The depth of 1477 m given by BOUVIER (1922) is probably incorrect and MANNING and HOLTHUIS (1981) note that most of the records for *Dynomene filholi* are from between 23 and 75 m. They doubt the *"Talisman"* record of 275-150 m but the *"Gazelle"* specimen (ZMB 1672) apparently came from 274 m. Thus the depth range for this species is from 35-275 m. Most of the material has come from bottoms of coralline algae and red coral with sand and rock.

SIZE. — The size range of *Dynomene filholi* material examined was from 3.6 x 3.3 mm to 14.6 x 12.0 mm for males, 3.8 x 3.6 mm to 10.5 x 8.2 mm for females and 5.8 x 4.9 mm to 10.5 x 8.2 mm for ovigerous females. However MANNING and HOLTHUIS (1981) report an overall size range for both sexes of 3-16 mm and 7-12 mm for ovigerous females.

Ovigerous females of *Dynomene filholi* have been reported in May (*"Pillsbury"* material), June, July and December (herein). A female 5.8 x 4.9 mm carried 30 eggs while a female 10.4 x 8.0 mm carried around 300 eggs. Egg size was 0.5 mm diameter. Ovigerous females collected in December carried eggs which were newly laid. The small size of ovigerous females suggests early maturity and small egg size indicates indirect development. Having a planktonic larval stage and an insular distribution suggests that larvae must be retained in the system of ocean currents surrounding these Atlantic islands. It is interesting to note that *D. filholi* has its breeding season during the second half of the calendar year whereas the very similar Indo-Pacific species, *D. hispida* and *D. praedator*, both carry eggs during the first half of the year.

DISCUSSION. — The name *Dynomene filholi* was first used by BOUVIER (1894) in the context of describing the gills to a Séance (10 November 1894) of the Société Philomathique de Paris, and then in his classic "*Sur l'origine Homarienne des crabes...*" paper (1896) where the carapace (his fig. 22), mouth appendages, a gill and male pleopod of the fifth abdominal segment (his fig. 23) are figured. But it was not until A. MILNE EDWARDS and BOUVIER (1900) published their monograph on the *"Travailleur"* and *"Talisman"* material that a substantial formal description and a list of material examined was published. However, even although BOUVIER (1894) only described the branchial apparatus, his use of the name *Dynomene filholi* must be regarded as the first valid example.

Clearly BOUVIER dissected the specimen (or the specimens) that he used for his 1894 paper. Since none remain, no types are now available and it was necessary to designate a neotype.

In their paper published in 1900, A. MILNE EDWARDS and BOUVIER refer to "..le grand mâle qui nous a servi de type,..." and again on page 9 they state "Ce dernier, qui est représenté dans la planche VIII, a servi de type pour notre description;..". These authors mention the measurements of this male (14.6 x 12.0 mm) and the place where it was collected (Cape Verde Islands, îlot Branco, 60 m). This male specimen is registered under MNHN-B 22080, along with two females. It is this male that I designate as neotype.

According to the list published by A. MILNE EDWARDS and BOUVIER, 28 specimens of *D. filholi* were collected by the *"Talisman"* from 4 stations. Only 14 remain at the Paris Museum. One from the station 107 (not examined by me) is held by the Museum of Comparative Zoology, Harvard, registration number MCZ 6559 and 2 others are held by the Zoologisk Museum at Copenhagen. Of the original 28 specimens, 11 are missing. But it may be these were dissected by BOUVIER for his 1894 and 1896 papers and discarded.

A. MILNE EDWARDS and BOUVIER (1900, pl. 8, figs 16-17) figure examples of the short setae, covering the surface, and the long setae arranged in "bouquets" on the carapace as well as fringing the abdomen. The electron microscope pictures confirm their results and add some more precise detail to the description and figures. *D. filholi* differs from the two preceding species in having dissimilar short and long setae. The short setae are unique amongst the dynomenids in having a subterminal brush of fine setules. Presumably these are specialized sensory setae.

BOUVIER (1896, fig. 23) and A. MILNE EDWARDS and BOUVIER (1900, pl. 7, figs 1-18) describe and illustrate the second maxilla, and all three maxillipeds of *D. filholi.* They also show an important feature of the second maxilla: the presence of three long denticulate setae on the posterior margin of the scaphognathite which probably have a role in cleaning the epibranchial surface of the gills. The presence of these setae is a primitive character because they are absent in the more derived Brachyura where gill cleaning is carried out by the long setose epipods of the maxillipeds. In *D. filholi* these epipods are well developed and their cleaning role is supplemented by the epipods on the pereopods. Three long scaphognathite setae are also found in *D. pilumnoides* but in *D. hispida* and *D. praedator*, there are only two setae.

A. MILNE EDWARDS and BOUVIER (1900) state that the branchial formula of *D. filholi* is the same as in *Dicranodromia mayheuxii* A. Milne Edwards, 1883 (the correct spelling is *D. mahieuxii*, see GUINOT, 1995, 236) with the addition of an epipod and podobranch on the fourth pereopod. However this is incorrect: in *Dynomene filholi* there are no gills on the fifth pereopod and there is only one arthrobranch on the third maxilliped. The branchial formula is 19 gills + 7 epipods. The gill structure of *D. filholi* is very different from the preceding species. A. MILNE EDWARDS & BOUVIER (1900, pl. 8, fig 18) provide an accurate cross section of the middle region of an anterior arthrobranch. The gill can be divided into two halves: a phyllobranchiate-like hypobranchial half, containing the efferent vessel, and a trichobranchiate-like epibranchial half, with six lobes arranged above the afferent vessel. As noted by BOUVIER (1896) the shorter epibranchial lobes tend to disappear towards the tip of the gill. A. MILNE EDWARDS & BOUVIER (1900) state that, in cross section, there are eight lobes but they counted the corners of the hypobranchial plate as "filaments".

A. MILNE EDWARDS & BOUVIER (1900) were the first to recognize, in a dynomenid species, that the subcheliform last pair of legs are sexually dimorphic: the extension of the propodus is much better developed in the female than in the male. In *Dynomene filholi* the last leg of the male is scarcely subcheliform. All other dynomenids also show this dimorphism. A small number (four) of spines, bearing many flattened teeth, on the female propodus is in keeping with the other species of *Dynomene.* However, the male shows some differences: there are only two spines on the propodus and these do not bear any teeth (in *D. hispida* and *D. praedator* there are five spines with many flattened teeth), while there is a lateral spine on the side of the dactyl which is unarmed in the other species of this genus. A similar dactyl spine is found in male *Metadynomene tanensis* and male *Paradynomene tuberculata* have a spine on the dorsal margin of the dactyl. These dactylar spines are reminiscent of those found in certain genera of the Dromiidae such as *Dromidiopsis* Borradaile, 1900, *Tunedromia* McLay, 1993, and *Lauridromia* McLay, 1993 where they are used, along with other spines, to assist in securing the sponge carried by the last two pairs of legs over the crab. However, in these dynomenids the spines are closely flattened against the surface of the dactyl so that they could not function in the same way as in the dromiids. These spines indicate a common ancestral relationship.

The figures of the first two male pleopods of *Dynomene filholi* by A. MILNE EDWARDS and BOUVIER (1900, pl. 7, 13-14) lack detail, but these pleopods are figured again by MONOD (1956, figs 84-88). The tip of the first male pleopod bears a curved apical plate surrounded by long setae as is found in most other dynomenids. However, MONOD's figures show that the second pleopod is armed with twice the number of subterminal spines seen in *D. hispida* and *D. praedator*, but there is only one long terminal spine. MONOD (1956, fig. 88) is inaccurate in the number of subterminal spines because it shows more than are there. BOUVIER (1896, fig. 23, V) includes a figure of one of the fifth pair of rudimentary male pleopods showing that it is biramous. There are two unequal lobes shown but one lobe (endopod) is an extension of the penultimate article while the other lobe (exopod) is separated by a joint. If the shorter inner lobe is regarded as the endopod then it must be assumed that fusion has occurred and the joint has been lost. The same situation is found in *D. hispida* and *D. pilumnoides*.

Examination of the stomach of a *Dynomene filholi* male 10.9 x 8.6 mm (MNHN-B 7028) from Principe Id, Guinea Gulf, revealed unidentifiable soft particulate organic fragments and some soft calcareous granules. The groups of stiff setae on the cheliped fingers may act as a sieving device for collecting food particles.

Dynomene filholi is most similar to *D. pilumnoides* (see Discussion below under the latter species). Since *D. filholi* is the only species of this genus inhabiting the Atlantic it is interesting to speculate about its origins. It seems to be a reasonable assumption that species of the genus *Dynomene* originated in the Tethys Sea so that the ancestors of *D. filholi* were Tethyan crabs. A southern colonization route for these crabs could have been available as early as the Upper Cretaceous (90-80 mybp) or sometime thereafter. *D. pilumnoides* has been recorded from the coast of Natal although no further south than this. At least at present there does not seem to be a dispersal route via the Cape because it is blocked by the local oceanic circulation pattern. This self-contained circulation pattern seems to have been in existence for a considerable time because there is a suite of endemic South African dromiid genera and species (see McLAY, 1993) which have been isolated perhaps since the Upper Cretaceous or Palaeocene (65 mybp). This interpretation requires that the Atlantic colonization by *Dynomene* must have been during the late Mesozoic or very Early Tertiary.

Dynomene pilumnoides Alcock, 1900

Figs 3 c-d, 8 d-e, 11, 12 e-f, 14 c, 17 d, 21 a-g

Dynomene pilumnoides Alcock, 1900: 133; 1901: 35, pl. 1, fig. 2. — STEBBING, 1905: 58 (list). — BARNARD, 1947: 371; 1950: 337, fig. 65 a-c. — SAKAI, 1965: 12, pl. 6, fig. 2; 1976: 29, pl. 6, fig. 3. — GUINOT, 1967: 242 (list). — SERÈNE, 1968: 37 (list). — PEYROT-CLAUSADE & SERÈNE, 1976: 1344 (key). — TAKEDA, 1977: 35 (list). — SERÈNE & VADON, 1981: 121. — KENSLEY, 1981: 37 (list). — MIYAKE, 1983: 11, pl. 4, fig. 2, 195 (list). — BABA, HAYASHI, & TORIYAMA, 1986: 310, fig. 163. — GARTH, HAIG & KNUDSEN, 1987: 241. — NAGAI, 1989: 43.

Maxillothrix actaeiformis Stebbing, 1921: 457, pl. 14 (Crust. pl. 109).

Dynomene hispida - YOKOYA, 1933: 95, text-fig. 37. Non Guérin-Méneville, 1832.

Dynomene actaeiformis - SERÈNE, 1968: 37 (list). — TAKEDA, 1977: 35 (list).

MATERIAL EXAMINED. — **Madagascar.** *"Vauban"* (A. CROSNIER coll.). *N.W. coast*: 12°41.50'S, 48°17.00'E, dredge, 160-170 m, 1.08.1973: 1 ♀ 14.6 x 12.0 mm; 1 ♀ ovig. 13.7 x 12.0 mm (MNHN-B 6913). — *W coast*: Dredge, about 18°50'S, no depth, 24.02.1973: 1 ♂ 10.0 x 8.2 mm (MNHN-B 6914). — *S.E. coast*: stn 72, 25°09.0'S, 17°14.2'E, 80-85 m, 3.03.1973: 1 ♀ 8.7 x 7.4 mm; 1 ♀ ovig. 10.0 x 8.3 mm. (MNHN-B 6904). — Fort-Dauphin, 90 m, no date: 1 ♂ 8.1 x 6.8 mm; 1 ♀ 6.9 x 6.2 mm (MNHN-B 6858).

Reunion. No locality, no depth, S. RIBES coll., no date: 1 ♂ 11.8 x 10.1 mm (MNHN).

Australia. *New South Wales*: Port Stephens, 32°42'S, 152°6'E, no depth, no date: 1 ♂ 17.2 x 14.1 mm (small balanomorph barnacle on dorsal surface of carapace); 1 ♀ ovig. 14.8 x 12.0 mm (AMS-P 42233). — Crowdy Head, 31°54'S, 153°00'E, 100 m, K. J. GRAHAM coll., 17.08.1977: 3 ♂ 8.0 x 6.5 - 22.8 x 17.4 mm; 1 ♀ 14.4 x 11.4 mm (AMS-P 26583).

Indonesia. DANISH EXPEDITION KEI ISLANDS: stn 3, 5°32'S, 132°36'E, 245 m, Th. MORTENSEN coll., 31.03.1922: 1 ♂ 10.0 x 8.9 mm (ZMUC).

Philippines. *"Pele"* (B. R. WILSON coll.). *Sulu Archipelago.* Pearl Bank: 3.2 km and 349° from Zal Id, 18 m, 22.02.1964: 1 ♀ ovig. 9.5 x 7.5 mm (MNHN-B 10376). — 6.4 km and 212° from Zal Id, 90 m, 22.02.1964: 1 ♀ 7.8 x 6.6 mm (MNHN-B 10375). — 14.4 km and 242° from Zal Id, 99-108 m, 22.02.1964: 1 ♀ 14.6 x 11.7 mm; 1 ♀ ovig. 12.7 x 10.6 mm (MNHN-B 10374). — 4 km and 182° from Zal Id, 90 m, 22.02.1964: 1 ♂ 9.2 x 7.8 mm (MNHN-B 10483).

MUSORSTOM 1: stn 57, 13°53.10'N, 120°13.20'E, 107-96 m, 26.03.1976: 1 ♂ 7.2 x 5.8 mm (see SERÈNE & VADON, 1981 who reported the specimen as a female).

Japan. Honshu Mie-Ken Wagu: 34°04.00'N, 136°51.30'E, no depth, no date: 2 ♂ 24.4 x 19.6, 28.5 x 22.1 mm (SMF 17127).

East of Toshima: 34°59.5'N, 139°36.3'E, 93-95 m, 1991: 1 ♂ 6.4 x 5.6 mm. — 34°19.79'N, 139°01.37'E, 134 m, coll. M. OSAWA, 1993: 1 ♀ 7.1 x 6.0 mm.

Hawaii Islands. *"Albatross"*: stn 3823, south coast of Molokai, Lae-O Ka Laau Light, 21°02'10"N, 157°15'45"W, 142-406 m, 1.04.1902: 1 ♂ 6.9 x 5.7 mm (USNM).

New Caledonia. LAGON: stn 393 bis, 22°46.00'S, 167°4.00'E, 284 m, 22.01.1985: 1 ♂ 8.0 x 6.6 mm.

MUSORSTOM 4: stn 164, 18°33.2'S, 163°13.0'E, 255 m, 16.09.1985: 1 ♀ 19.2 x 15.5 mm. — Stn 227, 22°46.00'S, 167°20.00'E, 300 m, 30.09.1985: 1 ♀ 5.0 x 4.5 mm.

CHALCAL 2: stn DW 69, 24°43.70'S, 168°07.90'E, 260 m, 27.10.1986: 1 ♀ 4.8 x 4.0 mm. — Stn DW 70, 24°46.00'S, 168°09.00'E, 232 m, 27.10.1986: 1 juv. 5.4 x 4.5 mm; 1 ♂ 5.6 x 4.6 mm. — Stn DW 84, 23°23.80'S, 168°07.00'E, 170 m, 31.10.1986: 2 ♂ 6.3 x 5.2, 7.2 x 6.0 mm.

SMIB 3: stn 18, 23°41.50'S, 167°59.40'E, 338 m, 23.05.1987: 1 ♂ 23.5 x 19.0 mm.

SMIB 4: stn DW 40, 24°46.20'S, 168°8.70'E, 260 m, 7.03.1989: 1 juv. 4.2 x 3.8 mm.

VOLSMAR: stn DW 7, 22°26.00'S, 171°44.10'E, 400 m, 1.06.1989: 2 ♀ 4.6 x 4.2, 12.4 x 10.3 mm.

SMIB 5: stn DW 94, 22°19.60'S, 168°42.80'E, 275 m, 12.09.1989: 1 ♀ ovig. 20.7 x 17.6 mm.

SMIB 8: stn DW 163, 24°49.10'S, 168°08.90'E, 310-460 m, 28.01.1993: 1 ♂ 13.2 x 10.6 mm; 1 ♀ 7.8 x 6.5 mm. — Stn DW 175, 23°14.10'S, 168°00.40'E, 235-240 m, 29.01.1993: 1 ♀ 10.3 x 9.0 mm.

Lagon, récif Laregnère, 12-16 m, 3.05.1993: 1 ♀ 7.5 x 6.2 mm.

BATHUS 3: stn CH 801, 23°39.00'S, 168°00'E, 270-300 m, 27.11.1993: 1 ♀ 9.8 x 8.9 mm. — Stn DW 836, 23°02'S, 166°59'E, 295-306 m, 30.11.1993: 1 ♀ 6.7 x 5.9 mm.

BATHUS 4: stn DW 943, 20°12.28'S, 164°30.58'E, 347-316 m, 09.08.1994: 1 ♀ 8.2 x 6.8 mm.

SMIB 10: stn DW 209, 24°49'S, 168°09'E, 329-560 m, 10.01.1995: 1 ♂ 27.0 x 22.0 mm.

Loyalty Islands. MUSORSTOM 6: stn DW 423, 20°20.85'S, 166°40.50'E, 280 m, 16.02.1989: 2 ♀ 10.1 x 8.6, 10.3 x 8.7 mm. — Stn DW 451, 20°59.60'S, 167°24.50'E, 330 m, 20.02.1989: 1 ♂ 9.7 x 8.2 mm. — Stn DW 472, 21°8.60'S, 167°54.70'E, 300 m, 22.02.1989: 1 ♂ 8.1 x 7.0 mm.

TYPES. — *Dynomene pilumnoides* Alcock, 1900: holotype is a male 11.0 x 10.0 mm, collected by the *"Investigator"*, from 11°27'N, 73°1.00'E, off Kiltan Id, Laccadive Ids, 90-54 m, held by the Indian Museum, Calcutta, registration number 9000/6.

Maxillothrix actaeiformis Stebbing, 1921: holotype not designated from amongst the four specimens, based on the number of carapaces in the container (at least two males and one female according to STEBBING, 1921), collected by the SS *"Pieter Faure"* from off the coast of Natal, located NW by N 12.6 km from the Umhlangakulu River, north of Durban (approximate coordinates 29°44'S, 31°5'E), stn PF-12348, 90 m, 4.04.1901, held by the South African Museum, registration number SAM-A839. This type material is in poor condition (Liz HOENSON pers. comm.). Two syntypes are held by the British Museum, registration number 1928. 12. 1. 10. According to the index card there is one specimen and fragments of another but the material in the container is just a lot of fragments (Miranda LOWE, pers. comm.). Thus all of the original material is in very poor condition.

DESCRIPTION. — Carapace wider than long, ratio of CW/CL 1.20-1.25, broadly rounded in outline but frontal and posterior margins truncated, surface smooth, quite convex, with a few minute granules in branchial area. Carapace surface and pereopods densely covered with setae of two kinds: short plumose setae, bent at right angles near the tip, clothing surface, but interspersed with longer filiform setae (6 x length of short setae and 0.20-0.25 x CW) which also fringe limbs and arranged in clumps on carapace where there are about fifteen to seventeen distinct groups (each with up to about four setae) which tend to be associated with rounded surface elevations. Density of setae completely obscures body surface but most of this is attributable to short rather than long setae. Structure of short and long setae is different. In short setae proximal 45% of shaft has very short setules (at end of which setae are sharply angled), then a region occupying about 45% where long, stout setules are directed almost at right angles to shaft, forming a dense bunch, and finally the distal 10% of setae which is smooth, slightly curved, and narrows to an acute tip. In long setae almost entire length is covered with small dendritic setules, all about same size, and setae are acutely tipped.

A shallow frontal carapace groove separates a pair of low rounded protuberances, and then divides into separate grooves which gradually become more faint. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately from small pits curving (slightly sinuously) anteriorly on to branchial region, while second shallower groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally, bordering anterior cardiac region. In effect the groove crossing the mid-line, connects two crescent-shaped grooves. Branchial groove not evident. Posterior cardiac area not defined. Anterolateral carapace margin begins just below level of postorbital corner, is evenly convex and bears four distinct, broad-based, equidistant teeth, each ending in a small, acute spine, and accompanied by a tuft of long setae. First two teeth directed anteriorly, third directed anterolaterally, and last directed more laterally. A posterolateral tooth, smaller than preceding anterolateral teeth, marks beginning of convergent posterolateral border alongside which lies the reduced last leg. Posterior carapace margin is recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, interrupted by a distinct notch closer to postorbital corner which is without granules; suborbital margin has a few small granules and angles towards an acute tooth (visible dorsally when setae are removed) then drops sharply into a notch before ending in a much smaller, blunt tooth at its inner corner. This tooth abuts second article of antenna. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region; distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth, above opening of antennal gland, is smaller. Second article wider than long; distal margin widest, to which is fixed the exopod curving over base of eyestalk and becoming broader and terminating bluntly. Exopod has a tuft of setae on its lateral margin. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and just matching length of exopod. Fourth antennal article smaller, as long as wide; remaining antennal articles directed laterally, extending well beyond postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.33. Eyestalk can be completely folded into orbit, and cornea is well developed, occupying all of tip. Epistome broadly triangular, surface slightly concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace marked by a narrow suture.

Subhepatic area smooth, very convex. A groove begins near base of the antenna, curving round under branchial region and meeting lateral carapace margin just anterior to last tooth at beginning of posterolateral border. A short cervical groove branches off and ascends towards gap between first and second anterolateral teeth, branching, with one branch meeting first anterolateral tooth ventrally and the other passing around behind second tooth. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has six or seven well developed, distally placed teeth on each side and a granulated border on outer margin. Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

Gill formula 19 gills + 7 epipods on each side, as found in *Dynomene hispida*. There is no podobranch on last pereopod. In cross section gills have the lateral margin deeply notched, dividing it into a hypobranchial plate (containing efferent vessel) and an epibranchial lobe (anterior lobe longer). Between these marginal lobes are a pair of lobes, similar to marginal lobes. Thus the epibranchial surface shows four rows of blunt lobes, decreasing in size from anterior to posterior side, which are arranged above afferent blood vessel. Hypobranchial setae poorly developed. Posterior margin of scaphognathite with three long setae. Hypobranchial margin of podobranchs bears same setae as on epipod.

Cheliped stout, much longer than first leg and stouter in the male, only slightly longer and stouter than first leg in the female; merus trigonal, inner face smooth and fitting closely against pterygostomial region of carapace, borders granulate, superior border has a subterminal broad, restriction which separates a thickened distal ridge, on which there are three small granules, from a row of three to five similar granules on superior border. Inner inferior margin of merus has an acute lateral spine distally which is especially prominent in large (CW > 20 mm) males where the spine forms a tooth which may itself be granulated. Outer face of carpus convex with six small granules, two more prominent acute tubercles on distal margin, inner superior border with a flattened, distomedially directed, spur (granulated in large males) which abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin is produced as a smooth obtuse flange fitting against merus when limb is withdrawn. These two structures give carpal article an unusual and distinctive shape. Outer face of propodus with two or three very small granules; superior face with three parallel rows of small granules; inner and inferior faces smooth, except that there is a small proximal spur on the inner propodal face. Fixed finger almost straight with six teeth increasing in size distally (large males have an additional basal tooth and some of the other teeth can be rudimentary); moveable

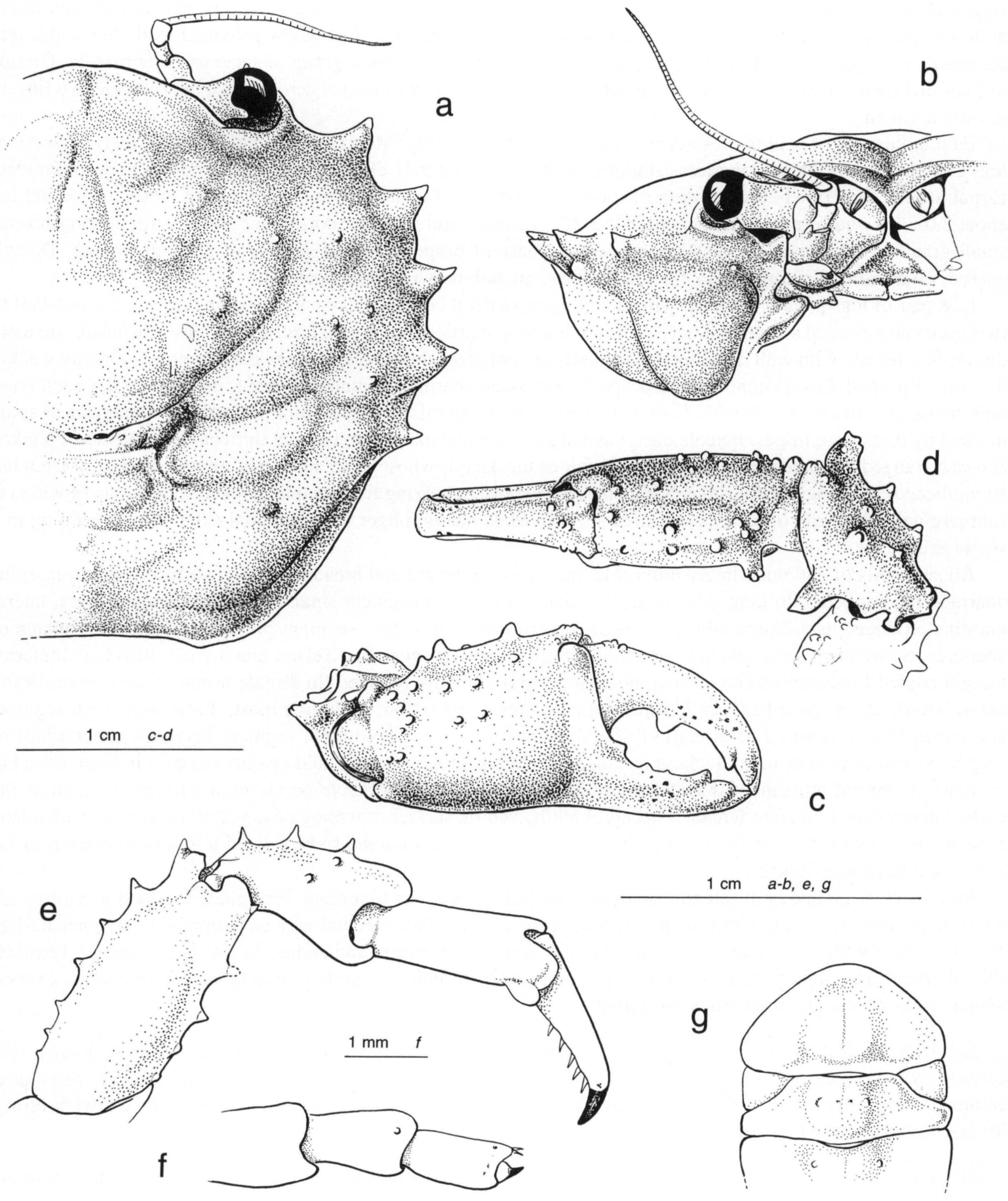

FIG. 21. — *Dynomene pilumnoides* Alcock, 1900: **a-g**, ♀ 14.6 x 11.7 mm, Sulu Archipelago, B. R. WILSON coll. (MNHN-B 10374): **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of female abdomen.

finger curved with four teeth, first mid-way and separated from remainder which are on tip; both fingers, thick, hollowed out internally, touching only at tips where the teeth interlock. Just below proximal teeth on fixed finger are two distinct pits in which several long setae are inserted with a similar group of setae on inner margin. Groups of long stiff setae, inserted mid-way along dactyl and fixed finger, are directed across space between the two fingers to form a screen.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with several small granules, length of merus of second leg about 2.0-3.0 x width and equal to about half of CL. Anterior and posterior dorsal margins of carpi bearing several small granules, and produced distally to overhang base of propodi. Dorsal surface of propodi smooth. Dactyli curved, inferior margin armed with 4-5 small spines, tip dark brown and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching only as far as a half to two-thirds along meral article of preceding limb; borders of articles unarmed. Last pair of legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing six, unequal, stout, hooked, spines each lined with marginal rows of 12 - 20 tiny flattened, acute teeth along middle region of inner surface, remainder of spine marked by transverse ridges. Female dactyl as long as propodal extension, bearing thirteen unequal, stout, hooked spines (arranged asymmetrically around perimeter of the dactyl) whose inner surface is smooth, devoid of teeth but strengthened by a longitudinal ridge. Male propodal extension bearing five unequal hooked spines, one of which is submarginal, all devoid of teeth along inner surface. Male dactyl longer than propodal extension and ending in a single acute claw.

All segments of abdomen freely moveable, increasing in length and breadth distally; surface smooth; margins unarmed but fringed with long setae. Anterior margin of second segment sinuous, medial region convex, lateral margins produced as a flange which fits over posterior margin of first segment preventing forward slippage of abdomen. Subsequent segments not overlapping with preceding segments. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In female uropod plates large, filling about two-thirds of space between last abdominal segment and telson, excluding most of last abdominal segment and telson from reaching lateral margin of abdomen. In male last abdominal segment occupies about a half of length. No effective abdominal locking mechanism: abdomen only loosely held against sternum in both sexes but in males its lateral movement is restricted by presence of a small tubercle on sternum adjacent to each of the second pereopods. In mature female it occupies all the ventral surface, covering coxae of all pereopods with telson covering proximal half of third maxillipeds. In male abdomen is not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. First male pleopod a semi-rolled tube with a small apical plate surrounded by long setae. Second male pleopod with an exopod on basis, needle-like distally, armed with a series of fifteen tiny, straight, acute, inset spines and ending in two larger spines. Terminal pair of spines are slightly curved at their tips. Third to fifth male pleopods rudimentary and biramous, exopod longer and connected to basal article by a joint.

COLOUR. — SAKAI (1965a) described the colouration of *Dynomene pilumnoides* as being yellowish red. MIYAKE (1983) shows the body and legs as light reddish-orange fringed with yellowish setae, and the eyestalks as being red. The picture of BABA, HAYASHI, and TORIYAMA (1986) shows the body and legs to be yellowish-brown fringed with dark brown setae.

GEOGRAPHIC DISTRIBUTION. — *Dynomene pilumnoides* has been recorded from Natal (as *Maxillothrix actaeiformis* Stebbing, 1921), Madagascar, Laccadive Ids, Philippine Ids, Japan, Australia, New Caledonia, Loyalty Id, Norfolk Ids, Enewetak Atoll, Marshall Ids and Hawaii. The material reported here from Australia, Norfolk Id, New Caledonia and Loyalty Ids represent new records and the specimen collected by the USFC Steamer *"Albatross"* in 1902, from Hawaii, has languished unrecognized in the collection of the U. S. National Museum for more than 90 years. This is a widespread Indo-Pacific species.

DEPTH. — Depth range of the material examined is 18-400 m, although most records are from 100-300 m. The specimens reported by BABA *et al* (1986) came from the Okinawa Trough, 362-540 m, but given the other more precise depth records, it does not seem justifiable to conclude that the lower depth limit for this species is 540 m. The lower depth limit is probably around 400 m. This species has been collected from rocky bottoms covered in lithothamnion algae, sponges, and corals. *Dynomene pilumnoides* does not seem to be associated with particular corals, although this could be the result of most specimens being collected from deeper water by dredge and separated from their host. The range obviously includes depths at which corals do not occur.

SIZE. — The maximum size for males is 28.5 x 22.1 mm, for females 20.7 x 17.6 mm, and the smallest ovigerous female is 9.5 x 7.5 mm. This female carried around 590 eggs while the largest ovigerous female with a complete brood (14.8 x 12.0 mm) carried about 1600 eggs. Mean egg diameter was 0.49 mm. The breeding season may be tentatively estimated as extending from February to September although no ovigerous females have been collected during the months from April to July. The maximum size for *Dynomene pilumnoides* is somewhat larger than for the preceding *Dynomene* spp. and the size of the smallest ovigerous female is also correspondingly larger. The larval stages of *D. pilumnoides* are unknown.

One female specimen (7.5 x 6.2 mm) collected in 1993 from a reef in the New Caledonia lagoon shows some peculiar features: there are no gonopores on the coxae of the second walking legs and the only indication of its sex is the presence of sternal sutures 7/8, terminating in the spermathecal openings, and five pairs of pleopods. However all pleopods are remarkably poorly developed, perhaps indicating that it has been parasitized.

DISCUSSION. — The exact status of *Dynomene pilumnoides* has been one of the main problems in understanding the relationships between the species of *Dynomene*, especially those from the Indian Ocean. ALCOCK's type specimen was a male 11.0 x 10.0 mm from 54-90 m off the Laccadive Ids. Although he created a new species for this single specimen, ALCOCK (1900) suggested that it could well prove to be a variety of *D. hispida*. Both species have a similar carapace shape, although the CW/CL ratio tends to be larger (approx. 1.30) for *D. hispida*, and the anterolateral carapace margins have four teeth, but the teeth are much smaller in *D. hispida*. The features which clearly distinguish *D. pilumnoides* from *D. hispida* are the presence of clumps of long filiform setae which are much longer than the surface covering of short setae (*D. hispida* carapace setae mostly short and not clumped), a notch in the supraorbital margin (no notch), postorbital corner without spines (five small acute spines), and only a single spine on the suborbital margin (five small acute spines). *D. pilumnoides* grows to a larger size and is usually collected from 100-300 m depth whereas *D. hispida* is a small dynomenid which occurs in shallow waters, often intertidally. It seems likely that ALCOCK did not have a specimen of *D. hispida* at his disposal which would have allowed a detailed comparison with *D. pilumnoides*. The differences between the species listed by ALCOCK (1900) are not diagnostic. However, the differences listed by ALCOCK (1901) are more useful and here he withdrew the suggestion that *D. pilumnoides* might be a variety of *D. hispida*. ALCOCK's description is seriously wrong in only one aspect: his statement that there are no rudimentary pleopods on the third to fifth abdominal segments in the male. (This feature is present in all dynomenid males although they are sometimes difficult to see clearly without special preparation.) Also his illustration does not show the longer carapace setae arranged in clumps.

Other features of *Dynomene pilumnoides*, not illustrated here, can be found in STEBBING (1921) (as *Maxillothrix actaeiformis*): mandible, second maxilla, second and third maxillipeds, and the first male pleopod. ODHNER (1925) pointed out that *Maxillothrix* is a junior synonym of *Dynomene* and therefore should not be placed amongst the Xanthidae as STEBBING had proposed. The synonymy of *M. actaeiformis* and *D. pilumnoides* was first recognized by BARNARD (1947).

The generic name *Maxillothrix* Stebbing, 1921 was created to reflect the presence of three long, unequal setae on the scaphognathite of the second maxilla. In fact similar setae had already been reported by BOUVIER (1896) for *Dynomene filholi* (see above) but STEBBING had placed his new genus amongst the Xanthidae, comparing the second maxilla with that found in *Nursia*, so the apparent uniqueness of these setae is understandable. STEBBING (1921) noted that the setae were reminiscent of the long scaphognathite spine in *Axius longispina* and he drew attention to the two long terminal setae on the second maxilla of *Homola andamanicus* (ALCOCK, 1901, pl. A). These setae probably have a role in cleaning the epibranchial surface of the gills.

BARNARD (1947, and 1950) continued to suggest that *Dynomene pilumnoides* is probably a synonym of *D. hispida,* but this cannot be correct because the suborbital margin is visible dorsally (suborbital margin straight and not projecting), CW/CL = 1.17-1.2 (CW/CL = 1.3), and the longer setae on carapace are clumped (setae not clumped). The specimens available to BARNARD were collected from 90 m depth, whereas *D. hispida* is an intertidal-shallow water species. The confusion about the status of the name *D. pilumnoides* Alcock, 1900 arose, at least in part, because of the errors and omissions of the original descriptions of ALCOCK and STEBBING (for *Maxillothrix actaeiformis*).

BARNARD (1950: 336) gave the branchial formula for *Dynomene pilumnoides* as 18 gills + 3 epipods. But this is incorrect because he missed the two arthrobranchs on the third maxilliped and overlooked the epipods on the pereopods. The branchial formula is 19 gills + 7 epipods. The gill structure of *D. pilumnoides* more closely resembles that of *D. filholi* than of *D. hispida* and *D. praedator.* The epibranchial surface of the gills is made up of four rows of elongate lobes which radiate out from the afferent vessel. The epipods and hypobranchial setae are similarly developed in all these species. Another character which *D. pilumnoides* and *D. filholi* share, is the presence of three long setae on the posterior margin of the scaphognathite. The other species of *Dynomene* only have two setae. In *D. pilumnoides* the hypobranchial margin of each podobranch carries long cleaning setae as found in *D. hispida* and *D. praedator.*

The subchelate structure of the last pairs of legs of females shows several differences from the other species of *Dynomene*: the propodal extension of the female bears six spines (four in the other species), and the teeth on the inner surface of these spines are fewer in number (12-20 teeth) and arranged in marginal rows in the middle region (rather than scattered along most of the spine). The dactylar spines of the female are strengthened by a longitudinal ridge. Male *D. pilumnoides*, along with *D. filholi,* lack the teeth on the propodal spines which are found in the other two species.

The second male pleopod of *Dynomene pilumnoides* is similar to that of *D. filholi* in having a large number (15) of subterminal spines. Also the rudimentary last three pairs of pleopods are biramous in both species.

Examination of the stomach contents of a *Dynomene pilumnoides* female 14.6 x 12.0 mm (MNHN-B 6913) from Madagascar revealed mostly soft amorphous material with a few sand grains and some chitinous brown tube-like fragments that may be hydroid in origin. It may be that this crab uses its chelae to spoon up sediment from which organic fragments are separated by the groups of setae on the cheliped fingers.

Dynomenid crabs very rarely have epizoites on their exoskeleton, perhaps because of the dense layer of setae. However, one large *Dynomene pilumnoides* male 28.5 x 22.1 mm (SMF 17127) from Japan, had a small polychaete tube on the right dorsal side of the carapace. It may be possible for fouling organisms to colonize larger crabs because of their longer intermoult intervals.

Dynomene pugnatrix de Man, 1889

Figs 5 d, 11, 22 a-g

Dynomene pugnatrix de Man, 1889: 444, pl. 10, fig. 13. — ALCOCK, 1901: 75 (list). — IHLE, 1913: 92 (list). — GUINOT, 1967: 242 (list). — SERÈNE, 1968: 36 (list). — TAKEDA, 1977: 35 (list).
Dynomene pugnatrix brevimana Rathbun, 1911: 196. — GUINOT, 1967: 242 (list). — SERÈNE, 1968: 37 (list).

MATERIAL EXAMINED. — **Mauritius**: No details, no depth, no date: 1 ♂ 9.8 x 7.2 mm, type specimen (SMF 4857).

Providence Island. PERCY SLADEN TRUST EXPEDITION: stn D4, 9°14.00'S, 51°02.00'E, 90-140 m, 4.10.1905: 1 ♀ ovig. 6.3 x 4.8 mm. type specimen of *D. pugnatrix brevimana* (USNM 41047).

TYPES. — *Dynomene pugnatrix* de Man, 1889: holotype is a male 9.8 x 7.2 mm, from Mauritius, held by the Natur-Museum Senckenberg, Frankfurt, registration number SMF 4857.

Dynomene pugnatrix brevimana Rathbun, 1911: holotype is an ovigerous female 6.3 x 4.8 mm, collected by the R/V *"Sealark"*, Percy Sladen Trust Expedition, from stn D4, 9°14.00'S, 51°02.00'E, Providence Id, north of Madagascar, 90-140 m, 4.10.1905, held at the Smithsonian Institute, Washington, registration number USNM 41047.

DESCRIPTION. — Carapace wider than long, ratio of CW/CL approx. 1.30, squarish in outline, surface convex, minutely granular. Carapace surface and pereopods sparsely covered with two kinds of setae of varying lengths up to 0.3 x CW. There are short stiff setae and longer "feathered" setae. The density of setae does not completely obscure body surface. Microscopic details of setae not examined.

Frontal carapace groove very faint, extending only a short distance from frontal margin. The normal pair of prominent rounded protuberances, separated by frontal groove, absent. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) crosses mid-line and runs directly anterolateral on to branchial region and mid-way along its length there is a short groove in the direction of median frontal margin. The second, shallower groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into a short anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally, bordering anterior cardiac region. In effect this second groove connects two crescent-shaped grooves. No branchial groove evident and posterior cardiac area only faintly defined. Anterolateral carapace margin begins below level of postorbital corner, initially it is a horizontal margin directed laterally, with two or three small granules, until meeting two small, subacute anterolateral teeth close together at corner. Behind these teeth margin runs posteriorly and has three similar equidistant teeth, first directed almost anteriorly, next two directed laterally, and finally there is a smaller submarginal tooth part-way along convergent posterolateral margin alongside which lies the reduced last leg. This gives a total of six teeth on the right-hand side, but on the left-hand side there is only one initial tooth, giving the more normal pattern for this genus of five teeth (the last of which is treated as being posterolateral). In the case of this species, absence of the branchial groove makes this distinction rather arbitrary. Posterior carapace margin recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, interrupted by a distinct notch closer to postorbital corner, following margin minutely granulated; suborbital margin with two small granules. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region, distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked, inferior tooth well developed, blunt, superior tooth above the opening of antennal gland slightly smaller. Second article wider than long, distal margin widest, to which is fixed the exopod curving over base of eyestalk and becoming broader and terminating bluntly. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and just matching length of exopod. Fourth antennal article smaller, as long as wide, remaining antennal articles directed laterally, extending well beyond postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.67. Eyestalk can be completely folded into orbit, and cornea well developed, occupying all of tip. Epistome broadly triangular, surface slightly concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace is marked by a narrow suture. Antennae, antennules and epistome fit closely together.

Subhepatic area convex, minutely granulated. A groove begins near base of antenna, curving round under branchial region and meeting lateral carapace margin just anterior to last tooth at beginning of posterolateral border. A short cervical groove branching off and ascending towards first anterolateral tooth. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has five or six small, blunt, distally placed teeth on each side. Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

No information about gill formula due to insufficient material, but structure of an arthrobranch taken from the cheliped is as follows: in cross section, the anterior and posterior margins of the gill are notched, dividing it into hypobranchial plates and epibranchial plates which end bluntly. The epibranchial plate on the anterior margin is larger and between these plates is a single row of short elongate lobes.

Cheliped slender, slightly longer than first leg. Merus trigonal, inner face smooth and fitting closely against pterygostomial region of carapace, borders granulate, outer face has a subterminal shallow, restriction which separates a thickened distal ridge devoid of granules from a pair of small subacute granules, preceded by a row of several smaller granules on superior border. Inner inferior margin of merus has an acute lateral spine. Outer face of carpus convex, smooth, inner superior border with a distomedially directed, sharp spur which abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin is produced as a smooth, obtuse, flange fitting against merus when limb is withdrawn. These two structures give carpal article an unusual and distinctive shape: inner face very narrow and outer face much broader. Surface of propodus smooth; fixed finger almost straight with three teeth at tip; moveable finger strongly curved with a single, blunt proximal tooth and three teeth at tip. Both fingers, thick, hollowed out internally, touching only at tips where last three teeth interlock. Just below proximal teeth on fixed finger are two distinct pits in which several long setae are inserted.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with five well developed spines in a row, increasing in size distally, separated by a gap from a single distal spine, and five well developed spines on posterior margin; length of merus of second leg about 2.4 x its width and equal to about three-quarters of CL. Dorsal surface of carpi bearing a row of five acute spines, and produced distally to overhang base of propodi. Dorsal surface of propodi with a row of four small spines. Dactyli curved, inferior margin armed with 10 small spines, tip brown and subacute.

Last pair of legs greatly reduced, adorned with long setae distally, lying along posterolateral border of carapace, reaching only as far as one third along meral article of preceding limb; borders of articles unarmed. Legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl; male with only weakly developed propodal extension. Structural details of dactyl and propodus have not been investigated.

All segments of abdomen freely moveable, surface smooth, margins unarmed but fringed with setae. Second segment narrowest, anterior margin sinuous, medial region convex, lateral margins produced as a flange which fits over posterior margin of first segment (which is the shortest) preventing forward slippage of abdomen. Subsequent segments increasing in length and breadth distally, not overlapping with preceding segments. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In male, uropod plates large, filling about three-quarters of the space between last abdominal segment and telson, excluding much of last abdominal segment and telson from reaching lateral margin of abdomen. No effective abdominal locking mechanism: abdomen only loosely held against sternum. Abdomen extends as far as bases of the third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. Five pairs of pleopods in male, first pleopod a semi-rolled tube ending in a curved, blunt apical plate surrounded by long setae, second pleopod needle-like with an exopod on the basis, remaining pleopods rudimentary. Microscopic details of second male pleopod unavailable.

COLOUR. — Unknown.

GEOGRAPHIC DISTRIBUTION. — The type locality is Mauritius and the other specimens reported by RATHBUN (1911) as *Dynomene pugnatrix brevimana* came from Providence Id, both of which are in the vicinity of Madagascar, although *D. pugnatrix* is not known from Madagascar itself. Thus *D. pugnatrix* is a western Indian Ocean species. It is interesting to compare this species with *D. filholi* which is an insular South Atlantic species.

DEPTH. — The depth range for *Dynomene pugnatrix* is 90-140 m (based on the specimens reported by RATHBUN (1911), as *D. pugnatrix brevimana*.

SIZE. — Only three specimens of *Dynomene pugnatrix* are known: one male, 9.8 x 7.2 mm (the type specimen), and two ovigerous females, one of which is 6.2 x 5.0 mm. The size of the other ovigerous female reported by RATHBUN (1911) is unknown. It is evident that this species reaches sexual maturity at a small size as do *D. hispida* and *D. praedator*. The specimen of *D. pugnatrix* examined carried 30 eggs but some eggs may have been lost because the brood did not fill the entire abdominal space. Egg diameter is 0.4 mm. These reproductive aspects are similar to the other *Dynomene* species.

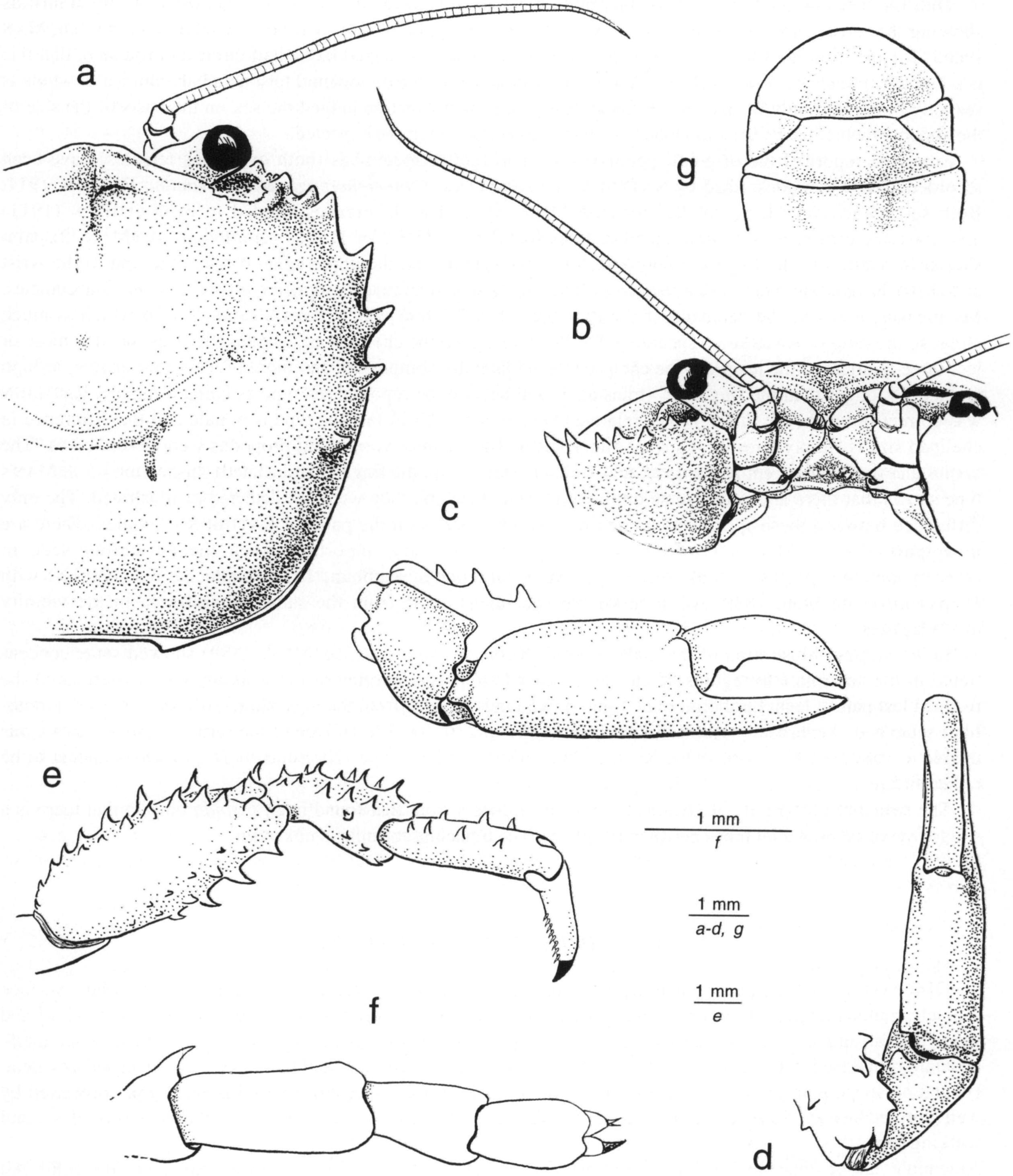

FIG. 22. — *Dynomene pugnatrix* de Man, 1889: **a-g**, ♂ 9.8 x 7.2 mm, type specimen, Mauritius (SMF 4857): **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of male abdomen.

DISCUSSION. — DE MAN (1889) illustrated the type specimen of *Dynomene pugnatrix* from Mauritius showing the left cheliped missing and stating that it was a female, but in fact the specimen is a male. DE MAN stated "I judge from the shape of the telson, whose last segment is shaped like a half circle and rounded, that this is a female" (translated from German). Apart from the pleopods, the dynomenid telson and abdomen as a whole is sexually dimorphic only in size, not in shape. It is also possible that he judged the sex on the basis of the size of the abdomen which, in dynomenid males, is much larger than might be expected.

Since the report of the original specimen only two further specimens (both ovigerous females) have been recorded. These were described by RATHBUN as a subspecies, *Dynomene pugnatrix brevimana* Rathbun, 1911. Both specimens are a little smaller than DE MAN's type. The differences alluded to by RATHBUN (1911) are 1) greater carapace width/length ratio, 6.3/4.8=1.3 vs 9.75/8.25= 1.2 (as reported by DE MAN, 2) palm shorter in relation to the fingers, 3) presence of a few spinules on the upper edge of the palm, and 4) the wrist and chelae have a few setae. A comparison of RATHBUN's specimen reveals some inconsistencies and inaccuracies. My measurements of the carapace of the type are 9.8 x 7.2 mm which gives a ratio of 1.36 which is much closer to the ratio of RATHBUN's specimen. DE MAN described the cheliped as "The length of the hand is more or less three-quarters of the length of the carapace. Hand laterally compressed and more or less twice as long as high and a little longer than the fingers..." (translated) and because he reported his type as being a female, RATHBUN was correct in noting the difference in relative cheliped size. But in fact the type is a male and the difference in cheliped size is simply a result of sexual dimorphism. The cheliped carpus and propodus were described as "The carpus and the hand are entirely smooth and without setae except the fingers" (translated). Inspection of DE MAN's type shows that there are in fact setae on the wrist and chela and they were not detected or illustrated. The only difference between these specimens is the presence of spinules on the palm of RATHBUN's females. There are no spinules on DE MAN's type but this does not seem very important given the variability seen in other dynomenid species. I think that *D. pugnatrix brevimana* Rathbun, 1911 should be synonymized with *D. pugnatrix* de Man, 1889. All three known specimens come from the same general area in the vicinity of Madagascar.

In his original illustration of the male type of *Dynomene pugnatrix*, DE MAN (1889) showed setae concentrated in the anterolateral regions of the carapace and along the margins of the walking legs as well as on the reduced last pair of legs. Furthermore he figured two kinds of setae from the legs: short, stiff "Kammhaar" (comb-like) setae and "Federhaar" (feather-like") setae (1889, pl. 10, fig. 13e-f). Due to the rarity of this species I was unable to verify DE MAN's observations using the electron microscope. The setae of *D. pugnatrix* appear to be rather different from those of the other species of this genus.

The structure of the gills of *Dynomene pugnatrix* differs from that found in *D. hispida* only in that there is a single row of epibranchial lobes between the plates. The branchial formula is unknown.

Genus ***HIRSUTODYNOMENE*** nov.

DIAGNOSIS. — Carapace much wider than long, moderately convex, commonly subcircular. Surface sparsely spinous (especially in anterobranchial region), areolate, covered with coarse setae, which are short and long, and arranged in tufts. Lateral carapace margin always well defined and armed with distinct teeth. Frontal groove well marked, split in two posteriorly; cervical, postcervical and branchial grooves usually evident. Frontal carapace margin broadly triangular, continuous; no rostrum or teeth. Eyestalks short, eyes protected by well defined orbits. Sternal sutures 7/8 of female end well apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside orbit at base of eyestalk. Antennal flagella shorter than carapace width. All articles of antenna moveable; first article (urinal) always beaked medially; second article has an exopod firmly fixed. Third maxillipeds opercular, completely covering buccal cavern, separated at their bases by a plate at same level as sternum; basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds equal, stouter than walking legs; dactyl strongly curved; fingers gaping basally. Last pair of legs very reduced; dactyl rudimentary, forming an obsolete subchelate mechanism with an extension of propodus. Gills usually 19 (including 6 podobranchs) + 7 epipods. Gill structure basically phyllobranchiate but plates are very variable in shape.

Abdomen of six segments and telson folded loosely under thorax; uropods large; no effective abdominal locking mechanism. Lateral movement of abdomen restricted by small sternal tubercle, at base of each of first walking legs, which lies alongside each uropod. Both sexes have five pairs of pleopods; first pair vestigial in female; last three pairs rudimentary in male. Male pleopods uniform in structure; first pair consist of a stout, setose semi-rolled tube with an apical plate; second pair needle-like with numerous subdistal spines, some of which overlap, sinuously arranged around the axis.

TYPE SPECIES. — *Dynomene spinosa* Rathbun, 1911.

OTHER SPECIES. — *Dynomene ursula* Stimpson, 1860.

ETYMOLOGY. — *Hirsutodynomene* is a combination of the latin *hirsutus*, meaning shaggy, alluding to the tomentum of these species, and the genus *Dynomene*. Gender is feminine.

DISCUSSION. — This new genus is erected for two species originally assigned to *Dynomene*. They clearly stand out amongst the other species because of their "shaggy" appearance, resulting from long, stiff setae, and their spiny, areolate carapace. The distribution of these two species does not overlap in the Pacific and they are clearly sister species.

Hirsutodynomene spinosa (Rathbun, 1911)

Figs 3 f, 5 e-f, 8 f, 9 c, 11, 13 a-b, d, 14 d, 17 e, 23 a-g

Dynomene spinosa Rathbun, 1911: 196, pl. 17, fig. 1. — IHLE, 1913: 92 (list). — BALSS, 1935: 115; 1938: 7. — MIYAKE, 1939: 198 (list). — WARD, 1942: 71. — HOLTHUIS, 1953: 3. — MORRISON, 1954: 13. — GUINOT, 1967: 242 (list); 1985: 448 (list). — SERÈNE, 1968: 36 (list). — TAKEDA, 1973: 81; 1977: 35 (list). — PEYROT-CLAUSADE & SERÈNE, 1976: 1343, pl. 2 A. — CHEN, 1980: 119, pl. 1, fig. 2. — DAI, YANG & LAN, 1981: 117, tex- fig. 1-4. — PEYROT-CLAUSADE, 1981: 750; 1984: 114. — DAI, YANG, SONG & CHEN, 1986: 27, pl. 3, 1. — GARTH, HAIG & KNUDSEN, 1987: 241. — DAI & YANG, 1991: 31, pl. 3, fig. 3. — POUPIN, 1996a: 24 (list).
Dynomene hispida - DE MAN, 1902: 689. [Not Guérin-Méneville, 1832].

MATERIAL EXAMINED. — **Madagascar**. Tuléar, stn 14-11-2, pente externe, 5 m, M. PEYROT-CLAUSADE coll., 1968: 1 ♀ 11.3 x 8.9 mm (MNHN-B 22077) (see PEYROT-CLAUSADE & SERÈNE, 1976; and PEYROT-CLAUSADE, 1984).

Glorieuses Islands. Grande Glorieuse. Intertidal zone, A. CROSNIER coll., 30.01.1971: 1 ♂ 16.4 x 14.3 mm (MNHN-B 6899).

Australia. *W coast*: Exmouth Gulf, Bundegi Reef, 21°53'S, 114°22'E, 3 m, under rock, N. COLEMAN coll., 14.08.1972: 1 ♂ 19.6 x 14.5 mm (AMS-P 19118).

Southeast Queensland, Flinders Reef, 26°59'S, 153°29'E, 6-20 m, 10.03.1989: 1 ♀ 27.7 x 20.4 mm (QM W16277).

Tasman Sea, Middleton Reef, 29°29.5'S, 159°06.2'E, no depth, P. FILMER-SANKEY coll., 5.12.1987: 1 ♂ 28.7 x 21.3 mm (10 poecilasmid barnacles on chelipeds) (AMS-P 39242). — No depth, P. HUTCHINGS coll., 8.12.1987: 1 ♀ ovig. 32.3 x 24.4 mm (AMS-P 39245). — Elizabeth Reef, 29°57.2'S, 159°01.2'E, 12 m, dead coral rubble, R. SPRINGTHORPE coll., 10.12.1987: 1 ♀ 19.5 x 14.8 mm (AMS-P 38264).

Cocos Keeling Islands. Horsburgh Id, 0-37 m, 9.02.1989: 1 ♂ 14.2 x 10.8 mm (WAM 139-94). — N end of West Id, 0-30 m, 21.02.1989: 1 ♀ 13.0 x 10.3 mm (WAM 138-94.). — NW end of West Keeling Id, 0-28 m, 23.02.1989, F. WELLS coll.: 1 ♀ 23.8 x 17.8 mm (WAM 723-89).

Indonesia. *Moluccas*. Amboina: no details, J. BROCK coll., 7.09.1885, J. G. DE MAN (1888) det.: 1 ♂ 17.8 x 13.7 mm (SMF 164). — Seram, Gorong Id. RUMPHIUS 2, stn GO 3, no depth, 27.01.1975, T. MONOD & R. SERÈNE coll. and det. as *Dynomene pilumnoides* : 1 ♂ 17.5 x 14.0 mm (MNHN-B 9906). — Ternate: no details, W. KUKENTHAL coll., 1894: 1 ♀ 18.5 x 14.3 mm (SMF 4856) (See DE MAN, 1902 who reported this specimen as *Dynomene hispida*). — *Timor*, Atapupu, coral reef, leg. *"Gazelle"*, no depth, no date: 1 ♂ 24.3 x 18.8 mm (ZMB 5138).

Vietnam. Institut océanographique, Nhatrang (coll. and det. R. SERÈNE): stn 1060, no locality, no depth, 1950: 1 ♂ 18.0 x 14.3 mm (ION. 9265) (ZRC 1970.6.20.1). — Stn. 87, no locality, no depth, 1950: 1 ♂ (dry) 7.4 x 6.0 mm (ION 1556) (ZRC 1970.6.20.2).

Mariana Islands. *Asuncion Id*, 19°40'N, 145°24'E, 1-6 m along rock wall in holes and corals, P. SCHUPP coll., 7.06.1992: 1 ♀ 24.2 x 18.0 mm (UGM).

Guam, Piti Lagoon, 13°27'N, 144°47'E, 1.0-2.5 m among dead coral, 20.09.1992: 1 ♂ 20.3 x 15.9 mm. — 1-2 m under rubble, H. T. CONLEY coll., 04.1997: 1 ♂ 10.2 x 8.1 mm. —Tumon Bay, 11 m on dead finely branched coral, R. K. KROPP & J. H. DOMINGUEZ coll., 7.11.1984: 1 ♀ 4.4 x 3.9 mm (UGM)

Japan. Kurashima Ids, Yaeyama Id, Okinawa, in dead coral branches, inner reef, M. OSAWA coll., 1993: 1 ♂ 22.2 x 17.0 mm.

Line Islands. WHIPP EXPEDITION: Palmyra Id, 5°52'N, 162°6'W, no depth, 1924: 1 ♂ 10.5 x 8.6 mm (BPBM 2297).

French Polynesia. *Tuamotu Ids*, Raroia Atoll, Homohomo Id, 16°3'S, 142°23'W, under rocks near shore in pavement pool zone, J. P. E. MORRISON coll., 21.07.1952: 1 ♀ 25.0 x 19.8 mm (USNM 94559) (see HOLTHUIS, 1953).

TYPES. — *Dynomene spinosa* Rathbun, 1911: holotype is a male 24.7 x 19.6 mm, collected by the R/V *"Sealark"*, Percy Sladen Trust Expedition, from 7°08.00'S, 56°16.00'E, Coetivy Id, 1905, held at the Smithsonian Institution, Washington, registration number USNM 41048 (note that there are two dry specimens in this lot, but the larger specimen is the holotype).

DESCRIPTION. — Carapace wider than long, ratio of CW/CL approx. 1.25-1.30, broadly rounded in outline but frontal and posterior margins truncated; surface convex, areolate, granulate, and spinous. There are about twenty five to thirty distinct areolae, more medial areolae smooth or minutely granulate, more lateral areolae adorned with larger acute granules, and those above anterolateral margin are adorned with short, acute spines. Behind branchial groove is a laterally directed region of granules, grading into spines towards last marginal tooth. Carapace surface and pereopods covered with setae of two kinds: short setae, bent at right angles near tip, clothing surface, but interspersed with longer filiform setae (6 x length of short setae and 0.20-0.25 x CW) which fringe limbs and are arranged in clumps on carapace where there are about twenty five distinct tufts, each with up to seven setae, which tend to be associated with areolae. The density of setae almost completely obscures body surface but most of this is attributable to short setae which, in some places, are separated by narrow areas lacking setae. Structure of short and long setae are different. In short setae proximal 40% of shaft is erect and lacks ornamentation, then a region occupying about 55% where setae are bent at right angles and long, stout setules radiate from shaft only on external side, forming a dense bunch, and finally distal 5% which is smooth, slightly curved, and narrows to an acute tip. In long setae proximal 95% is covered with small setules which distally increase in density, but not in size, and last 5% is smooth, slightly curved and narrows to an acute tip.

A narrow frontal carapace groove separates a pair of prominent rounded protuberances, and then divides into separate grooves which diverge and then curve back medially. Between these grooves is an elongate granulate ridge. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately from small pits and runs directly anterolateral on to branchial region and mid-way along their length they are joined by grooves running back from frontal groove The second, shallower groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows first groove for a short distance, while second portion curves posterolaterally, bordering anterior cardiac region. In effect groove crossing mid-line, connects two crescent-shaped grooves. A faint branchial groove is evident and posterior cardiac area is defined. Anterolateral carapace margin begins at level of postorbital corner, is evenly convex and bears four distinct, broad-based, equidistant teeth, each ending in a well developed, upwardly curved, acute spine; first tooth directed anterolaterally and remainder directed laterally. Each anterolateral tooth has an associated tuft of long setae. A posterolateral tooth, which is smaller than preceding anterolateral teeth, marks beginning of convergent posterolateral border alongside which lies the reduced last leg. Posterior carapace margin is recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, interrupted by a distinct notch closer to postorbital corner, followed by four or five acute spines; suborbital margin with three similar spines followed by an acute tooth (visible dorsally when setae are removed) and then descending to a much smaller tooth at its inner corner. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region; distal margin bearing a dense fringe of longer setae, obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well

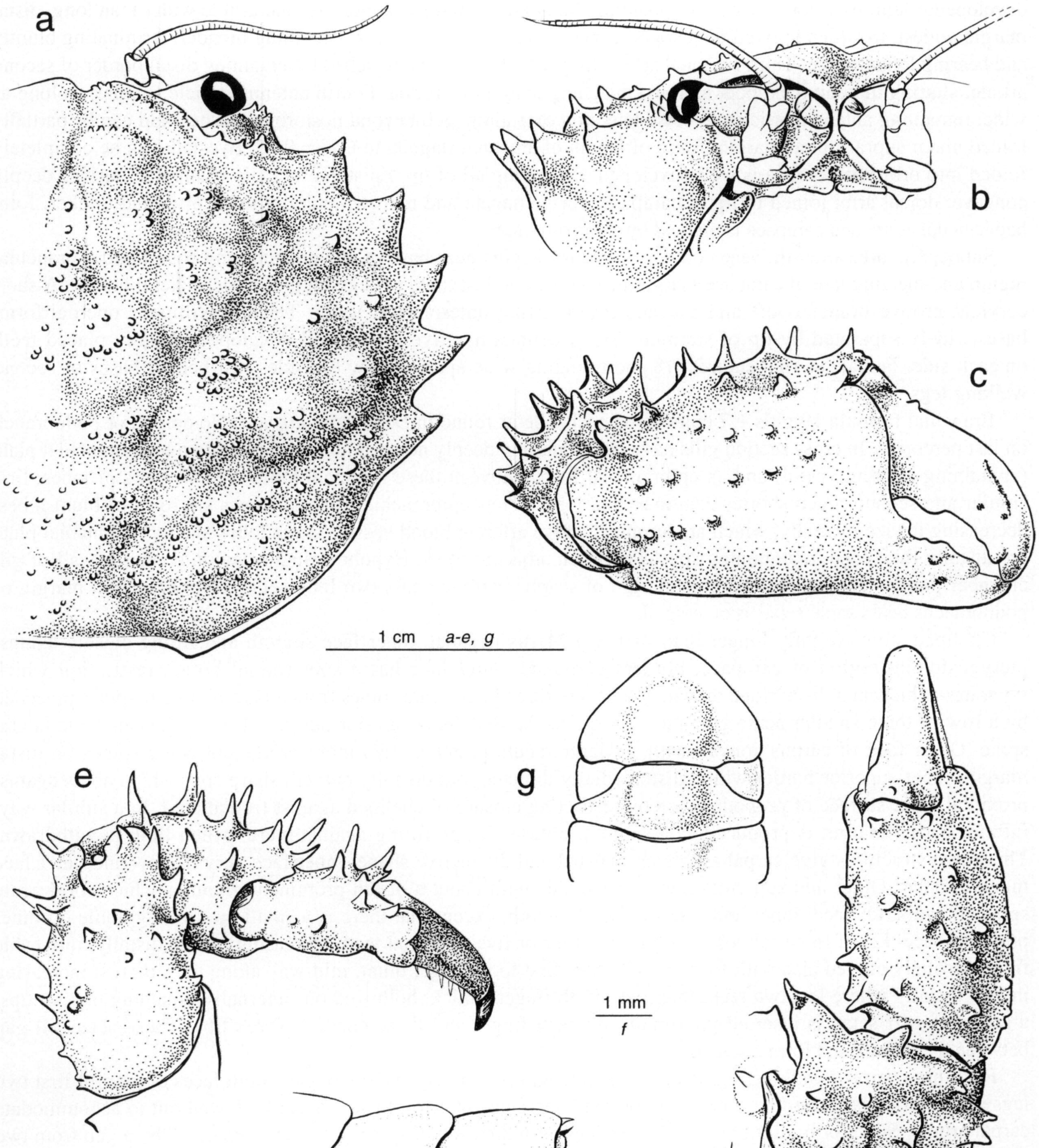

FIG. 23. — *Hirsutodynomene spinosa* (Rathbun, 1911): **a-g**, ♂ 16.4 x 14.3 mm, Glorieuses Ids (MNHN-B 6899): **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of male abdomen.

developed, blunt, superior tooth above opening of antennal gland is smaller. Second article wider than long, distal margin widest, to which is fixed the exopod curving over base of eyestalk, becoming broader, terminating bluntly and bearing longer setae. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and just matching length of exopod. Fourth antennal article smaller, as long as wide; remaining antennal articles directed laterally, extending well beyond postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.45. Eyestalk can be completely folded into orbit, and cornea is well developed, occupying all of tip. Epistome broadly triangular, surface deeply concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace is marked by a narrow suture.

Subhepatic area smooth, very convex. A groove begins near base of antenna, curving round under branchial region and meeting lateral carapace margin just anterior to last tooth at beginning of posterolateral border. A short cervical groove branches off and ascends towards first anterolateral tooth. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has five or six well developed, distally placed teeth on each side. Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

Branchial formula 19 gills + 7 epipods on each side as found in *Dynomene hispida*. No epipod or podobranch on last pereopod. In cross section gills have lateral margin deeply notched, dividing gill into a hypobranchial plate (containing efferent vessel) and an epibranchial lobe. Between these marginal lobes are two pairs of lobes, first similar and second much shorter than marginal lobes. Thus epibranchial surface shows six rows of blunt lobes, decreasing in size medially, which are arranged above afferent blood vessel. These lobes and hypobranchial plate are distally thickened, maintaining spaces between adjacent rows. Hypobranchial setae on posterior wall of gill chamber poorly developed. Posterior margin of scaphognathite bears two long setae. Hypobranchial margin of podobranchs bears same setae as on epipod.

Cheliped stout, slightly longer than first leg. Merus trigonal, inner face smooth and fitting closely against pterygostomial region of carapace, borders granulate, outer face has a subterminal broad, restriction which separates a thickened distal ridge on which there are three large acute spines from a pair of similar spines preceded by a row of three smaller acute granules on superior border. Inner inferior margin of merus has an acute lateral spine. Outer face of carpus convex with six large, acute granules, two more prominent acute spines on distal margin; inner superior border with a distomedially directed, but dorsally curved, sharp spur which abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin is produced as a smooth, obtuse, flange fitting against merus when limb is withdrawn. These two structures give carpal article an unusual and distinctive shape: inner face very narrow and outer face much broader. Outer and superior faces of propodus with about a dozen prominent granules which form acute spines on superior face; inner and inferior faces smooth, except that there is a small proximal granule on inner propodal face. Fixed finger almost straight with four or five proximal teeth increasing in size distally; moveable finger strongly curved also with four or five teeth; first tooth large, blunt, mid-way along margin, rest increasing in size distally where last two teeth interlock. Both fingers, thick, hollowed out internally, touching only at tips; a group of stiff setae is inserted proximally on each finger and these curve towards tips. These setae fill gap between the fingers and form a screen.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with three small spines, in a row, separated by a gap from two larger distal spines, and three large distal spines on posterior margin, length of merus of second leg about 1.6 x its width and equal to about half of CL. Dorsal surface of carpi bearing three longitudinal rows each of five acute spines, and produced distally to overhang base of propodi. Dorsal surface of propodi with three similar rows each of two or three spines. Dactyli curved, inferior margin armed with 4-5 small spines, tip brown (in some cases the whole dactyl is black) and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching only as far as half way along meral article of preceding limb, borders of articles unarmed. Last pair of legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing eight, unequal, stout, hooked, acute, spines, the four largest lined with tiny, striated flattened and conical teeth along almost their entire inner surface, the remaining four more sparsely covered with teeth. Female dactyl as long as propodal extension, bearing sixteen unequal, stout, hooked spines (arranged asymmetrically around perimeter of dactyl) whose concave inner surface is wrinkled and mostly devoid of tiny teeth. Male propodal extension bearing five unequal curved spines the four largest of which have lateral rows of about six tiny teeth. Male dactyl longer than propodal extension and ending in a single acute claw.

All segments of abdomen freely moveable, surface smooth, margins unarmed but fringed with long setae. Second segment narrowest, anterior margin sinuous, medial region convex, lateral margins produced as a flange which fits over posterior margin of first segment (which is shortest) preventing forward slippage of abdomen. Subsequent segments increasing in length and breadth distally, not overlapping with preceding segments. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In female uropod plates large, filling about two thirds of space between last abdominal segment and telson, excluding most of last abdominal segment and telson from reaching lateral margin of abdomen. In male last abdominal segment occupies about a half of length. No effective abdominal locking mechanism: abdomen only loosely held against sternum in both sexes; sideways movement restricted by small sternal tubercle beside telson. In mature female abdomen occupies all of ventral surface, covering coxae of all pereopods with telson covering proximal half of third maxillipeds. In male abdomen not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. First male pleopod a semi-rolled tube with a small apical plate surrounded by long setae. Second male pleopod with an exopod on the basis, needle-like distally, armed with a series of sixteen tiny, straight, acute, inset spines and ending in two larger straight spines. Subterminal spines unevenly spaced, ninth and tenth spines overlap, and follow a sinuous path. Third to fifth male pleopods rudimentary and biramous, exopod longer and jointed to basal article.

COLOUR. — Preserved specimens have a dense covering of light brown setae and the dactyli (or only their tips) of the first four pereopods are black or dark brown.

GEOGRAPHIC DISTRIBUTION. — In the Indian Ocean *Hirsutodynomene spinosa* is known from Madagascar, Mauritius, Glorieuses Ids, Coetivy Id (the type locality, Western India), Chagos Archipelago, Cocos Keeling Ids, and Western Australia. Records from Indonesia include Timor, Ternate, and Moluccas. In the Pacific this species is known from Southeast Queensland, Middleton Reef, Elizabeth Reef, Palau, Marshall Ids, Vietnam, Mariana Ids, Xisha Ids, Japan, Enewetak Atoll, Palmyra Id, Tuamotu, Raroia, Marquesas Ids. The material examined in this study establishes new records for Australia, Middleton and Elizabeth Reefs (Tasman Sea), Mariana Ids, Japan, and Palmyra Id. It should be noted that although BALSS (1935) included this species in his report on the collections made by the Hamburg Museum Expedition to South Western Australia, 1905, the material cited did not come from Western Australia but from the Marquesas and Palau Ids. *H. spinosa* is clearly a widespread Indo-Pacific species.

DEPTH. — *Hirsutodynomene spinosa* has been collected from intertidal habitats and to a depth of approximately 15 m. *H. spinosa* is an inhabitant of shallow water coral reefs.

SIZE. — The maximum size for males is 28.7 x 21.3 mm, for females 32.3 x 29.4 mm. Only one ovigerous female (32.3 x 29.4 mm) has been recorded in December from Middleton Reef, Tasman Sea and it carried about 3800 eggs with a diameter of 0.5 mm. Although *H. spinosa* is one of the larger dynomenids, it evidently produces eggs of similar size to the other species and probably has planktotrophic larvae.

DISCUSSION. — *Hirsutodynomene spinosa* (Rathbun, 1911) was first described by RATHBUN on the basis of three males collected from Coetivy Id by the Percy Sladen Trust Expedition of 1905. The first female was reported by BALSS (1935) from the Marquesas Ids.

RATHBUN (1911) referred to the shorter setae of *Hirsutodynomene spinosa* as being "club-shaped" and the bunches of setae as being long and slender. Microscopic examination shows that the distal portion of the short setae is bent at right angles and ornamented, on the outer side, with sharp setules which might give the setae a club-shaped appearance. The long setae are clothed for almost their entire length with much smaller setules.

The gills of *Hirsutodynomene spinosa* are similar to those of *Dynomene filholi*. On the epibranchial surface there are sequential rows of six lobes along the length of the gill, except towards the tip where the smaller medial lobes are lost. In prepared material the lobes tend to be clumped together, even interlocking, but in live animals the lobes are probably free, kept apart by their thickened tips. As in the species of *Dynomene*, the hypobranchial setae in the posterior region of the branchial chamber of *H. spinosa* are poorly developed. The posterior margin of the scaphognathite bears two long setae and the hypobranchial margin of each podobranch carries cleaning setae as found in *H. ursula*.

The male pleopods of *Hirsutodynomene spinosa* are similar to those of the species of *Dynomene*. The tip of the first pleopod bears a dense ring of long setae surrounding an oval apical plate. The second pleopod has a large number of subterminal spines, not all evenly spaced, which follow a sinuous path along the shaft and it ends with two straight terminal spines. Also the last three pairs of pleopods are biramous and the connection of the exopod with the basal article is marked by a joint.

The two species in this genus have non-overlapping distributions with *Hirsutodynomene spinosa* being a widespread Indo-West Pacific species and *H. ursula* being restricted to the eastern Pacific. The main differences between these species (see Table 2) are discussed below under *H. ursula*.

The habitat of *Hirsutodynomene spinosa* seems to be dead coral branches and rubble. MORRISON (1954) recorded *H. spinosa* from the inshore, more pooled area of the leeward outer reef at Raroia, Tuamotu along with hermit crabs, *Cryptodromia canaliculata*, *Pachygrapsus plicatus*, *Micippoides angustifrons*, *Thalamita picta*, *Eriphia sebana* and several xanthids. PEYROT-CLAUSADE (1981) recorded it from dead clumps of *Acropora* sp. on Tuléar Reef, Madagascar where (along with *Dynomene hispida*) it made up only about 1-2% of the anomuran and brachyuran fauna. On both the Tuléar and Reunion reefs *H. spinosa* was always less common than *D. hispida* which had a greater depth range (PEYROT-CLAUSADE, 1984). Although both these species are shallow water dynomenids, *H. spinosa* grows to a much larger size.

Examination of the gut contents of a male *Hirsutodynomene spinosa* 14.2 x 10.8 mm from the Cocos Keeling Ids revealed a stomach packed almost entirely with sand grains and a small amount of aggregated amorphous organic material. There were no recognizable animal or plant fragments. Food is probably obtained by using the spooned cheliped fingers and their stiff setae to sift out fine particulate organic material from coral sediments.

Hirsutodynomene ursula (Stimpson, 1860)

Figs 4 a-c, 6 a-b, 9 a-b, 11, 14 f, 17 f, 24 a-g

Dynomene ursula Stimpson, 1860: 239. — A. MILNE EDWARDS, 1879: 9, figs 16-19. — ALCOCK, 1901: 74 (list). — RATHBUN, 1937: 54, pl. 12, figs 1-4. — SCHMITT, 1939: 25. — GARTH, 1946: 349, pl. 61, figs 5-6; 1948: 16; 1961: 121 (list); 1965: 6; 1966: 5; 1991: 125. — BIRKELAND *et al.*, 1975: 67. — TAKEDA, 1977: 35 (list). — PRAHL & ALBERICO, 1986: 98 (list). — PRAHL, 1986: 96. — RODRIGUEZ DE LA CRUZ, 1987: 113. — VILLALOBOS-HIRIART *et al.*, 1989: 53 (list). — CORREA-SANDOVAL, 1991: 2. — LEMAITRE & ALVAREZ-LEON, 1992: 50. — AGUILERA & GUZMAN, 1992: 4 (list). — HENDRICKX, 1995: 127 (list); 1997: 29, fig. 39 a-c. — VARGAS *et al.*, 1996: 99 (list).

MATERIAL EXAMINED. — **Galapagos**. ALLAN HANCOCK GALAPAGOS EXPEDITION: stn 30-33, Hood Id, Gardner Bay, no depth, W. L. SCHMITT coll., 26.01.1933, M. J. RATHBUN id.: 1 ♂ 11.7 x 9.6 mm; 1 ♀ 15.0 x 12.3 mm (USNM 68313). — Charles Id, no depth, W. L. SCHMITT coll., 27.01.1933, M. J. RATHBUN id.: 2 ♂ 9.1 x 7.4 mm, 11.1 x 8.6 mm (USNM 68314).

Mexico. *Espiritu Santo Id. "Velero"*: stn 638-37, San Gabriel Bay, shore, 7.03.1937: 1 ♂ 13.4 x 10.3 mm; 1 ♀ 13.0 x 10.3 mm (LACM). — Stn 1110-40, 2-4 m, 14.02.1940, J. GARTH id.: 1 ♀ 7.2 x 5.7 mm (LACM).

Panama. *Secas Ids*. Stn 252-34, on *Porites* coral, 22.02.1934, M. J. RATHBUN id.: 1 ♀ ovig. 10.9 x 8.8 mm (LACM).

"Velero": stn 867-38, shore, 2.03.1938: 8 ♂ 8.4 x 6.6 - 12.7 x 10.0 mm; 5 ♀ ovig. 9.5 x 7.5 - 12.3 x 9.8 mm (LACM).

Ecuador. *La Plata Id. "Askoy"*: stn 80, 12.04.1941, J. GARTH id.: 3 ♂ 7.5 x 6.3 - 19.4 x 15.7 mm; 1 ♀ 5.0 x 4.4 mm; 1 ♀ ovig. 15.0 x 12.2 mm (LACM).

ARGOSY 34: no depth, J. GARTH coll., 5.03.1963: 1 ♀ ovig. 19.4 x 14.7 mm (USNM 247230).

TYPES. — *Dynomene ursula* Stimpson, 1860: holotype is a male 15.2 x 12.7 mm, collected by Mr J. XANTUS from 22°50.00'N, 109°55.00'W, Cape St. Lucas, Baja California, and according to the original paper is held by the Smithsonian Institute, Washington, but RATHBUN (1937) stated that the specimen is not extant. However there is a syntype held by the Museum of Comparative Zoology, Harvard, registration number MCZ 1378.

DESCRIPTION. — Carapace wider than long, ratio of CW/CL approx. 1.25-1.30, broadly rounded in outline but frontal and posterior margins truncated; surface convex, areolate, sparsely granulate, and spinous. There are about twenty to twenty five distinct areolae, more medial areolae smooth or minutely granulate, more lateral areolae adorned with larger acute granules, and those above anterolateral margin adorned with short, acute spines. Behind branchial groove is a laterally directed region of granules ending at base of last marginal tooth. Carapace surface and pereopods covered with setae of two kinds: short erect serrate setae clothing surface, but interspersed with longer serrate setae (3 x length of short setae and 0.05-0.07 x CW) which also fringe limbs and arranged in clumps on carapace where there are about twenty distinct tufts, each with up to five setae, which tend to be associated with areolae. Density of setae does not completely obscure body surface. Structure of short and long setae differs. In short setae the proximal 23% of shaft lacks ornamentation, followed by a region of 45% where tiny setules arranged in bands, then a region occupying about 22% where long, stout setules radiate from all sides of shaft, forming a dense bunch, and finally the distal 5% which is smooth, and narrows to an acute tip. The whole seta may be slightly curved but is not bent at right angles. In long setae the proximal 15% is smooth, following 80% covered with small setules which increase distally in density and size (but not reaching size of setules on short setae), and the last 5% is smooth, slightly curved and narrows to an acute tip.

A narrow frontal carapace groove separates a pair of prominent rounded protuberances, and then divides into separate grooves which diverge and then curve back medially. Between these grooves is an elongate granulate ridge. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately from small pits and runs directly anterolateral on to branchial region and mid-way along their length they are joined by grooves running back from frontal groove. Second shallower groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally, bordering anterior cardiac region. In effect groove crossing mid-line, connects two crescent-shaped grooves. A faint branchial groove is evident and posterior cardiac area is defined. Anterolateral carapace margin begins at level of postorbital corner, evenly convex and bears four distinct, broad-based, equidistant well developed teeth, each ending bluntly; first tooth directed anteriorly, second anterolaterally, and remainder directed laterally. Each anterolateral tooth has an associated tuft of long setae. A posterolateral tooth marks beginning of convergent posterolateral border alongside which lies the reduced last leg. Posterior carapace margin recessed in order to accommodate first segment of abdomen visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, interrupted by a distinct notch closer to postorbital corner, followed by three small blunt granules before corner; suborbital margin with three larger blunt granules, first two visible dorsally, second and third (tooth-like) closer together but separated by a deep notch with third terminating the suborbital margin. Orbits clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region; distal margin bearing a dense fringe of longer setae, obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit behind second antenna. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed; blunt, superior tooth above opening of antennal gland smaller. Second article about as wide as long; distal margin widest, to which is fixed the exopod curving over base of eyestalk, becoming broader, terminating bluntly and bearing longer setae. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod. Fourth antennal article smaller, as long as wide, together with third article just matching length of exopod; remaining antennal articles directed laterally, extending well beyond postorbital corner, and partially folded under supraorbital margin. Ratio of length of antennal flagella to CW = 0.45. Eyestalk can be completely folded into orbit, and the cornea is well developed,

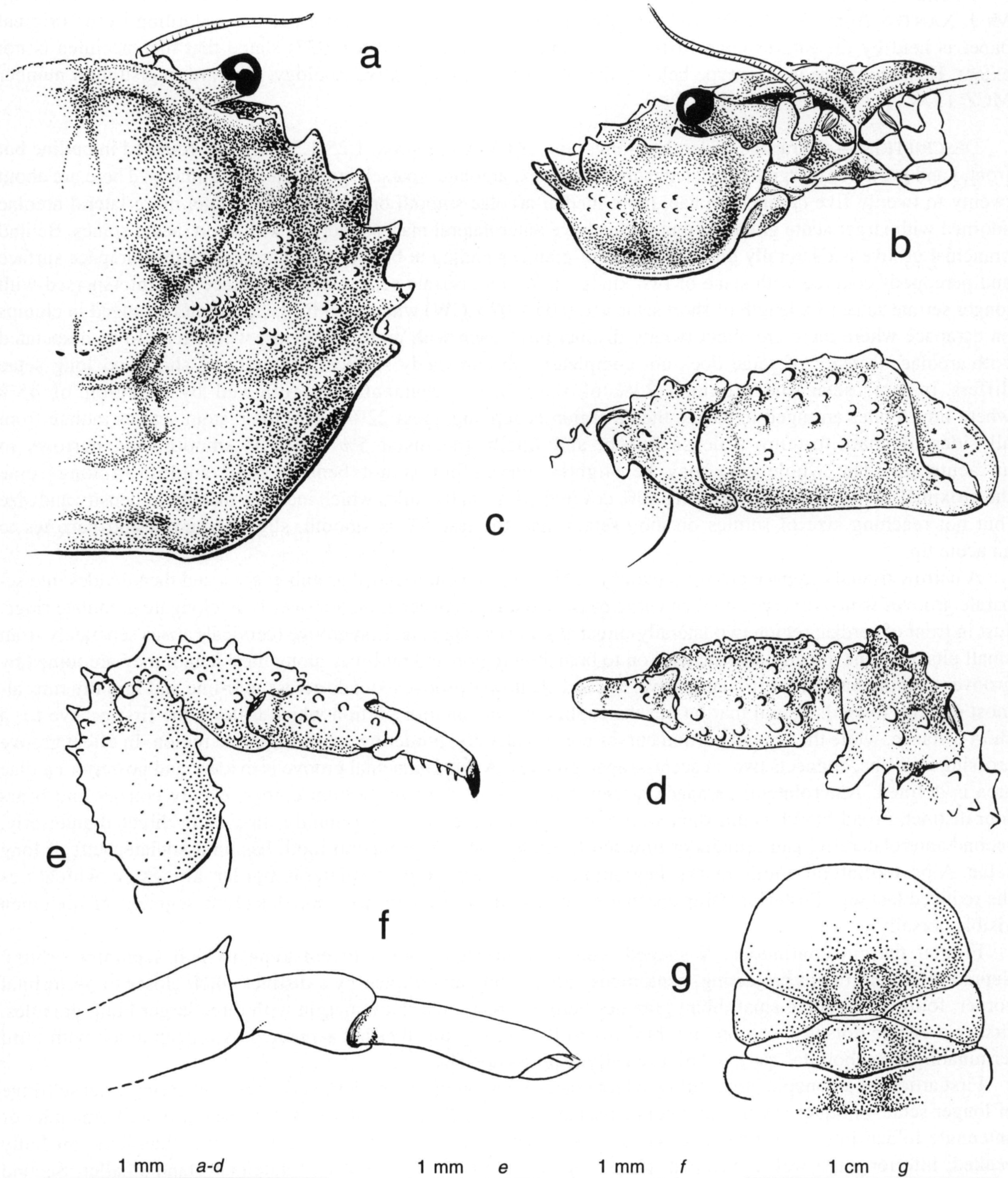

FIG. 24. — *Hirsutodynomene ursula* (Stimpson, 1860), ♀ ovig. 19.4 x 14.7 mm, La Plata Island, Ecuador (USNM 247230): **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of female abdomen.

occupying all of tip. Epistome broadly triangular, surface deeply concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace marked by a narrow suture.

Subhepatic area very convex with a few scattered granules. A groove (pleural suture) begins near base of antenna, curving round under branchial region and meeting lateral carapace margin just anterior to last tooth at beginning of posterolateral border. A short cervical groove branches off and ascends towards first anterolateral tooth before dividing into two branches, one curving towards postorbital corner and the other curving beneath second anterolateral tooth. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has seven or eight well developed, distally placed teeth on each side. Female sternal sutures 7/8 short, ending wide apart on low tubercles just behind bases of second walking legs.

Branchial formula 19 gills + 7 epipods on each side. There is no podobranch or epipod on last pereopod. Gill structure is variable. In cross section the anterior of each pair of arthrobranchs show maximum development of epibranchial lobes: there are a series of six elongate lobes developed above afferent vessel, two narrow, short median lobes flanked by longer lobes, with wider and longer lobes on the outside. The short median lobes are lost towards the tip of gill. At base of outer lobes there is a deep notch on each side dividing off the hypobranchial plate containing the efferent vessel. On posterior arthrobranchs, and all pleurobranchs, there are only four epibranchial lobes and the median lobes are lost towards tip of gill. Hypobranchial setae at posterior end of branchial chamber poorly developed. Posterior margin of scaphognathite with two long setae. Hypobranchial margin of podobranchs bear same setae as on epipod.

Cheliped stout, slightly longer than first leg. Merus trigonal; inner face smooth fitting closely against pterygostomial region of carapace, borders granulate; outer face has a subterminal broad, restriction which separates a thickened distal ridge, on which there are three spines, from a pair of similar spines preceded by a row of six smaller granules on superior border. Inner inferior margin of merus has a small blunt lateral spine. Outer face of carpus convex with six small blunt granules, two more prominent blunt spines on distal margin; inner superior border with a distomedially directed, but dorsally curved, blunt spur which abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin is produced as a smooth, obtuse, flange fitting against merus when limb is withdrawn. These two structures give carpal article an unusual and distinctive shape: inner face very narrow and outer face much broader. Outer and superior faces of propodus with about a dozen small blunt granules, inner and inferior faces smooth, except that there is a small proximal granule on inner propodal face. Fixed finger almost straight with four or five teeth increasing in size distally, second tooth placed midway and prominent, last three teeth dividing up tip of finger; moveable finger strongly curved bearing four teeth, first blunt, second more acute directed towards tip and last two interlocking with teeth of fixed finger. Both fingers, thick, hollowed out internally, touching only at tips; a group of stiff setae inserted proximally on each finger and these curve towards tips filling gap between fingers.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate; both faces of meri of first two legs and anterior face third leg merus smooth and nacreous; inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with a row of three or four small spines increasing in size distally, separated by a gap from two small distal spines; no spines on distal posterior margin; length of merus of second leg about 1.2 x its width and equal to about 0.4 x CL. Dorsal surface of carpi armed with seven or eight small spines not arranged in rows, and produced distally to overhang base of propodi. Dorsal surface of propodi armed with four or five small spines. Dactyli curved, inferior margin armed with 4-5 small spines, tip brown (in some cases whole dactyl is black) and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching only as far as half way along meral article of preceding limb; borders of articles unarmed. Last pair of legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing ten, unequal, stout, hooked, acute, spines with lateral rows of 8-10 tiny, flattened teeth proximally, separated by a striated ridge. Distally the striae of this ridge grade into a surface that is densely convoluted. Female dactyl as long as propodal extension, bearing thirteen unequal, stout, hooked spines (arranged asymmetrically around perimeter of dactyl) whose concave inner surface is wrinkled or convoluted and mostly devoid of tiny teeth except for a few small blunt marginal teeth on distal two-thirds. Male propodal extension bearing six unequal curved spines which have tiny scattered marginal teeth. These spines are not arranged in the typical manner for dynomenids: instead of lying in an asymmetrical row around the perimeter, they are very disorganized, facing in different directions and leaning at different angles. Male dactyl longer than propodal extension and ending in a single acute claw.

All segments of abdomen freely moveable, surface smooth, margins unarmed but fringed with long setae. Second segment narrowest; anterior margin sinuous, medial region convex, lateral margins produced as a flange which fits over posterior margin of first segment (which is shortest) preventing forward slippage of abdomen. Subsequent segments increasing in length and breadth distally, not overlapping with preceding segments. Telson much wider than long, anterior margin angled to accommodate uropod, posterior margin broadly rounded. In female uropod plates are large, filling about ninety percent of space between last abdominal segment and telson, excluding most of last abdominal segment and telson from reaching lateral margin of abdomen. In male last abdominal segment occupies about three quarters of peripheral margin. No effective abdominal locking mechanism: abdomen only loosely held against sternum in both sexes, sideways movement restricted by small sternal tubercle beside telson or uropods. In mature females sternal tubercles absent; abdomen occupies all of ventral surface, covering coxae of all pereopods with telson covering proximal half of third maxillipeds. Male abdomen not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. First male pleopod a semi-rolled tube with a small apical plate surrounded by long setae. Second male pleopod with an exopod on basis, needle-like distally, armed with a series of twenty prominent, straight, acute, spines and ending in two larger curved spines. Subterminal spines unevenly spaced, seventh, eighth, and ninth spines form an overlapping group as do thirteenth and fourteenth spines, and follow a sinuous path. Third to fifth male pleopods rudimentary and biramous, exopod longer and jointed with basal article.

COLOUR. — In his original description STIMPSON (1860) noted that the color of *Hirsutodynomene ursula* is more or less reddish or crimson, the setae a light golden color, and the ambulatory legs have sharp, black, curved unguiles (claws). A. MILNE EDWARDS (1879) gave the colour as being crimson, and in places carmine. RATHBUN (1937) noted that the dactyli of the last pair of legs are without pigment.

GEOGRAPHIC DISTRIBUTION. — The type locality for *Hirsutodynomene ursula* is Cape San Lucas, Baja California. RATHBUN (1937) states that the type specimen is not extant. The range extends from the Gulf of California in the north to La Plata Id, Ecuador in the south, and offshore it occurs on the Galapagos Ids and Clipperton Id. Thus *H. ursula* is an eastern Pacific species.

DEPTH. — The depth range for *Hirsutodynomene ursula* is 0-99 m (rarely 125 m). Most specimens have been collected from rocks and dead coral, and some have been recorded as coming from *Porites* sp. and *Pocillopora* sp. but it is not clear whether these were living or dead colonies. There is no strong evidence of dependence on living corals. *H. ursula* has a much greater depth range than *H. spinosa* which has not been recorded deeper than 15 m.

SIZE. — The maximum sizes for *Hirsutodynomene ursula* are 27.2 x 20.4 mm for males, and 21.8 x 16.5 mm for females. The smallest ovigerous female examined was 9.5 x 7.5 mm, carrying around 120 eggs, and the largest ovigerous female, 19.4 x 14.7 mm, carrying around 2800 eggs. Mean egg diameter was 0.45 mm. This egg size suggests that this species has planktotrophic larvae. Ovigerous females have been mainly collected during December to April with one female from Clipperton Id collected in August (GARTH, 1965). Concentration of breeding in the early part of the calendar year is similar to the *Dynomene* species.

DISCUSSION. — GARTH (1946) remarked upon the remarkable similarity of *Hirsutodynomene ursula* to the xanthids: "With no other Galapagos species of Brachyura is the field collector so likely to be misled as to identity as with *D. ursula.* Unless he notices that the fourth pair of walking legs are reduced to minute size and carried dorsally, he will believe himself to have found a species of *Pilumnus.*" Indeed, initial sorting of the Galapagos collections resulted in all the dynomenid specimens being placed with the Xanthidae. An untrained observer would be easily misled by the black pereopod dactyli. (It should be noted here that dynomenids do not in fact carry their last pereopods "dorsally". They are carried horizontally).

The main differences between the two species in this genus (see Table 2) are that in *Hirsutodynomene spinosa* there are about 12 spines (and associated areolae) on the carapace (only about 6 in *H. ursula*), the suborbital margin has 5 short acute spines (only blunt granules), the carpal projection on the cheliped is a sharp spine (a blunt lobe), the carapace is densely covered with setae (sparsely covered), and the short setae are bent at right angles near the tip (short setae not bent).

Other differences between *Hirsutodynomene spinosa* and *H. ursula* are seen in the last pair of legs: both have a similar number of propodal spines in the female but those of *H. spinosa* are densely covered with teeth while in *H. ursula* the teeth are confined to the proximal lateral margins and the rest of the spine has a roughened, convoluted surface. In both species these spines are opposed by concave, wrinkled dactylar spines with a few small teeth but *H. spinosa* has more spines. The males have a similar number of propodal spines but in *H. ursula* these spines are very disorganized and arranged irregularly around the distal perimeter. There are no differences in the male dactyli. Commenting about the last pair of legs of *H. ursula*, STIMPSON (1860) said they are "... not prehensile, since the animal does not cover itself with a foreign body like the Dromiae; and 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." This is the earliest speculation about the role of the last leg of a dynomenid. STIMPSON clearly believed that this limb is vestigial and redundant.

RATHBUN (1937) describes the two kinds of setae on the surface of *Hirsutodynomene ursula*: "...the first kind very short, clavate, or even pedicellate, and densely crowded; the second long and nearly as thick as the first, but fusiform, with pointed extremities, and sparsely distributed over the surface, generally in groups of three or four, of unequal lengths." The short erect setae are in fact plumose with a dense distal zone of long setules and most of the shaft only sparsely covered with short setules. The long setae are mostly covered with short setules. These long setae are very similar in *H. ursula* and *H. spinosa* but the short setae show several differences in their shape and setule ornamentation.

The gill structure of *Hirsutodynomene ursula* is similar to that of *H. spinosa* but shows more variation between gills. The anterior arthrobranchs of *H. ursula* are the same, but the other large gills show a reduced number of median lobes. These are more phyllobranchiate-like because more of the gill consists of flattened plates. The gills of *H. spinosa* are more trichobranchiate-like in having a large number of elongate epibranchial lobes. Both species show the pattern seen in other dynomenids of a tendency to lose epibranchial lobes towards the tip of the gills. Hypobranchial setae at the back of the gill chamber are poorly developed and there are two long setae on the posterior margin of the scaphognathite. Setae on the hypobranchial margin of each podobranch aid the cleaning role of the epipods.

The second male pleopod of *Hirsutodynomene ursula* has a larger number of subterminal spines than *H. spinosa* and these spines are longer, and not inset into the surface of the pleopod. In both species these spines are unevenly distributed along the pleopod, but more so in *H. ursula*, where there are two overlapping groups. Both species have the last three pairs of pleopods biramous and rudimentary but in *H. ursula* the articles are of similar length, whereas in *H. spinosa* the exopod is longer. The junction of the exopod and basal article is marked by a joint in both species.

The two species have mutually exclusive distributions: *Hirsutodynomene ursula* in the Eastern Pacific and along the coast of the Americas, and *H. spinosa* across the Western Pacific and the Indian Ocean. The western-most locality for *H. ursula* is Clipperton Id (109°W), while the eastern-most locality for *H. spinosa* is the Tuamotu Ids (142°W).

The stomach of a male *Hirsutodynomene ursula*, 13.4 x 10.3 mm, from Espiritu Santo Id, was almost entirely filled with sand grains and some amorphous aggregates of organic material. There were no recognizable plant or animal fragments present. Food is probably obtained by using the spooned cheliped fingers and their stiff setae to sift out fine particulate organic material from coral sediments. The contents are identical to those found in *H. spinosa* (see above). In the body cavity, beside the stomach, two encysted nematodes were observed.

On the Galapagos Ids, GARTH (1991) found that in a sample (n = 169) of 20 species of rocky shore Brachyura from Sullivan Bay, Isla Santiago, *Hirsutodynomene ursula* was common, making up 5.3% of the total. This species is the only dynomenid known from the Galapagos Ids.

Character	*H. spinosa*	*H. ursula*
Density of setae	Very dense over most of carapace	Some areas of sparse setae on carapace
Short setae	Bent at right angles	Not bent at right angles
Carapace surface	Areolate and bearing about 12 spines	Areolate and bearing about 6 spines
Suborbital margin	Armed with about 5 short, acute spines	Armed with only a few blunt granules
Inner carpal margin of cheliped	Bearing a sharp spine	Bearing a blunt lobe
P5 ♀ Propodus	8 spines with numerous teeth on inner margin	10 spines with marginal rows of teeth
P5 ♀ Dactyl	16 spines	13 spines
P5 ♂ Propodus	5 spines arranged around distal perimeter	6 spines not arranged around perimeter
Second ♂ Pleopod	16 short, inset subterminal spines	20 long subterminal spines, not inset

TABLE 2. — Comparison of the two species of *Hirsutodynomene*.

Genus *METADYNOMENE* nov.

DIAGNOSIS. — Carapace as wide as long or slightly wider than long, moderately convex, subcircular; surface smooth. Tomentum composed of uniformly short, soft setae, which accentuate unevenness of carapace forming transverse troughs. Lateral carapace margin well defined and marked by indentations or armed with distinct teeth. Frontal groove well marked, split in two posteriorly; cervical, postcervical and branchial grooves usually evident. Frontal carapace margin broadly triangular, continuous, no rostrum or teeth Eyestalks short; eyes protected by well defined orbits. Sternal sutures 7/8 of female end well apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside orbit at base of eyestalk. Antennal flagella shorter than carapace width. All articles of antenna moveable; first article (urinal) always beaked medially; second article has an exopod firmly fixed. Third maxillipeds opercular, completely covering buccal cavern, separated at their bases by a plate at same level as sternum; basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds equal, stouter than walking legs; fingers not strongly curved and touching for at least half their length. Last pair of legs sexually dimorphic, very reduced; dactyl rudimentary, forming an obsolete subchelate mechanism with an extension of propodus. Gill structure basically phyllobranchiate but plates have a variable number of epibranchial lobes.

Abdomen of six segments and telson folded loosely under thorax; uropods large, no effective abdominal locking mechanism. Sideways movement restricted by small spines or ridges on coxae of second and third pereopods, adjacent to the margins of telson and penultimate abdominal segments. Both sexes have five pairs of pleopods; first pair vestigial in female; last three pairs rudimentary in male. Male pleopods uniform in structure; first pair consist of a stout, setose semi-rolled tube with an apical plate; second pair needle-like, bearing a row of curved spines on anterior surface.

TYPE SPECIES. — *Dynomene devaneyi* Takeda, 1977.

OTHER SPECIES. — *Dynomene tanensis* Yokoya, 1933, *Metadynomene crosnieri* sp. nov.

ETYMOLOGY. — *Metadynomene* is a combination of *meta*, meaning *after*, and the genus *Dynomene*. Gender is feminine.

DISCUSSION. — This new genus is erected for a group of three species, two of which were originally assigned to *Dynomene*. The third species is newly described herein. All of these species are characterized by having a carapace about as wide as long, or only slightly wider than long, densely covered with short, soft setae which give the surface an uneven, undulating appearance with transverse troughs, and chelipeds with fingers not strongly down-curved and touching for about half their length. All the known species are substantially larger than the other dynomenids and occur in deeper waters. *Metadynomene crosnieri* sp. nov. is known only from the type locality, *M. devaneyi* (Takeda, 1977) from the type locality and Marquesas Islands, whereas the third species, *M. tanensis* (Yokoya, 1933), is widespread in the Pacific.

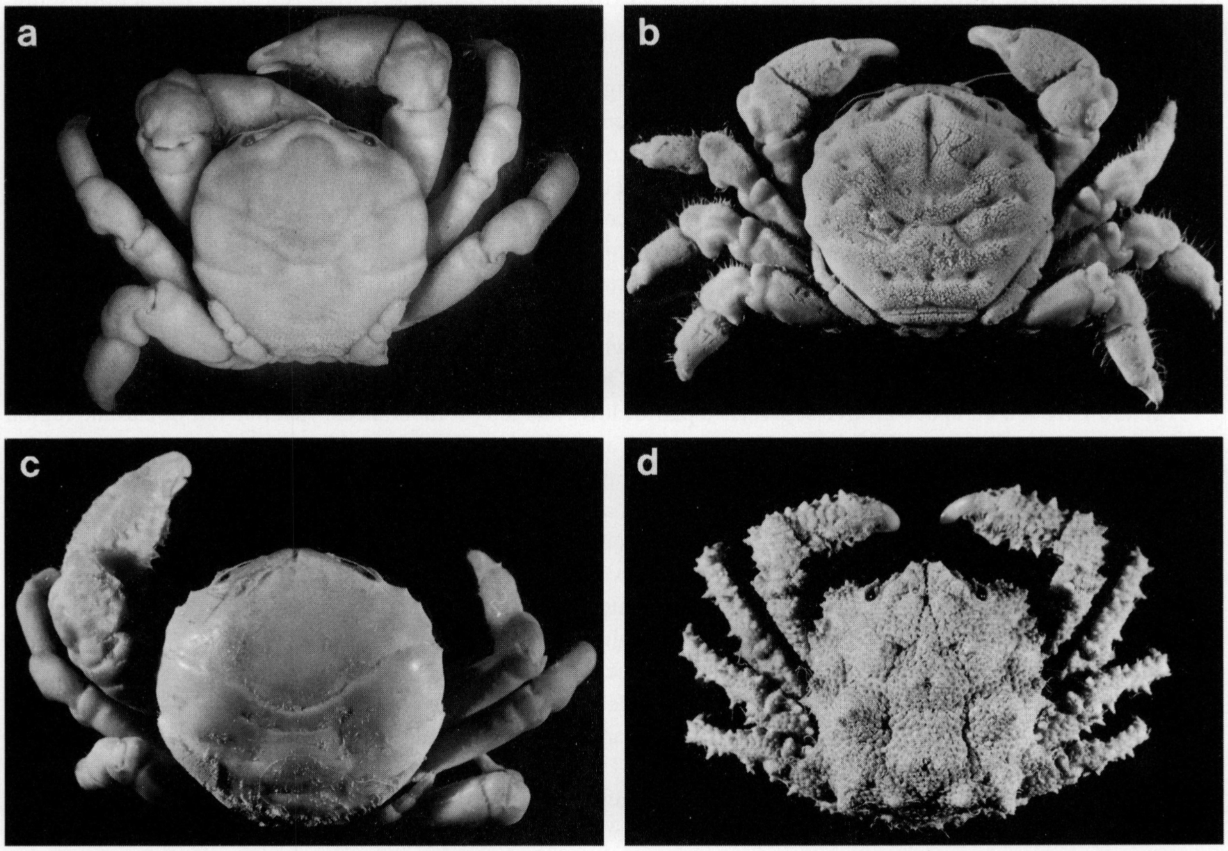

FIG. 25. — **a**, *Metadynomene devaneyi* (Takeda, 1977) ♂ 21.2 x 20.1 mm, holotype, S. E. Oahu, Hawaii, *"Star II"*, 367 m (BPBM-S 8509): dorsal view of whole crab, left second pereopod and right fourth pereopod not shown. — **b**, *Metadynomene tanensis* (Yokoya, 1933), ♀ 13.5 x 12.5 mm, New Caledonia, SMIB 8, 305-355 m: dorsal view of whole crab. — **c**, *Metadynomene crosnieri* sp. nov., ♂ 23.2 x 22.7 mm, Glorieuses Ids, BENTHEDI, 330-440 m (MNHN-B 22510): dorsal view of whole crab, setae removed from right half of carapace, right cheliped, left third pereopod and left fifth pereopod are missing. — **d**, *Paradynomene tuberculata* Sakai, 1963, ♂ 21.5 x 22.3 mm, Loyalty Ids, MUSORSTOM 6, stn DW 406, 373 m: dorsal view of whole crab.

Metadynomene devaneyi (Takeda, 1977)

Figs 11, 25 a, 26 a-c

Dynomene devaneyi Takeda, 1977: 31, figs 1-3; 1978, fig. 1. — MCLAY, 1991: 465, fig. 4b.
Not *Dynomene devaneyi* - GUINOT, 1993: 1227 (= *Metadynomene crosnieri* sp. nov.).

MATERIAL EXAMINED. — **Hawaii**. *"Star II Submersible"*: S.E Oahu, off Makapuu Point, Kaiwi Channel, 21°18'N, 157°39'W, 367 m, 28.02.1974, collected from precious coral (*Corallium* sp.) beds: 1 ♂ 21.2 x 20.1 mm, holotype (BPBM-S 8509); 1 ♀ 15.6 x 15.2 mm, allotype (BPBM-S 8510).

Marquesas Islands. MUSORSTOM 9: stn CP 1290, Ua Huka, 8°53'S, 139°38'W, 341-344 m, 8.09.1997: 1 ♀ 18.4 x 18.3 mm. — Stn CP 1306, Nuka Hiva, 8°55.2'S, 140°14'W, 283-448 m, 10.09.1997: 1 ♂ 29.0 x 28.3 mm; 1 ♀ ovig. 25.0 x 25.3 mm.

TYPES. — *Dynomene devaneyi* Takeda, 1977: holotype is a male 21.2 x 20.1 mm, collected by the submersible *"Star II"* from 21°18'N, 157°39'W, Southeastern Oahu, off Makapuu Point, Kaiwi Channel, Hawaii, 367 m, 28.02.1974, held by the Bernice P. Bishop Museum, Honolulu, registration number BPBM-S 8509. The same institution holds a paratype male 22.7 x 21.6 mm (BPBM 1975.77, lot no. 2), and an allotype female 15.6 x 15.2 mm (BPBM-S 8510). A paratype male 21.0 x 20.0 mm, is held by the National Science Museum, Tokyo, registration number NSMT Cr. 5075 (ex BPBM 1974.04, lot no. 4).

DESCRIPTION. — Carapace slightly wider than long, ratio of CW/CL = 1.03-1.05, rectangular in outline; surface mostly flat, convexity greater in anterior-posterior direction than laterally, smooth, except for deeply marked grooves (see below). Carapace surface densely covered with setae of only one kind: very short, soft setae, clothing entire surface. Pereopods covered with short setae as well as a few longer filiform setae (5 x length of short setae and 0.10 x CW) which fringe limbs, locally concentrated on dactyli. Density of short setae completely obscures body surface and on carapace they present a symmetrical undulating aspect, reflecting gentle undulations in carapace surface: one oblique trough lies behind supraorbital margin, with a short median longitudinal trough extending posteriorly, then a trough curving anterolaterally which marks cervical groove, followed by a trough running across midline, just in front of cardiac area, which splits into two lateral troughs, and finally a short trough crossing cardiac area. Microscopic details of setae not investigated.

A shallow frontal carapace groove separates a pair of low rounded protuberances. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately (but very close together) from small gastric pits curving (slightly sinuously) anterolaterally on to branchial region towards a faint notch mid-way along anterolateral margin, while second groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows posterior to the first groove but does not reach lateral carapace margin, while second portion curves posterolaterally, bordering anterior cardiac region, to become branchial groove, meeting margin at posterolateral tooth. Posterior cardiac area marked by a shallow groove crossing mid-line. Anterolateral carapace margin begins at level of postorbital corner, evenly convex, without teeth, and interrupted by a shallow notch where cervical groove meets the edge, midway towards branchial notch which marks beginning of posterolateral border. Reduced last leg lies alongside posterolateral border which angles obliquely towards rear of carapace. Posterior carapace margin recessed in order to accommodate distal section of first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, not interrupted by a notch, and without granules. Suborbital margin, convex, without teeth, projecting, shelf-like and visible dorsally. Orbits oblique and clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region, distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth, above the opening of antennal gland, smaller but more acute and directed ventrally. Second article wider than long, distal margin widest, to which is fixed the exopod curving over base of eyestalk, becoming broader and terminating bluntly. Third antennal article is longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and just matching length of exopod. Fourth antennal article smaller, as long as wide; remainder of the antennal articles directed laterally, extending well beyond postorbital corner, and can be partially folded under the supra-orbital margin. Ratio of length of antennal flagella to CW = 0.33. Eyestalk can be completely folded into orbit; cornea well developed, occupying all of tip. Epistome broadly triangular, surface slightly concave; dorsal arm, joined to tip of carapace, narrow; lateral arms longer and thicker. Joint between epistome and carapace is marked by a narrow suture.

Subhepatic area smooth, very convex. A groove begins near base of antenna, curving round under branchial region and meets branchial groove at posterolateral notch. A short continuation of cervical groove bends anteriorly

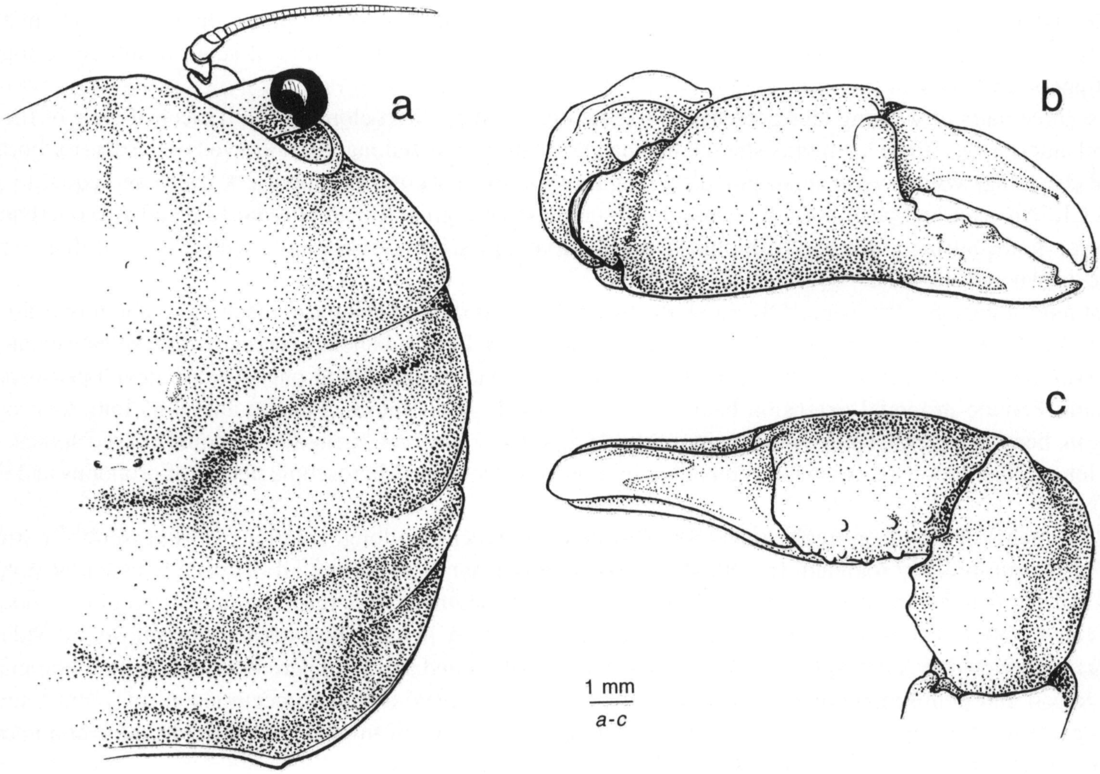

FIG. 26. — *Metadynomene devaneyi* (Takeda, 1977): **a-c**, ♀ 15.6 x 15.2 mm, allotype, S. E. Oahu, Hawaii, *"Star II"*, 367 m (BPBM-S 8510): **a**, dorsal view of right half of carapace; **b**, outer face of right cheliped; **c**, dorsal view of right cheliped.

to meet groove at margin of branchial area. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has twelve teeth increasing in size distally. Female sternal grooves short, ending wide apart in a V-shaped groove created by a low medial parallel ridge, just behind bases of second walking legs. Sternal sutures 7/8 concealed by a dense layer of long soft setae from adjacent coxa of third walking leg.

Branchial formula same as *M. tanensis*, except than there is no podobranch on last pereopod. A cross section of an arthrobranch shows lateral margin deeply notched, dividing gill into a hypobranchial plate (containing efferent vessel) and an epibranchial lobe. Between these marginal lobes are a pair of shorter lobes. Thus the epibranchial surface shows four rows of blunt lobes, which are arranged above afferent blood vessel. Towards tip of gill the length and number of lobes is gradually reduced. Hypobranchial setae in posterior region of branchial chamber well developed.

Cheliped stout, much longer and stouter than first leg. Merus trigonal, inner face smooth and fitting closely against pterygostomial region of carapace; borders granulate, superior border has a subterminal broad, restriction which separates a thickened, smooth distal ridge, from a row of three small granules; inferior face has three subdistal, blunt tubercles. Outer face of carpus convex, smooth, no longitudinal channel, two prominent blunt tubercles on distal margin; inner superior border with three blunt tubercles, distal one largest which abuts against the proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, the inferior carpal margin is produced as a smooth obtuse flange fitting against merus when limb is withdrawn. Outer face of propodus smooth, superior face with three small granules, inner and inferior faces smooth, except that there is a small proximal tubercle on inner propodal face. Fixed finger almost straight with seven or eight almost obsolete teeth increasing in size distally; moveable finger not strongly curved, with one small proximal tooth and three teeth at tip, interlocking with opposing teeth. A narrowing band of setae extend on to outer face of moveable finger. Just below proximal teeth of fixed finger are two small pits in which several long setae are inserted. Both fingers, thick, hollowed out internally, with a small proximal gape, touching for about three-quarters their length. In hollowed out interior of each finger there are small tufts of setae which come together when fingers are closed.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out. Superior border of meri of these legs with several small granules, length of merus of second leg about 2 x width and equal to about half of CL. Anterior and posterior dorsal margins of carpi without granules, and produced distally to overhang the base of propodi. Surface of propodi smooth. Dactyli curved, inferior margin armed with 2-3 small distal spines, tip pale brown and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching to about two-thirds of meral article of preceding pereopod; borders of articles unarmed. Legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing several, small, stout, spines. Female dactyl as long as propodal extension, bearing several, small, stout, spines. Male propodal extension bearing five unequal curved spines. Male dactyl longer than propodal extension and ending in a single acute claw. Microscopic details of propodus and dactyl unknown.

All segments of abdomen freely moveable. Telson much wider than long, anterior margin essentially straight, posterior margin broadly rounded. In both sexes uropod plates are large, filling all of space between penultimate abdominal segment and telson, excluding all of last abdominal segment from reaching lateral margin of abdomen. No effective abdominal locking mechanism: abdomen only loosely held against sternum in both sexes. Sideways movement restricted by small spines (can be bifid) on coxae of second and third pereopods, adjacent to the margins of the telson and penultimate abdominal segments. In mature female abdomen occupies all of ventral surface, covering coxae of all pereopods with telson covering proximal third of third maxillipeds. In male abdomen not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial and uniramous, remainder biramous. Five pairs of pleopods in male; first pleopod a semi-rolled tube ending in a curved apical plate surrounded by long setae; second pleopod needle-like with an exopod on basis (as illustrated by TAKEDA, 1977, fig. 1A-C). Microscopic details of second pleopod unavailable. Remaining pleopods rudimentary. Third pleopod comparatively well developed, fourth and fifth pleopods smaller, all are biramous.

COLOUR. — Covered in a pale tan velvet tomentum.

GEOGRAPHIC DISTRIBUTION. — *Metadynomene devaneyi* is known from Oahu Id, Hawaii (type locality) where it was collected from precious coral (*Corallium* sp.) beds, and the Marquesas Islands (new record).

DEPTH. — The depth off southeast Oahu was 367 m, and at the Marquesas Islands 283-448 m and 341-344 m.

SIZE. — Seven specimens of *Metadynomene devaneyi* (4 males and 3 females) are known: maximum size for males is 29.0 x 27.3 mm and for females is 25.0 x 25.3 mm. An ovigerous female has been collected from the Marquesas in September. It carried approximately 2200 eggs, diameter 0.7 mm, a smaller number than comparable *M. tanensis* females.

DISCUSSION. — Some details can be added to the original description. TAKEDA (1977, fig. 1A-C) figured the first two male pleopods of *Metadynomene devaneyi* but did not show any details, especially of the second pleopods, which are only visible under high magnification. The male type specimen has three pairs rudimentary biramous pleopods. The dactyli of the walking legs are armed with two or three small distal spines. The major differences between the three species of this genus are discussed below (see Table 3) under *M. crosnieri* sp. nov.

The branchial formula of *Metadynomene devaneyi* (19 gills + 7 epipods) is very similar to *M. tanensis* except that there is no podobranch on the last pereopod. McLAY (1991, fig. 4b, as *Dynomene devaneyi*) described the structure of the gills of *M. devaneyi* showing several asymmetrical epibranchial lobes. The number of lobes is dependent upon where, along the gill, the cross section is made. The epibranchial lobes and hypobranchial plates do not always correspond exactly. Whereas the plates are clearly arranged in sequence, the lobes tend to arise independently so that in one section there may be as many as five lobes, and in another section there may be only three. Furthermore, the number of lobes decreases towards the ends of the gill. In a scanning electron microscope picture the lobes are sometimes clumped and it is difficult to see the exact relationship between the lobes and the hypobranchial plates. However, the multi-lobed gill structure is similar to that found in the species of *Hirsutodynomene* (see above). Hypobranchial setae at the back of the gill chamber are much better developed in *M. devaneyi*.

McLAY (1991) compared some features of *Metadynomene devaneyi* with those of the primitive dromiid *Sphaerodromia*, contrasting the shape of the front of the carapace, the structure of the antenna, female sternal sutures 7/8, and male pleopods - all of which are very similar. However, *M. devaneyi* has a large number of pereopodal epipods and podobranchs, the gills are multi-lobed, trichobranchiate-like, rather than phyllobranchiate. In *Sphaerodromia* the abdomen is held in place by denticulate ridges on coxae of first two walking legs against the lateral margins, while in *M. devaneyi* there is no effective abdominal locking mechanism.

The gut of a female, 18.4 x 18.3 mm, from the Marquesas Islands contained amorphous organic material and sand grains.

Metadynomene tanensis (Yokoya, 1933)

Figs 4 d, 6 c, 7 f, 9 d-e, 11, 13 c, e-f, 14 e, 25 b, 27, 28

Dynomene tanensis Yokoya, 1933: 96, text-fig. 38. — SAKAI, 1936: 45; 1940: 54 (list). — SERÈNE, 1968: 36 (list). — TAKEDA, 1977: 35 (list). — POUPIN, 1996b: 26, pl. 12f (colour photo).

Dynomene praedator - SAKAI, 1976: 30, text-fig. 17. — NAGA & TSUCHIDA, 1995: 108, pl. 1, fig. 2. Not *Dynomene praedator* A. Milne Edwards, 1879.

MATERIAL EXAMINED. — **Taiwan**. Nan-Fan-Auo Fishing Harbour, from a boat, no locality, no depth, no date, coll. J. F. HUANG : 1 ♂ 9.0 x 8.0 mm. (only colour photo seen) (NTOU).

Indonesia. DANISH EXPEDITION KEI ISLANDS: stn 12, 5°31'S, 132°35'E, 325 m, coll. T. MORTENSEN, 9.04.1922: 1 ♀ 5.5 x 5.0 mm (ZMUC).

KARUBAR: stn DW 18, 5°18'S, 133°01'E, 205-212 m, 24.10.1991: 1 ♂ 9.0 x 8.2 mm; 1 ♀ 10.9 x 10.0 mm.

New Caledonia. Dragage du *"Vauban"*: stn D 15, 22°49'S, 167°12'E, 390-395 m, 10.04.1978: 1 ♀ 6.4 x 6.0 mm. — Stn D 24, 22°48'S, 167°12'E, 355-360 m, 13.04.1978: 3 ♀ 11.2 x 10.5 - 13.4 x 12.6 mm.

BIOCAL: stn DW 50, 23°06.50'S, 167°53.74'E, 240-260 m, 31.08.1985: 1 ♀ 22.8 x 20.5 mm.

MUSORSTOM 4: stn 193, 18°56.30'S, 163°23.20'E, 415 m, 19.09.1985: 1 ♀ 15.9 x 14.6 mm. — Stn 212, 22°47.40'S, 167°10.50'E, 375-380 m, 28.09.1985: 1 ♂ 7.2 x 6.8 mm; 1 ♀ 13.0 x 12.1 mm. — Stn 213, 22°51.30'S, 167°12.00'E, 405-430 m, 28.09.1985: 1 ♂ 18.9 x 18.1 mm. — Stn 214, 22°53.80'S, 167°13.90'E, 425-440 m, 28.09.1985: 1 ♂ 13.6 x 12.6 mm; 1 ♀ 13.0 x 12.2 mm. — Stn 215, 22°57.70'S, 167°17.00'E, 485-520 m, 28.09.1985: 3 ♂ 7.2 x 7.0 - 16.9 x 16.0 mm; 4 ♀ 14.4 x 13.9 - 19.2 x 18.9 mm. — Stn 230, 22°52.50'S, 167°11.80'E, 390-420 m, 30.09.1985: 1 ♂ 22.8 x 21.6 mm; 1 ♀ 15.8 x 14.6 mm.

SMIB 2: stn DW 1, 22°52.7'S, 167°12.6'E, 438-444 m, 17.09.1986: 2 ♂ 13.5 x 12.5, 17.8 x 16.6 mm. — Stn DW 3, 22°56.0'S, 167°18.8'E, 412-428 m, 17.09.1986: 1 ♂ 13.1 x 12.3 mm. — Stn DW 5, 22°56.3'S, 167°14.4'E, 398-410 m, 17.09.1986: 2 ♀ 11.0 x 10.4, 13.1 x 12.6 mm. — Stn DW 6, 22°56.2'S, 167°15.9'E, 442-460 m, 17.09.1986: 1 ♀ 16.7 x 15.2 mm. — Stn DW 16, 22°51.2'S, 167°11.7'E, 390 m, 19.09.1986: 1 ♀ 19.6 x 17.5 mm. — Stn DW 17, 22°55.1'S, 167°14.5'E, 428-448 m, 19.09.1986: 2 ♂ 12.9 x 12.0, 18.4 x 17.5 mm; 1 ♀ 13.7 x 12.6 mm.

SMIB 3: stn DW 25, 22°56.1'S, 167°16.2'E, 437 m, 24.05.1987: 1 ♂ 16.5 x 15.8 mm. — Stn DW 27, 22°55.2'S, 167°16.2'E, 457 m, 24.05.1987: 1 ♀ ovig. 17.6 x 16.3 mm.

SMIB 4: stn DW 65, 22°55.3'S, 167°14.5'E, 420 m, 10.03.1989: 1 ♀ 15.6 x 14.4 mm.

SMIB 6: stn DW 125, 18°57.4'S, 163°23.5'E, 335-350 m, 3.03.1990: 1 ♂ 19.8 x 18.0 mm.

BERYX 11: stn CP 46, 23°42'S, 168°01'E, 300-350 m, 20.10.1992: 2 ♀ 11.2 x 10.0, 20.0 x 18.0 mm.

SMIB 8: stn DW 163, 24°49'S, 168°09'E, 310-460 m, 28.01.1993: 1 ♂ 11.9 x 11.0 mm. — Stn DW 185, 23°16'S, 168°04'E, 311-355 m, 31.01.1993: 3 ♀ 4.8 x 4.8 - 16.0 x 15.4 mm. — Stn DW 190, 23°18'S, 168°05'E, 305-310 m, 31.01.1993: 1 ♀ 16.2 x 14.8 mm. — Stn DW 193, 22°59'S, 168°19'E, 500-508 m, 1.02.1993: 1 ♂ 7.4 x 6.8 mm. — Stn DW 197, 22°51'S, 168°12'E, 414-436 m, 1.02.1993: 1 ♂ 22.1 x 21.2 mm; 4 ♀ 8.6. x 7.5 - 19.0 x 18.4 mm. — Stn DW 198, 22°52'S, 168°12'E, 414-430 m, 1.02.1993: 2 ♀ 5.0 x 4.8, 16.2 x 15.3 mm. — Stn DW 199, 22°52'S, 168°12'E, 408-410 m, 1.02.1993: 2 ♀ 11.3 x 10.6, 21.0 x 19.8 mm.

BATHUS 2: stn CP 736, 23°03'S, 166°58'E, 452-464 m, 13.05.1993: 1 ♀ ovig. 16.3 x 15.4 mm.

Bathus 3: stn CP 805, 33°41'S, 168°01'E, 278-310 m, 27.11.1993: 1 ♂ 23.7 x 21.4 mm. — Stn CP 811, 23°41'S, 168°15'E, 383-408 m, 28.11.1993: 1 ♀ 24.8 x 22.4 mm. — Stn DW 829, 23°21'S, 168°02'E, 386-390 m, 29.11.1993: 1 ♂ 17.4 x 16.1 mm. — Stn DW 830, 23°20'S, 168°01'E, 361-365 m, 29.11.1993: 1 ♂ 8.7 x 8.2 mm, 7 ♀ 4.6 x 4.5 - 17.3 x 16.3 mm.

Halical 1: stn DW 01, 18°56'S, 163°24'E, 380-400 m, 23.11.1994: 1 ♂ 12.9 x 12.0 mm. — Stn DW 04, 18°55'S, 163°24'E, 350-365 m, 26.11.1994: 1 ♀ 14.5 x 13.7 mm.

Loyalty Islands. Musorstom 6: stn DW 459, 21°01.39'S, 167°31.45'E, 420 m, 20.02.1989: 1 ♀ 16.8 x 15.4 mm. — Stn 460, 21°01.72'S, 167°31.45'E, 420 m, 20.02.1989: 1 ♂ 16.4 x 15.2 mm. — Stn 464, 21°02.30'S, 167°31.60'E, 430 m, 21.02.1989: 2 ♀ 15.5 x 14.6, 16.9 x 15.8 mm.

Chesterfield Islands. Chalcal 1: stn CP 8, 19°43.80'S, 158°35.25'E, 348 m, 19.07.1984: 1 ♀ ovig. 16.0 x 14.3 mm.

Musorstom 5: stn 361, 19°52.50'S, 158°38.10'E, 400 m, 19.10.1986: 1 ♂ 19.8 x 17.9 mm.

Vanuatu. Musorstom 8: stn DW 965, 20°20'S, 169°51'E, 361-377 m, 21.09.1994: 1 ♀ 9.0 x 8.4 mm. — Stn CP 982, 19°22'S, 169°26'E, 408-410 m, 23.09.1994: 1 ♂ 7.7 x 7.2 mm.

French Polynesia (coll. SMSRB and J. Poupin). *Tuamotu Archipelago*, Fangatafu: stn 487, 22°14.1'S, 138°47.2'W, 310 m, 25.04.1995: 1 ♂ 29.1 x 27.6 mm.

Types. — *Dynomene tanensis* Yokoya, 1933: holotype is an ovigerous female 23.5 x 22.2 mm, collected by the S.S. *"Soyo-Maru"*, from 30°06'N, 130°50'E (approximate coordinates), east of Tanegasima Id, Japan, 219 m, between 1923 and 1930. I have been unable to trace the specimen so I assume that the specimen no longer exists.

Description. — Carapace slightly wider than long, ratio of CW/CL 1.05-1.10, rectangular in outline, surface smooth, quite convex, with a few minute granules in branchial area. Carapace surface densely covered with setae of only one kind: very short, soft setae, which are minutely serrated, clothing entire surface. Pereopods covered with short setae as well as a few longer filiform setae (5 x length of short setae and 0.10 x CW) which fringe limbs. Density of short setae completely obscures body surface and on carapace they present a symmetrical undulating aspect reflecting gentle undulations in carapace surface: one oblique trough lies behind supraorbital margin, with a short median longitudinal trough extending posteriorly, then a trough curving anterolaterally which marks cervical groove, followed by a trough running across midline, just in front of cardiac area, which splits into two lateral troughs, and finally a short trough crossing cardiac area. All setae have same structure: proximal 20% of shaft smooth, followed by a region covered in long setules which increase in size distally, projecting almost at right angles to shaft, and finally an unornamented region, slightly curved and narrowing to an acute tip.

A shallow frontal carapace groove separates a pair of low rounded protuberances, and then divides into two separate, short, faint grooves on a flattened area. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately (but very close together) from small gastric pits curving (slightly sinuously) anterolaterally on to branchial region towards gap between second and third anterolateral teeth, while second, shallower groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows first groove but does not reach lateral carapace margin, while second portion curves posterolaterally, bordering anterior cardiac region, meeting a branchial groove running to base of last anterolateral tooth. Posterior cardiac area marked by a distinct groove crossing mid-line. Anterolateral carapace margin begins at level of postorbital corner, slightly convex and bears three distinct, broad-based blunt teeth. First tooth smallest and close to postorbital corner followed closely by second tooth, both directed almost anteriorly. Third tooth (largest) more distant and directed laterally. A posterolateral tooth marks beginning of convergent posterolateral border alongside which lies reduced last leg. Posterior carapace margin recessed in order to accommodate distal section of first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, minutely granulated, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, not interrupted by a notch, and without granules. Suborbital margin, convex, without teeth, projecting, shelf-like and easily visible dorsally. Orbits oblique and clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region; distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth, above the opening of antennal gland, smaller but more acute and directed ventrally. Second article wider than long, distal

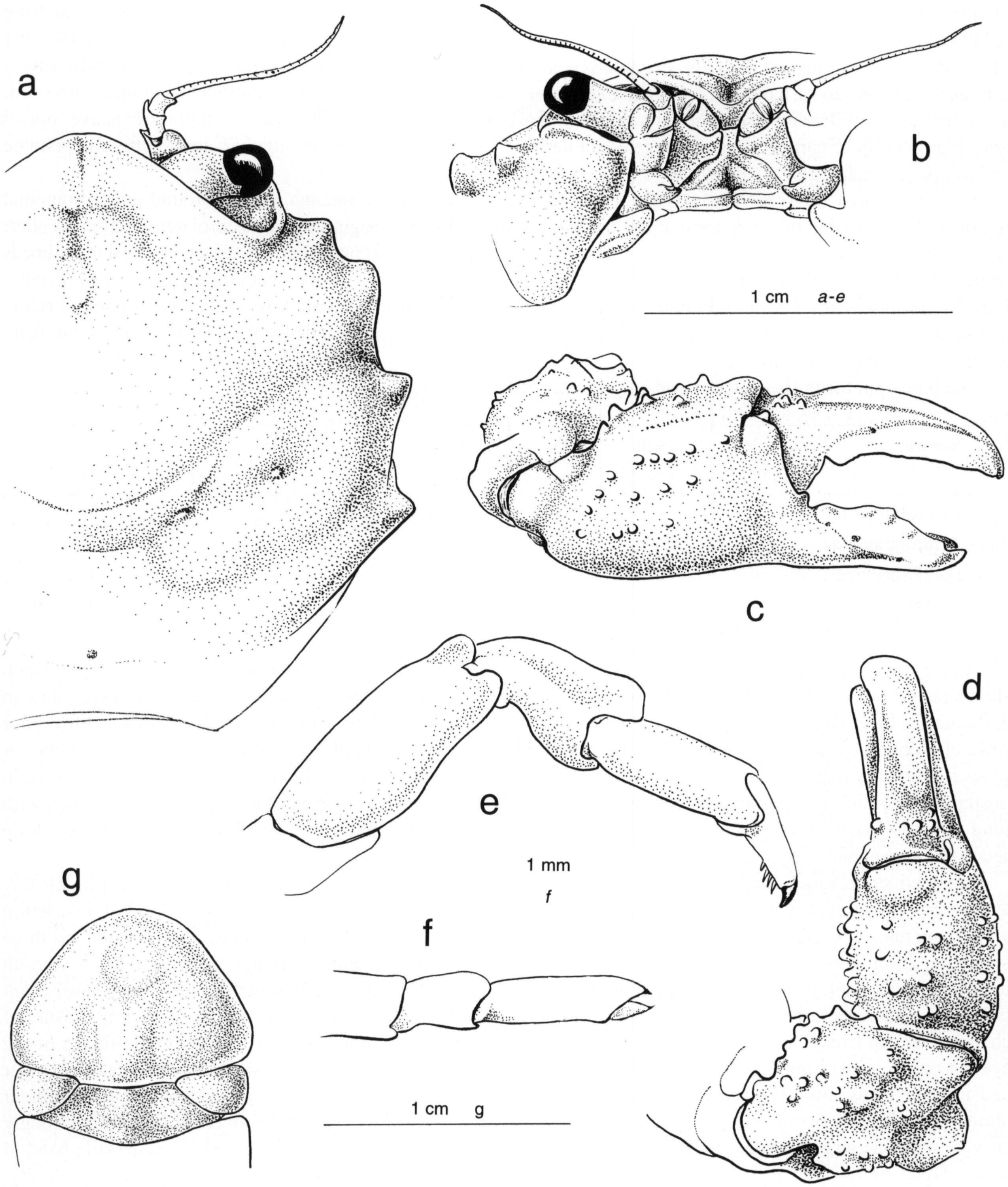

FIG. 27. — *Metadynomene tanensis* (Yokoya, 1933), ♀ 19.2 x 18.9 mm, New Caledonia, MUSORSTOM 4, stn 215, 485-520 m: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of female abdomen.

margin widest, to which is fixed the exopod curving over base of eyestalk and becoming broader and terminating bluntly. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and just matching length of exopod. Fourth antennal article smaller, as long as wide; remainder of antennal articles directed laterally, extending well beyond postorbital corner, and partially folded under supraorbital margin. Ratio of length of antennal flagella to CW = 0.33. Eyestalk can be completely folded into orbit, and cornea is well developed, occupying all of tip. Epistome broadly triangular, surface slightly concave; dorsal arm, joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace is marked by a narrow suture.

Subhepatic area smooth, very convex. A groove begins near base of antenna, curving round under branchial region and meeting lateral carapace margin just anterior to last tooth at beginning of posterolateral border. A short cervical groove branches off and ascends towards gap between first and second anterolateral teeth. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has twelve teeth increasing in size distally. Female sternal sutures 7/8 short, ending wide apart in a V-shaped groove created by a low medial parallel ridge, just behind bases of second walking legs. Sternal sutures 7/8 concealed by a dense layer of long soft setae from adjacent coxa of third walking leg.

The branchial formula is 20 gills and 7 epipodites on each side:

Somite	VII	VIII	IX	X	XI	XII	XIII	XIV
	(Mxp1)	(Mxp2)	(Mxp3)	(P1)	(P2)	(P3)	(P4)	(P5)
Pleurobranchiae	-	-	-	-	1	1	1	-
Arthrobranchiae	-		2	2	2	2	2	-
Podobranchiae	-	1	1	1	1	1	1	1
Epipods	1	1	1	1	1	1	1	-

A podobranch is definitely present on last pereopod but there is no epipod. A cross section of an arthrobranch shows lateral margin deeply notched, dividing gill into a hypobranchial plate (containing efferent vessel) and an epibranchial lobe. Between these marginal lobes are a pair of shorter lobes. Thus epibranchial surface shows four rows of blunt lobes, which are arranged above afferent blood vessel. Towards tip of the gill, length and number of lobes is gradually reduced. Second maxilla has two long setae extending into gill chamber. Hypobranchial setae in posterior region of branchial chamber are well developed. Hypobranchial margin of each podobranch armed with long setae as found on epipods to which they are attached. Posterior margin of scaphognathite bears two long setae. Hypobranchial margin of podobranchs bears same setae as on epipod.

Cheliped stout, much longer and stouter than first leg. Merus trigonal, inner face smooth and fitting closely against pterygostomial region of carapace; borders granulate, superior border has a subterminal broad, restriction which separates a thickened, smooth distal ridge, from a row of four to five small granules; inferior face has three subdistal, blunt tubercles. Outer face of carpus convex with many small granules, separated by a smooth longitudinal channel, two more prominent blunt tubercles on distal margin; inner superior border with three blunt tubercles, distal one largest which abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin is produced as a smooth obtuse flange fitting against merus when limb is withdrawn. Outer and superior faces of propodus with several small granules, inner and inferior faces smooth, except that there is a small proximal tubercle on inner propodal face. Fixed finger almost straight with seven or eight almost obsolete teeth increasing in size distally; moveable finger not strongly curved, with one large proximal tooth and four teeth at tip, interlocking with opposing teeth. A narrowing band of setae extend on to outer face of moveable finger. Both fingers, thick, hollowed out internally, gaping basally, touching for about half their length. In hollowed out interior of each finger there are prominent small tufts of long setae which come together when fingers are closed.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with several small granules, length of merus of second leg about 2.5 x width and equal to about half of CL. Anterior and posterior dorsal margins of carpi without granules, and produced distally to overhang base of propodi. Surface of propodi smooth. Dactyli curved, inferior margin armed with 3-4 small distal spines, tip dark brown and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching almost to end of meral article of preceding limb; borders of articles unarmed. Legs subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male with only weakly developed propodal extension. Female propodal extension bearing eight, unequal, stout, hooked, spines with tiny flattened teeth along most of concave inner surface, and distal area free of teeth. Female dactyl as long as propodal extension, bearing eleven unequal, stout, hooked spines (arranged asymmetrically around perimeter of the dactyl) whose concave inner surface is devoid of tiny teeth. Male propodal extension bearing five unequal curved spines without teeth. Male dactyl longer than propodal extension and ending in a single acute claw which has a tiny acute spine on its outer margin.

All segments of abdomen freely moveable. Telson much wider than long, anterior margin essentially straight, posterior margin broadly rounded. In both sexes uropod plates are large, filling all of space between penultimate abdominal segment and telson, excluding all of last abdominal segment from reaching lateral margin of abdomen. Abdominal locking mechanism consists of a small ridge or spine on coxae of first and second walking legs adjacent to uropods and penultimate abdominal segment respectively. Abdomen only loosely held against sternum in both sexes. In mature female, coxal spines absent; abdomen occupies all of ventral surface, covering coxae of all pereopods with telson covering proximal half of third maxillipeds. In male, abdomen not quite so broad and telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. (Seventeen percent of females had male first pleopods instead of the normal vestigial type. See discussion below). First male pleopod a semi-rolled tube with a small apical plate surrounded by long setae. Second pleopod with an exopod on basis, needle-like distally, armed with a series of twenty four tiny, curved, acute, inset spines and ending in two larger curved spines. Subterminal spines evenly spaced and not following a sinuous path. Third to fifth male pleopods rudimentary and biramous, both articles about same length and not separated from base by a joint.

COLOUR. — The colour picture in POUPIN (1996b) shows the whole body covered with a pale tan velvet tomentum, which is a darker brown colour on the carpi of each pereopod. Cheliped fingers may have a pink colouration.

GEOGRAPHIC DISTRIBUTION. — The type locality given by YOKOYA (1933) is "east of Tanegasima Id". The distribution of *Metadynomene tanensis* includes Japan, Taiwan, Indonesia, New Caledonia (including Loyalty Ids, and Chesterfield Ids), and Tuamotu, French Polynesia. The records for Taiwan, Indonesia, New Caledonia and Tuamotu are new.

DEPTH. — The depth range of the material examined is 205-520 m, although the majority of specimens come from 300-400 m. The lower depth limit is a little uncertain but it is at least 500 m. The type specimen, an ovigerous female approx. 23.5 x 22.2 mm, came from a depth of 219 m. *Metadynomene tanensis* is clearly a deep water western Pacific species.

SIZE. — The maximum size for males is 29.1 x 27.6 mm, for females 24.8 x 22.4 mm, and the smallest ovigerous female is 16.0 x 14.3 mm. Although sexually mature females have been recorded from almost every month, only 4 ovigerous females are known. These females were collected in May, when the eggs were newly laid or showed little development, and July, when the eggs were eyed and ready to hatch. This suggests that the breeding season of *Metadynomene tanensis* may be restricted to a short period and that females may only have a single brood of eggs each year. This may be a consequence of living at a depth where water temperatures are much lower. Only one female, 17.6 x 16.3 mm, gave a reliable egg count of 2800. The mean egg diameter is 0.62 mm, which is somewhat larger than for the shallow water dynomenids, but probably still consistent with the assumption that this species has planktotrophic larvae. The largest female with an immature sized abdomen was 11.2 x 10.5 mm, and the smallest female with a mature sized abdomen was 11.3 x 10.6 mm. Therefore females probably mature at a size within the range of 11.0-12.0 mm CW.

DISCUSSION. — This enigmatic species has been largely ignored and in the Japanese carcinological literature its status has been uncertain (see below). The only report of *Metadynomene tanensis* is the original description by YOKOYA (1933). The description is brief and his figure 38 is not entirely in agreement with the text which is as follows:

" Carapace and appendages of legs covered with short and dense hairs; and with a few long setae on the margins of the legs. Carapace subcircular, regions marked by some transverse grooves; five anterolateral teeth very shallow and obtuse. Front broad triangular, grooved in the medial line. Upper and lower margin of orbit smooth, outer angle rounded. Meri and carpi of legs irregularly tuberculated. Chelipeds subequal, stouter and longer than succeeding legs; fingers naked near the extremities, with deeply excavated extremities, inner edges dentate, gaping at the base when closed; last leg slender and shorter than one half of the preceding leg, the tip minutely chelate."

YOKOYA (1933, fig. 38) shows an ovigerous female which still has all the setae and the last pair of legs is shown as having the same orientation as the other walking legs. However this cannot be accurate because in all dynomenids the last pair of legs are always straight and lie alongside the posterolateral margins of the carapace. Most of the text could apply to any of the other species in this genus except for the details about the anterolateral teeth. Thus the interpretation of these teeth is critical to establishing the use of this name. The text states that there are five shallow and obtuse anterolateral teeth, but the figure shows only two teeth plus the posterolateral tooth. In their natural state the specimens examined here closely resemble YOKOYA's figure and they agree in having the stated number of teeth. If it is assumed that there were indeed five teeth on the type specimen, then they must have been made up as follows: the first tooth close to the orbit (shown in his figure), the second and smaller third teeth (not shown in the figure), the fourth tooth (shown), and the fifth tooth (shown) must be the posterolateral tooth. Thus the features of the present material can be reconciled with both the text and the figure. One additional feature of YOKOYA's figure, which is not mentioned in the text, is the shape of the cheliped carpal article. The outer face of this article appears deeply sculptured because of the arrangement of tubercles and apart from the differences in the anterolateral margin, this characteristic is sufficient to separate it from *M. devaneyi* in which the surface of the carpal article is much less sculptured. For these reasons it seems valid to identify the present material as being *Metadynomene tanensis* (Yokoya, 1933). The major differences between the three species of this genus are discussed below (see Table 3) under *M. crosnieri* sp. nov..

Although the two species are clearly different, there has been some confusion between *Dynomene praedator* and *Metadynomene tanensis* from Japan. SAKAI (1936) listed *Dynomene tanensis* but stated that he had not seen any specimens. Without giving any reasons, SERÈNE (1968) stated that these two species were synonyms. For *D. praedator* from Japan, SAKAI (1976) used a text-figure which showed *M. tanensis* and placed *Dynomene tanensis* Yokoya, 1933 in the list of synonyms for *Dynomene praedator*. The habitat information which he gives is almost certainly for *D. praedator*, i.e. "coral reefs, shallow waters", and the records of material examined (from Yoron Id, Taketomi Id, and the Bonin Ids) are probably for this species. There is no record from Sagami Bay (SAKAI, 1965) and it is only in 1976 that there is any evidence he had seen a specimen of *M. tanensis* (from Ishigaki Id, depth not given, 1 male approx. 15.0 x 13.5 mm) which he referred to *D. praedator*. In his list of the Japanese fauna MIYAKE (1983) also assumed that *D. tanensis* is a synonym of *D. praedator*. Thus it is important to clearly establish that these are two valid species and that both occur in Japanese waters. *D. praedator* is a shallow water species (0-50 m) while *M. tanensis* occurs in much deeper water (205-520 m).

The setae of *M. tanensis* clothe almost the entire body surface and are for the most part densely covered in long setules, giving the surface of the crab a soft velvet-like appearance. Although there are a few longer setae, all setae have the same microscopic structure. In this respect *M. tanensis* is similar to *Dynomene hispida* and *D. praedator* but the setules are longer and cover more of the shaft. Also the bare tip is relatively much shorter.

Metadynomene tanensis is the only dynomenid examined in which the branchial formula is 20 gills + 7 epipods. This species has a small podobranch on the last pereopod but this is absent in the other dynomenids. Besides the seven epipods *M. tanensis* has two long setae on the posterior margin of the scaphognathite and a well developed field of hypobranchial setae at the back of the gill chamber. These are all part of the mechanism used for gill cleaning and they are aided by the presence of long cleaning setae on the hypobranchial margin of each podobranch. These setae probably clean the bases of the adjacent gills. The structure of the gills is very similar to that of *M. devaneyi* with four epibranchial lobes associated with each gill plate.

The propodus and dactyl of the last pair of legs in females show some similarity to those found in the species of *Dynomene*: they have dentate propodal spines, and edentate dactylar spines. Similarly, the males have five edentate propodal spines, as in *D. filholi* and *D. pilumnoides*, but the dactyl is most unusual in having an acute spine on one side. This identical structure has only been observed in one other dynomenid species, *D. filholi*, although a similar spine on the dorsal margin is present in *Paradynomene tuberculata*. The structure is reminiscent of that found in some dromiids (see Discussion under *D. filholi*).

The first two pairs of male pleopods agree closely with those of *Metadynomene devaneyi* as figured by TAKEDA (1977, fig. 1a-c). Examination of the *M. tanensis* second pleopod, using the scanning electron microscope, shows that it is armed with a large number (24) of tiny curved spines. Similar large numbers of spines are found in *Hirsutodynomene ursula*, *H. spinosa*, and *Dynomene pilumnoides* although in these species the spines are not curved. As with most of the other dynomenids the last three pairs of pleopods in *M. tanensis* are biramous but there is no sign of any joint between the separate articles and the basal article.

Examination of the stomach contents of a male, 19.8 x 17.9 mm, from New Caledonia showed mostly fine sand grains, soft unidentifiable organic material as well as chopped dark brown chitinous fragments. Like most of the other dynomenids, *Metadynomene tanensis* may obtain most of its food by sieving sand, using the setae on the cheliped fingers and third maxillipeds, and perhaps some by scavenging.

OCCURRENCE OF GYNANDROMORPH FEMALES

Metadynomene tanensis was one of the more common species in the collection studied. A total of 73 specimens were examined: 25 males and 48 females. The sex ratio was 1.92 females/male, but the most interesting feature was the occurrence of females with male first pleopods. While the second to fifth biramous pleopods were developed in the normal way, these gynandromorphic females had male pleopods in place of the normally vestigial uniramous first pleopods. Seventeen percent of the females were gynandromorphs and most of them were sexually mature: the smallest was CW = 13.0 mm and the largest was CW = 19.2 mm. One female, CW = 13.7 mm, had one male pleopod and one normal vestigial pleopod. Although it was not possible to examine the internal organs, these abnormal females seemed to be normal in every other respect, having well developed genital apertures in the coxae of the third pereopods and an abdomen as well developed as in normal females. They are probably reproductively successful, although none were carrying eggs. The female pleopods on the second to fifth abdominal segments were of the normal size and structure, and there was no evidence of parasitism. The male pleopods of the gynandromorphs were only about half the size that would be expected for a male of the same size. None of the females of any of the other dynomenid species examined showed any evidence of developing male first pleopods.

Relative growth of the abdomen and chelipeds in *Metadynomene tanensis* is shown in Fig. 28 a-b. The size of normal females ranged from CW = 4.8 to CW = 24.8 mm and included three ovigerous females. Relative width of the last abdominal segment for small crabs shows no difference between females and males, but there is a sudden increase for females larger than about CW = 11.0 mm, suggesting a pubertal moult. The abdomen of males continues to grow at the same relative rate as for small crabs. The abnormal crabs do not differ in their abdomen size from mature females. With cheliped propodus length (or depth for that matter), both males and females show a similar pattern until they reach about CW = 15.0 mm when male chelipeds become relatively larger. This suggests that males may reach sexual maturity at a larger size than females. For abnormal crabs, the relative growth of both the abdomen and the chelipeds shows a pattern which conforms to that of females.

The smallest of the abnormal specimens, CW = 6.4 mm, was unusual in that the male pleopods were the longest while the remaining female pleopods (biramous) were very small. Since the genital apertures are not developed at this size, and both sexes have five pairs of pleopods, the only criterion for deciding on gender is whether the last four pairs of pleopods are biramous (female) or uniramous (male). Since the abdomen size of males and females up to about CW = 11.0 mm does not differ, it is unclear whether this specimen is a masculinized female or a feminized male. In Fig. 28 a-b this specimen is shown as an abnormal female. Another small female, CW = 8.6 mm, had uniramous vestigial first pleopods with the rest biramous but all the pleopods were very small and not properly developed. Again, the original sex of this specimen is uncertain because it is the same as the first case, except that its first pleopod did not show any male characteristics.

Assuming that the mature abnormal crabs have passed through the same stages as the two small crabs discussed above, then it is not clear whether they represent crabs which started out as males or as females. If we assume that they were originally males, then this would help to explain why the overall sex ratio is biased in favour of females. Perhaps there are some individuals in the population which have delayed sex determination, retaining the potential to become either male or female. While the rate of occurrence of abnormal crabs would be 17% if we assume that they are masculinized females, it would be 8/40 = 20% if they were feminized males and the overall sex ratio would be 1.21 females/male rather than 1.92. There is no evidence of sex change such as would be found in a sequential hermaphrodite because females reach sexual maturity at about CW = 11 mm and males at about 15 mm CW. Another hypothesis is that these abnormal crabs represent "errors in development", but 17% seems to be a very high rate of occurrence. An alternative explanation is that the development of these two small abnormal crabs has been modified by a parasite, but there was no external evidence of parasitism. Moreover, the parasite hypothesis would not account for the occurrence of the abnormal mature females.

The occurrence of gynandromorphic individuals is rare amongst Malacostraca and appears to be limited to the decapods (CHARNIAUX-COTTON, 1975). Bilateral gynandromorphs have been reported for *Metapenaeus monoceros* (GEORGE, 1963), a species of *Lucifer* (see MANNING & HOLTHUIS, 1981), *Nephrops norvegicus* (FARMER, 1972), *Homarus americanus* (CHACE & MOORE, 1959) and *H. gammarus* (GORDON, 1957), *Jasus frontalis* (reported as *Palinurus frontalis* by BURGEN, 1902) and *J. edwardsii* from New Zealand (pers. obs.), and *Cambarus propinquus* (reported as *Orconectes propinquus* by HAY, 1905). Some cases involve the presence of supernumerary genital openings e.g. *Astacus astacus* (reported as *A. fluviatilis* by BENHAM, 1891). Immature female *Procambarus clarkii* which received androgenic gland implants developed male first pleopods and, when mature, vitellogenesis was inhibited (TAKETOMI & NISHIKAWA, 1996).

Bilateral gynandromorphs have also been reported in brachyurans such as *Chionoecetes opilio* (TAYLOR, 1986), and *Callinectes sapidus* (CARGO, 1980; JOHNSON & OTTO, 1981). More complex and peculiar malformations have been found in several other brachyurans. VEILLET (1945) described an unusual *Carcinus maenas* (Portunidae) in which there were two male pleopods and a male genital aperture on the right side, while on the left side there was a male first pleopod and four female pleopods, with a female genital aperture in the thorax. FROGLIA and MANNING (1978) reported a gynandromorph specimen of the grapsid *Brachynotus gemmellari* which had male first pleopods but female second pleopods. MANNING (1993) reported a similar case of a segmental gynandromorph in the pinnotherid *Nepinnotheres androgynus* which had a wide abdomen with male pleopods and female pleopods, but lacked female gonopores. Another peculiar case was reported by GORDON (1963) for a male *Pleistacantha moseleyi* which had five pairs of pleopods: normal male first and second pleopods, except that the second carried an exopodite, followed by three pairs of semi-biramous pleopods. MANNING and HOLTHUIS (1981) found one gynandromorph specimen of *Ebalia tuberculata* Miers (Leucosiidae) which had one half of the abdomen with female characteristics while the other half had male characteristics. Sternal female gonopores were present and four normal female pleopods were found on the right hand side of the abdomen, but on the left hand side there were male pleopods on the first two segments, followed by normal female pleopods on the third to fifth segments. Evidently, female characters were dominant in this crab. ROPER (1979) found that around 1% of *Leptomithrax longipes* (Majidae) had poorly developed female gonopores, abdomens of intermediate size and varying degrees of development of male pleopods on the first abdominal segment while the third to fifth segments had normal female pleopods. He concluded that these specimens were males showing various degrees of feminization which may have been attributable to the effects of a bacterium. HARTNOLL (1960) found a specimen of *Hyas coarctatus* Leach (Majidae) which had both female and male genital openings while there was a pair of male pleopods followed by three pairs of female pleopods on the abdomen. Several morphological features were intermediate in size between typical males and females. This crab most closely approximates the hermaphroditic condition.

In the abnormal specimens of *Metadynomene tanensis* only the pleopods of the first abdominal segment were modified to the male form. Whereas in *Ebalia tuberculata* the first male pleopod was of normal size, in *M. tanensis* the pleopods were only about half the size that would be expected in a male of the same size. In both these species female characters were evidently dominant. The *E. tuberculata* specimen is a case of bilateral gynandromorphism while *B. gemmellari*, *N. androgynus* and most of the *M. tanensis* specimens, were segmental gynandromorphs, although one *M. tanensis* female had one male first pleopod as well as a typical female first pleopod. In most of the decapods mentioned above, gynandromorphism is very rare, except in the case of *Nephrops norvegicus* where up to 12% of males can be affected (RIDEWOOD, 1909). CHARNIAUX-COTTON (1975) concludes that, at least in the case of bilateral gynandromorphs, the cause of feminization is genetic in origin, resulting from the loss of the male chromosome from a blastomere at an early stage of cleavage, so that

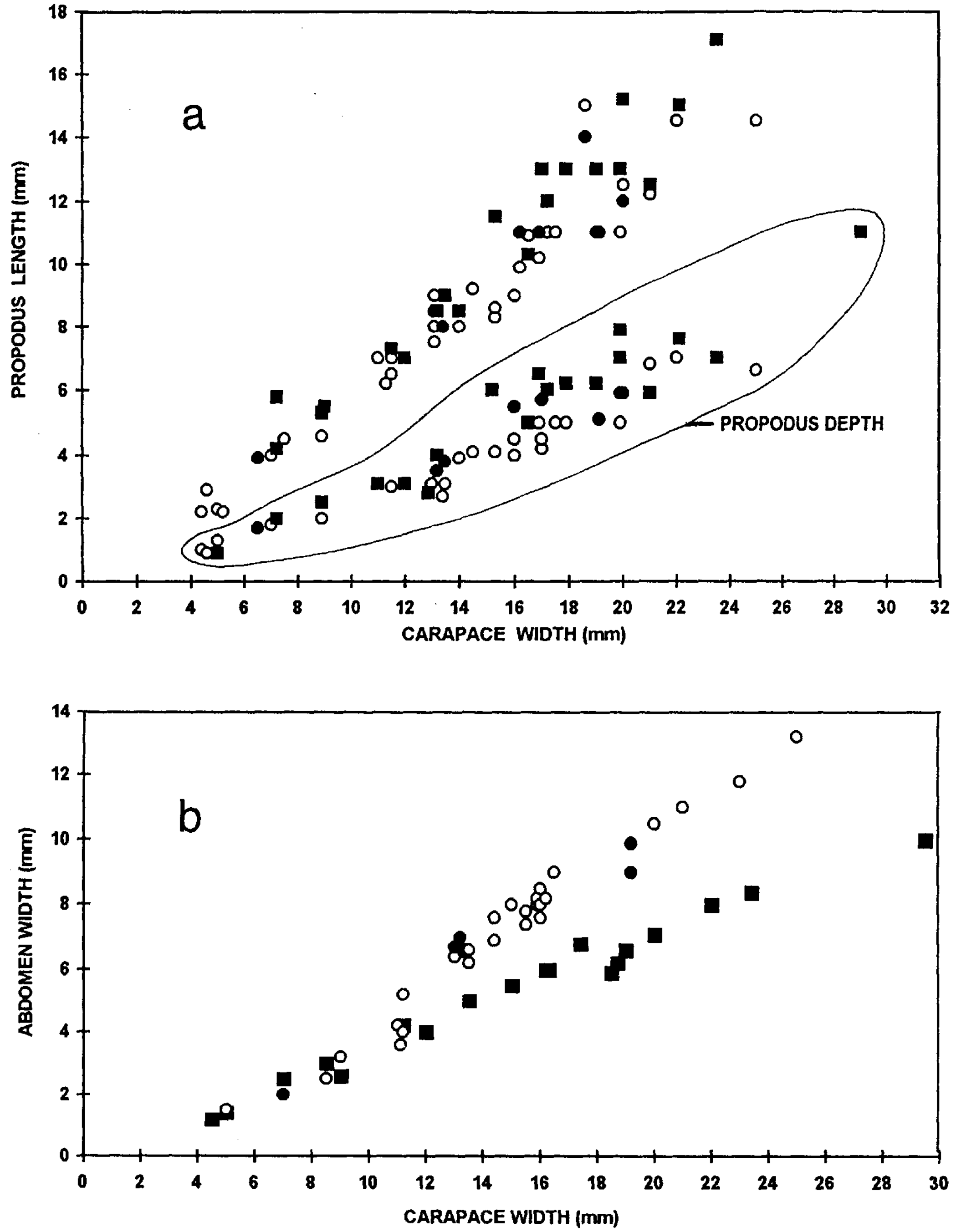

FIG. 28. — Relative growth of *Metadynomene tanensis* (Yokoya, 1933): **a**, cheliped propodus length and depth plotted against carapace width; **b**, width of penultimate abdominal segment plotted against carapace width (mm). Open circles are for males, closed circles are for females, and triangles are for gynandromorphic individuals.

one half of the animal develops as a male while the other develops as female. It seems most likely that the cause of the pleopod abnormalities in *M. tanensis* is also genetic in origin and may be environmentally induced. Given that male decapods are usually the heterogametic sex (LECHER *et al.*, 1995), it may well be that the abnormal animals are feminized males rather than masculinized females.

Metadynomene crosnieri sp. nov.

Figs 25 c, 29

Dynomene devaneyi - GUINOT, 1993: 1227 [Not Takeda, 1977].

MATERIAL EXAMINED. — **Glorieuses Islands.** BENTHEDI: 11°32.00'S, 47°16.40'E, 330-440 m, 7.06.1977: 1 ♂ 23.2 x 22.7 mm (MNHN-B 22510, originally identified as *D. devaneyi* by C. L. McLAY).

TYPES. — The holotype is a male 23.2 x 22.7 mm, collected during the BENTHEDI Expedition from 11°32.0'S, 47°16.4'E, off the Glorieuses Ids, Indian Ocean, 330-440 m, 7.06.1977, held at the Muséum national d'Histoire naturelle, Paris, registration number MNHN-B 22510.

DESCRIPTION. — Carapace about as wide as long, ratio of CW/CL = 1.02, rectangular in outline; surface smooth, quite convex, no granules. Carapace surface densely covered with setae of only one kind: very short, soft setae, which are minutely serrated, clothing entire surface. Pereopods covered with short setae as well as a few longer filiform setae (5 x length of short setae and 0.10 x CW) which occur sparsely on limbs with a tuft associated with dactyli of second to fourth pereopods. Density of short setae completely obscures body surface and on carapace they present a symmetrical undulating aspect reflecting gentle undulations in carapace surface: one oblique trough lies behind supraorbital margin, with a short median longitudinal trough extending posteriorly, then a trough curving anterolaterally which marks cervical groove, followed by a trough running across midline, just in front of cardiac area, which splits into two lateral troughs, and finally a short trough crossing cardiac area. Microscopic details of setae not investigated.

A shallow frontal carapace groove separates a pair of low rounded protuberances, and then divides into two separate, short, faint grooves on a flattened area. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately (but very close together) from small gastric pits curving (slightly sinuously) anterolaterally on to branchial region towards gap between second and third anterolateral teeth, while the second, shallower groove extends across mid-line and initially runs almost directly towards lateral margin but then splits into an anterior portion which follows the first groove for a short distance, while the second portion curves posterolaterally, bordering anterior cardiac region, meeting a branchial groove running to base of last anterolateral tooth. Posterior cardiac area marked by a distinct groove crossing mid-line. Anterolateral carapace margin begins at level of postorbital corner, slightly convex and bears three similar, very small, subacute teeth. First tooth close to postorbital corner followed closely by second tooth, both directed almost anteriorly. Third and fourth teeth, directed laterally, more distant and separated from first two by a marginal swelling above which is a small tubercle. There is also a small tubercle just above base of posterolateral tooth. On righthand side (illustrated) fourth anterolateral tooth is absent. A posterolateral tooth, behind branchial groove, marks beginning of convergent posterolateral border alongside which lies the reduced last leg. The posterior carapace margin recessed in order to accommodate distal section of first segment of abdomen which is visible dorsally.

Frontal margin continuous, V-shaped, minutely granulated, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin not projecting, continuous above orbits, not interrupted by a notch, and without granules around postorbital corner. Suborbital margin, convex, without teeth, not projecting, scarcely visible dorsally. Orbits oblique and clearly exposed dorsally. First article of antennule large, filling a large part of ventral orbital region, distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit.

First article of antenna moveable, wider than long, medially beaked; inferior tooth well developed, subacute; superior tooth, above opening of antennal gland, blunt, smaller and directed ventrally. Second article wider than

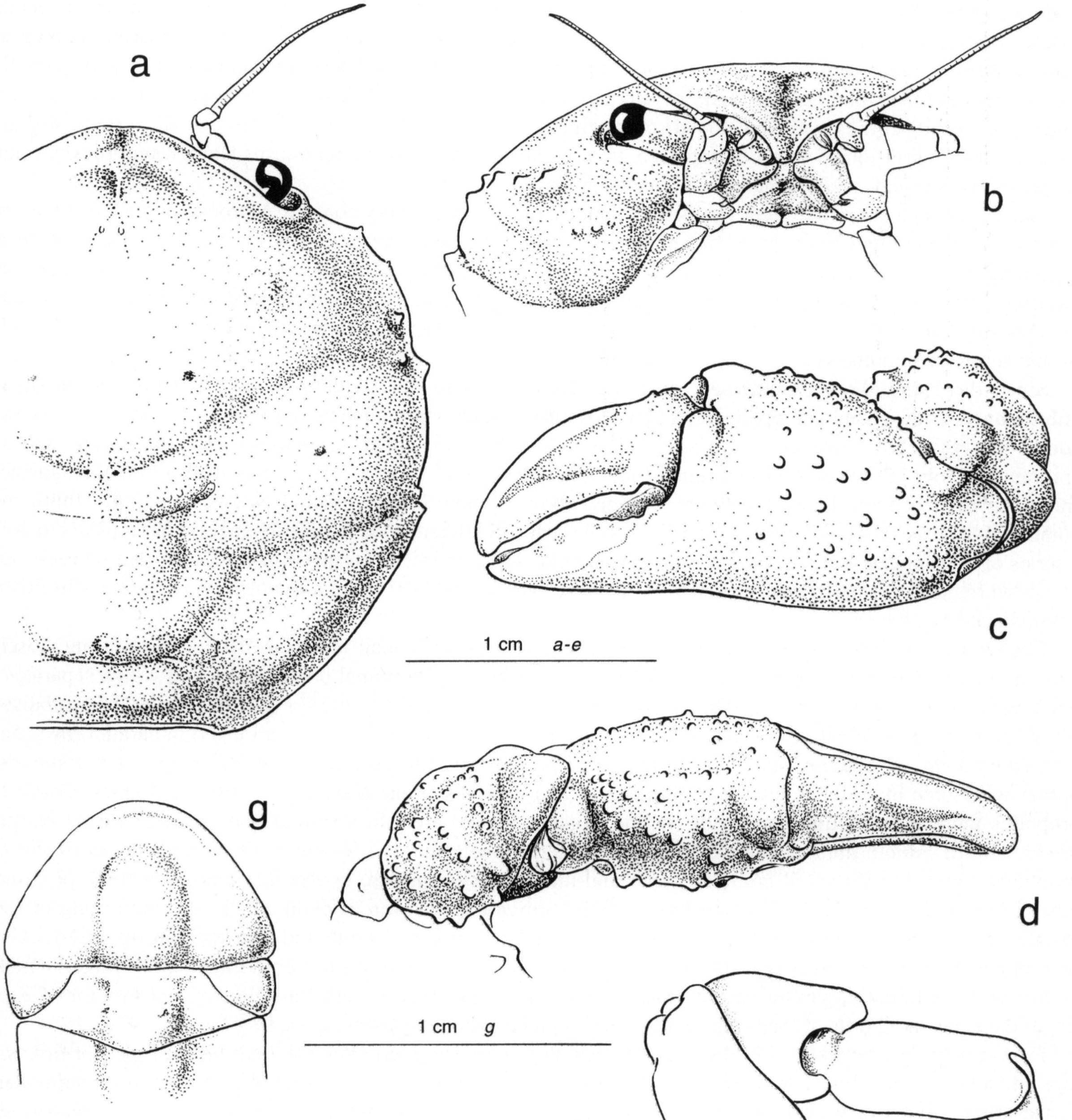

FIG. 29. — *Metadynomene crosnieri* sp. nov., ♂ 23.2 x 22.7 mm, holotype, Glorieuses Ids, BENTHEDI, 330-440 m: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of left cheliped; **d**, dorsal view of left cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of male abdomen.

long, distal margin widest, to which is fixed the exopod curving over base of eyestalk and becoming broader and terminating bluntly. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and exceeding length of exopod. Fourth antennal article smaller, as long as wide, remainder of antennal articles directed laterally, extending well beyond postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.35. Eyestalk can be completely folded into orbit; cornea well developed, occupying all of tip. Epistome broadly triangular, surface slightly concave; dorsal arm joined to tip of carapace, very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace marked by a narrow suture.

Subhepatic area smooth, except for three or four minute granules, very convex. A groove begins near base of antenna, curving round under branchial region and meeting lateral carapace margin just anterior to tooth at beginning of posterolateral border. A short cervical groove branches off and ascends towards base of marginal swelling between first and second pairs of anterolateral teeth. Third maxillipeds operculiform, bases widely separated by tip of sternum. Crista dentata has thirteen well developed teeth increasing in size distally. Female sternal sutures 7/8 unknown.

Since there is only one specimen, branchial formula could not be determined but examination of an arthrobranch from second pereopod shows that gills differ slightly from preceding species: a cross section shows lateral margin deeply notched, dividing gill into a hypobranchial plate (containing efferent vessel) and an epibranchial lobe. Between these marginal lobes are two pairs of shorter lobes. Thus the epibranchial surface shows six rows of blunt lobes, which are arranged above afferent blood vessel. Towards tip of gill, length and number of lobes is gradually reduced. There are well separated afferent and efferent channels in basal plate but with a series of six elongate lobes developed on outer margin. These lobes are arranged into a longer pair on each side of gill with another, smaller pair medially. At base of outer lobes there is a small notch on each side, but this is not produced as a lobe.

Cheliped stout, much longer and stouter than first leg. Merus trigonal; inner face smooth and fitting closely against pterygostomial region of carapace; superior border has a subterminal broad, restriction which separates a thickened, smooth distal ridge, from a row of five to six small granules; inferior face has three blunt subdistal tubercles. Outer face of carpus convex with many small granules, which tend to be arranged in parallel rows, and divided by a smooth longitudinal channel, two more prominent blunt tubercles on distal margin; inner superior border with three blunt tubercles, all of similar size and most distal one abuts against proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin produced as a smooth obtuse flange fitting against merus when limb is withdrawn. Outer and superior faces of propodus with scattered small granules; inner and inferior faces smooth, except that there is a small proximal tubercle on inner propodal face. Fixed finger almost straight with seven or eight small teeth increasing in size distally; moveable finger not strongly curved, with one large proximal tooth and four teeth at tip, interlocking with opposing teeth. A narrowing band of setae extend on to outer face of moveable finger. Both fingers, thick, hollowed out internally, gaping basally, touching for about half their length. In hollowed out interior of each finger there are small tufts of long setae which come together when fingers are closed.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus smooth and nacreous, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with several small granules, length of merus of second leg about 2.6 x width and equal to about half of CL. Anterior and posterior dorsal margins of carpi without granules, and produced distally to overhang the base of propodi. Surface of propodi smooth. Dactyli curved, inferior margin armed with four small distal spines, tip brown and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace, reaching about halfway to end of meral article of preceding pereopod; borders of articles unarmed. Male propodal extension bearing five unequal curved spines. Male dactyl longer than propodal extension and ending in a single acute claw. Microscopic details of dactyl and propodal spines unknown. Female unknown.

All segments of abdomen freely moveable. Telson much wider than long, anterior margin essentially straight; posterior margin broadly rounded. Uropod plates large, filling all of space between penultimate abdominal segment and telson, excluding all of last abdominal segment from reaching lateral margin of abdomen. No effective abdominal locking mechanism: small bifid tubercle on coxa of first walking leg beside uropods restricts sideways movement. Abdomen only loosely held against sternum. Telson only extends as far as bases of third maxillipeds.

Five pairs of pleopods in male; first pleopod a semi-rolled tube ending in a curved apical plate surrounded by long setae; second pleopod needle-like with an exopod on basis, remaining pleopods rudimentary and biramous. Microscopic details unavailable. Female unknown.

ETYMOLOGY. — This new species is named after Alain CROSNIER in recognition of his enormous contribution to the study of decapod crustaceans.

COLOUR. — Whole body covered with a pale tan velvet tomentum.

GEOGRAPHIC DISTRIBUTION. — *Metadynomene crosnieri* is known only from the type locality near the Glorieuses Ids, south of the Seychelle Ids, Indian Ocean.

DEPTH. — The depth of the type locality is between 330 and 440 m.

SIZE. — Only the male type specimen is known, 23.2 x 22.7 mm.

DISCUSSION. — At a casual glance the three species in this genus are extraordinarily similar: they are relatively large dynomenids and all have a short, soft, undulating tomentum. Indeed the specimen of *M. crosnieri* was originally mis-identified as *M. devaneyi*. Of the external differences between the species (see Table 3) the most important are those of the anterolateral carapace margin and the prominence of the suborbital margin. *M. devaneyi* is distinctive in not having any anterolateral teeth while *M. crosnieri* has four small subacute teeth. The anterolateral teeth in *M. tanensis* are somewhat variable but there are usually at least three well developed teeth. In all cases it is necessary to carefully remove the tomentum to expose the anterolateral margin.

TABLE 3. — Comparison of the *Metadynomene* species.

	M. devaneyi	*M. tanensis*	*M. crosnieri*
Carapace surface	No granules	A few minute granules in branchial area	No granules
Carapace grooves	Well marked	Only faintly marked	Well marked
Anterolateral teeth	None: only a faint notch marking cervical groove	Three well developed teeth, second tooth can have two smaller teeth close by	Four small subacute teeth
Posterolateral tooth	None	Strong tooth	Weak tooth
Suborbital margin	Projecting and visible dorsally	Projecting and visible dorsally	Not projecting and not visible dorsally
Cheliped propodus	Outer face smooth, superior face with three small granules	Outer and superior faces with several small granules	Outer and superior faces with several small granules
Cheliped carpus outer face	Smooth except for two prominent blunt tubercles	Many small granules and three blunt unequal tubercles	Many small granules, arranged in rows, and two prominent blunt tubercles
Gills	Five dorsal lobes	Three dorsal lobes	Six dorsal lobes

There are some minor differences between the gills of the three species of *Metadynomene*. *M. crosnieri* has the largest number of epibranchial lobes (six) while the other two species have four. Thus in all species the epibranchial portion of the gills is trichobranchiate-like, while the hypobranchial portion is more phyllobranchiate-like. In *M. devaneyi* and *M. tanensis* the hypobranchial cleaning setae are well developed. In *M. tanensis* there is a podobranch on the last pereopod, but this gill is absent in *M. devaneyi.*

GUINOT (1993, as *Dynomene devaneyi*) described the abdominal locking structures of *Metadynomene crosnieri* and the rudimentary third male pleopod. The male abdomen is only loosely retained by small bifid teeth on the coxae of the second pereopods. The rudimentary third to fifth male pleopods are biramous as in the other two species of this genus.

The species of *Metadynomene* show a remarkable resemblance to the dromiid *Dromia wilsoni* (Fulton & Grant, 1902). The short undulating tomentum gives a superficial similarity, but inspection of the last two pairs of legs reveals that these dynomenids are very different. Material sorted by a non-specialist often has these species mixed together. Since all these species live in deeper water, these features may be convergent.

None of the species of *Metadynomene* have overlapping distributions: *M. crosnieri* is known from the Indian Ocean, *M. tanensis* from the western Pacific and *M. devaneyi* from much further east at Hawaii. Given their high degree of similarity it may be that these species are of quite recent origin.

Genus ***ACANTHODROMIA*** A. Milne Edwards, 1880

Acanthodromia A. Milne Edwards, 1880: 31. — BOUVIER, 1896: 56. — ALCOCK, 1899: 134; 1901: 36. — ORTMANN, 1899: 1155. — A. MILNE EDWARDS & BOUVIER, 1902: 22. — RATHBUN, 1937: 55.

DIAGNOSIS. — Carapace longer than wide, convex, ovoid; surface bristling with long spines. Lateral carapace margin poorly defined, without distinct teeth but bearing numerous spines. Carapace grooves not well marked, but lateral cardiac and branchial grooves faintly evident. Frontal carapace margin broadly triangular, spinous; eyestalks short; eyes protected by well defined orbits. Sternal sutures 7/8 of female end well apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside orbit at base of eyestalk. Antennal flagella shorter than carapace width. All articles of antenna moveable, first article (urinal) not beaked medially and second article has an exopod firmly fixed. Third maxillipeds opercular, completely covering buccal cavern, separated at their bases by a plate at same level as sternum; basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata absent. Chelipeds equal, stouter than walking legs; last pair of legs very reduced; dactyl rudimentary, forming an obsolete subchelate mechanism with an extension of propodus. Gills usually 19 (including 6 podobranchs) + 7 epipods. Gill structure basically phyllobranchiate.

Abdomen of six segments and telson folded loosely under thorax, uropods large. Abdominal locking mechanism present, using well developed coxal projections. Surface of abdominal segments spinous, except for fourth segment which bears one or more large, pearl-like, medial tubercles. Females have five pairs of pleopods, first pair vestigial, remainder biramous and of normal size. Male pleopods unknown.

TYPE SPECIES. — *Acanthodromia erinacea* A. Milne Edwards, 1880, by monotypy. Gender is feminine.

OTHER SPECIES. — *Dynomene margarita* Alcock, 1899.

DISCUSSION. — The original definition of *Acanthodromia* by A. MILNE EDWARDS (1880) included reference to the shape of the carapace (narrow and ovoid) and its fronto-orbital region, third maxillipeds, walking legs, and the rudimentary and cheliform last legs. A. MILNE EDWARDS placed this genus in his family "Dromiens", between *Dromia* and *Dynomene*, along with other dromiids and the homolodromiid genus *Dicranodromia* A. Milne Edwards, 1880. Later A. MILNE EDWARDS and BOUVIER (1902) separated these into three sub-families, retaining *Dynomene* and *Acanthodromia* in the Dynominae. They noted that *Acanthodromia* represented a curious mixture of primitive (e.g. carapace longer than wide) and "secondary" (e.g. non filamentous gills) characters which distinguished it from *Dynomene*. To these can be added the absence of a beaked first antennal article and a crista dentata. The main reason for including *Acanthodromia* in the Dynomenidae is the structure of the reduced last pair of legs. To include it any where else would require the assumption that these limbs had evolved more than once.

WRIGHT and COLLINS (1972: 24) have suggested that the genus *Acanthodromia* should be included in the fossil family Prosopidae Von Meyer, 1860, sub-family Pithonothinae Glaessner, 1933, thus making it the only genus of this family to survive to recent times. They considered that "*Acanthodromia* appears to be no more than a spinose *Plagiophthalmus* Bell, 1863 in which the main furrows are obsolescent." However this seems ill-advised because, although the carapace of *Acanthodromia* is longer than wide, it lacks a distinct carapace margin which is a feature of *Plagiophthalmus*. Thus the indication by BRIGGS *et al* (1993) that the Prosopidae have a fossil record extending from the mid Jurassic to the present day is incorrect.

Acanthodromia erinacea A. Milne Edwards, 1880

Figs 6 d, 9 f, 10 a, 30

Acanthodromia erinacea A. Milne Edwards, 1880: 31. — BOUVIER, 1896: 56, figs 18-21. — YOUNG, 1900: 336. — ALCOCK, 1901: 75 (list). — A. MILNE EDWARDS & BOUVIER, 1902: 23, text-figs 7-8, pl. 3, figs 5-15, pl. 4, figs 1-4. — IHLE, 1913: 92 (list). — RATHBUN, 1937: 55, pl. 12, figs 5-6. — RICE, 1981: 174.

MATERIAL EXAMINED. — **Guadeloupe**. *"Blake"*: stn 166, 275 m, coll. A. AGASSIZ, 21.01.1878: 1 ♀ ovig. 16.7 x 17.7 mm, holotype (MCZ 6509).

Mexico. *Yucatan*. *"Albatross"*: stn 2354, Arrowsmith Bank, 238 m, 22.01.1885: 1 ♀ 9.5 x 11.5 mm. (USNM 9547).

TYPES. — The holotype is an ovigerous female 16.7 x 17.7 mm, collected by A. AGASSIZ from *"Blake"* stn 166, 15°55.50'N, 61°37.05'W, Leeward Ids, off Guadeloupe, 275 m, 21.01.1878, held at the Museum of Comparative Zoology, Harvard University, registration number MCZ 6509. A paratype specimen, consisting of only a carapace, was collected from *"Blake"* stn 232, 13°6.45'N, 61°6.55'W, Windward Ids, off St. Vincent, 158 m, 21.02.1879, registration number MCZ 2641.

DESCRIPTION. — Carapace longer than wide, ratio of CW/CL = 0.90-0.94, ovoid in outline, surface evenly convex, with a dense cover of acute spines and spinules with occasional long setae. Microscopic details of setae not investigated. Density of spines completely obscures body surface. Frontal, cervical, and post-cervical grooves not evident, crescentic lateral cardiac grooves and branchial groove faint, posterior cardiac area not defined. Anterolateral carapace margin poorly defined, begins below level of postorbital corner, subparallel and adorned with longer spines but these are not arranged in a well-defined row. Posterolateral border convergent alongside which lies the reduced last leg. Posterior carapace margin recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin V-shaped, spinous, ventrally-directed, joined to epistome (which separates orbits). Supraorbital margin projecting, continuous above orbits, eave-like, not interrupted by a notch, adorned with long spines which become smaller near postorbital corner and curved posteriorly. Suborbital margin concave adorned by long spines with a larger spine at inner corner. Cornea of eye and suborbital margin clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region; prominent spine mid-way along length; distal margin spinous, obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, bearing a row of three or four spines, not medially beaked, opening of antennal gland is on medial margin and concealed against base of antennule. Second article spinous, longer than wide; medial margin longest produced as a spine, to which third article is fixed. Exopod short, spinous, blunt extending behind third antennal article and curving over base of eyestalk. Third and fourth antennal articles as wide as long, lying over distal end of exopod and continued as a flagellum which is 0.6 x CW. Eyestalk can be completely folded into orbit (where it is well protected by marginal spines), outer surface spinous; cornea light brown, well developed, occupying all of tip. Epistome triangular, surface slightly concave; dorsal arm joined to tip of carapace, margins bearing spines; lateral arms shorter. Joint between epistome and carapace marked by a narrow suture.

Subhepatic area inflated, covered with tubercles. A groove (pleural suture or linea dromica) begins near base of the antenna, curving round under branchial region and towards anterolateral carapace margin about mid-way along its length. A short groove branches off, ascending and curving towards postorbital corner marking posterior margin of inflated subhepatic area. Third maxillipeds operculiform, bases separated by tip of sternum, without crista dentata; coxae armed with prominent medial projections under which telson fits when at rest. Female sternal sutures 7/8 short, ending wide apart under an overhanging lip immediately below female gonopores.

Branchial formula according to A. MILNE EDWARDS and BOUVIER (1902: 24) is 19 gills + 7 epipods (see Discussion below). In cross section gills consist of pairs plates, one on each side of gill axis, with epibranchial tips of each plate ending in a blunt thickened lobe. Lateral margins of each plate faintly notched about mid-way along their length.

Cheliped stouter and longer than first leg. Merus trigonal, inner face roughened with rounded tubercles and fitting closely against pterygostomial region of carapace; borders spinous, superior border has a faint subterminal restriction which separates a thickened distal ridge, on which there are several spines, from a row of five or six similar spines on superior border. Outer face of carpus convex with small blunt tubercles interspersed among longer, sharper spines; inner superior border lacks a flattened, distomedially directed, spur restricting closure of cheliped. Instead, both superior and inferior inner margins of carpus are spinous like outer face. Entire surface of propodus covered with spines which are longer on superior and outer faces. Outer surface of fingers covered with tubercles and small spines. Dactyl strongly downcurved, margin sinuous but not interrupted by teeth except at tip where there are two blunt teeth, roof of finger strongly concave. Fixed finger almost straight with three evenly spaced, blunt teeth on outer margin, three further teeth on tip (interlocking with pair of teeth on dactyl), inner margin without teeth and floor strongly concave. Small groups of long stiff setae, inserted near base of dactyl and fixed finger, are directed across space between the two fingers. Spoon-shaped fingers gape proximally on internal face but there is only a small gape externally.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus covered with low rounded tubercles; inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with numerous long spines, length of merus of second leg about 1.5 x width and equal to about one third of CL. Dorsal margins of carpi bearing several long spines, and produced distally to overhang base of propodi. Propodi bearing numerous long spines. Dactyli curved, bearing numerous shorter spines; inferior margin armed with five small spines similar to tip which is dark brown and subacute.

Last pair of legs greatly reduced, lying along posterolateral border of carapace above bases of walking legs, reaching to about half-way along meral article of preceding limb; borders of articles spinous; basis-ischium and merus fused. In female last pair of legs subchelate with well developed distal extension of propodus which opposes dactyl. Propodal extension bearing seven, unequal, stout, hooked, spines facing laterally, with marginal rows of 6-10 tiny flattened teeth proximally on concave inner surface, and distal area free of teeth. These marginal teeth are curved inwards, without meeting the opposite row, and directed distomedially. Female dactyl as long as propodal extension, bearing eight unequal, stout, hooked spines (arranged asymmetrically around perimeter of dactyl) whose inner surface is edentate. Male unknown.

All segments of abdomen freely moveable, length and breadth of all segments similar, surface spinous, with occasional setae, margins unarmed. First segment partially concealed under posterior border of carapace, visible portion fits into recess and articulates with carapace margin; anterior margin of second segment sinuous; medial region convex and inserted under margin of preceding segment; lateral margins produced as a flange which fits over posterior margin of first segment thereby preventing forward slippage of abdomen. Subsequent segments articulated in a similar manner. Anterior half of fourth segment with two small pearl-like medial tubercles almost totally united except for a narrow proximal fissure. Rest of medial region behind these two rounded tubercles bears several spines. Fifth abdominal segment has a pair of similar but smaller tubercles, separated by a fissure which extends posteriorly on to sixth segment, between the tubercles. Telson spinous, much wider than long; anterior margin angled to accommodate uropod; posterior margin broadly rounded. In female uropod plates are large, filling about half of the space between last abdominal segment and telson, excluding much of last abdominal segment from reaching lateral margin of abdomen. Male characters unknown. Abdominal locking mechanism well developed: when at rest, abdomen of mature female lies between bordering flanges on first three pereopods with telson beneath coxal projections of third maxillipeds.

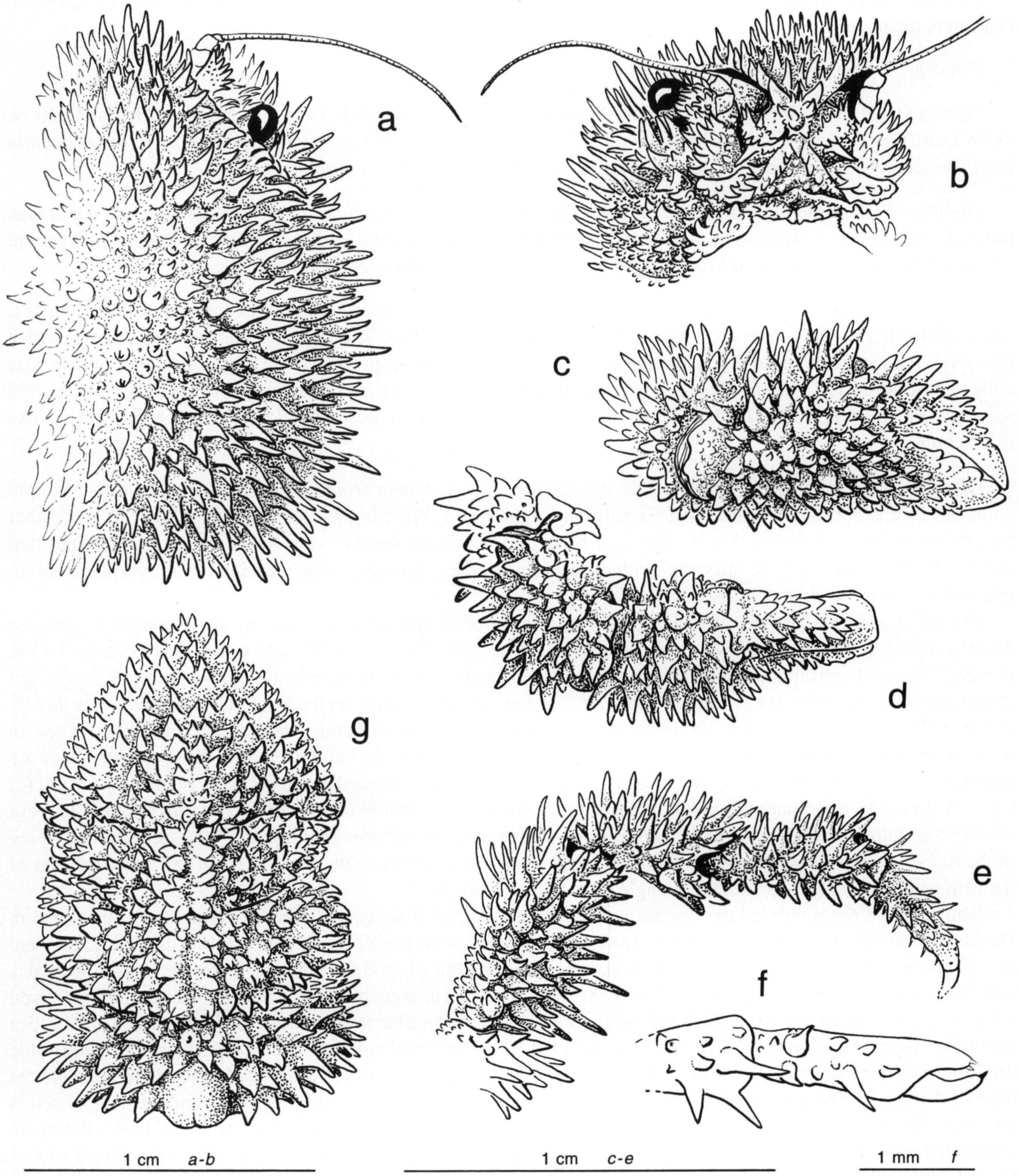

FIG. 30. — *Acanthodromia erinacea* A. Milne Edwards, 1880, ♀ ovig. 16.7 x 17.7 mm, holotype, Guadeloupe, *"Blake"*, stn 166, 275 m (MCZ 6509): **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of female abdomen (uropods concealed by strong spinulation).

Five pairs of pleopods in female, first pair vestigial and not carrying eggs, remainder biramous. Male pleopod characters unknown.

COLOUR. — Pale cream when preserved.

GEOGRAPHIC DISTRIBUTION. — Along the chain of Caribbean islands from the Arrowsmith Bank (20°N, 86°W), off the Yucatan coast of Mexico, to St. Vincent (13°N, 61°W) in the Windward Ids. *Acanthodromia erinacea* seems to be an insular species like the other Atlantic dynomenid, *Dynomene filholi.*

DEPTH. — The depth range for this species is 158-540 m. *Acanthodromia erinacea* lives at a greater depth than most of the species of *Dynomene*. The only information about its habitat comes from the specimen collected at 158 m off St. Vincent, Windward Ids where the substrate is described as "coral bottom".

SIZE. — Only three females of *Acanthodromia erinacea* are known as well as a carapace of unknown sex. These collection records have been summarized by RATHBUN (1937). The largest female (the holotype), which was ovigerous, measured 16.7 x 17.7 mm and carried about 100 eggs of 0.5 mm diameter. This female was collected in January, 1878 and the eggs were newly laid. The egg size is similar to that of the other dynomenid species. RICE (1981) examined eggs from a female collected in February 1933 which were very close to hatching.

DISCUSSION. — RICE (1981) described the pre-zoea of *Acanthodromia erinacea* dissected from the eggs of a crab collected by the Johnson-Smithsonian Expedition off Mona Id, West Indies. Although the material was rather unsatisfactory, he concluded that the larva of this species is most similar to those of the Dromiidae and that anomuran characteristics are strongly evident in both families. This pre-zoea remains the only known larval material of any of the dynomenids.

The most accurate and detailed description of the reduced last pereopods of any dynomenid is given for *Acanthodromia erinacea* by A. MILNE EDWARDS and BOUVIER (1896, pl. 3, fig. 12) where they describe for the female "...la pince parfaite qui termine ces appendices est munie de soies spiniformes sur le bord des doigts, qui sont deux fois plus courts que la région palmaire". The presence of spines on the propodus and dactyl has largely escaped the attention of other dynomenid researchers. The number and arrangement of these spines in *Acanthodromia erinacea* is similar to that found in the other dynomenids, but the teeth on the propodal spines are unusual in being curved inwards. The number of these teeth is very reduced compared to *Dynomene hispida*, for e.g., but similar to the situation found in *Paradynomene tuberculata* and *Hirsutodynomene ursula* females. In these species the teeth are only found on the margins and are restricted to the proximal region of the spines. The last leg of the *A. erinacea* male is unknown. In both *P. tuberculata* and *A. erinacea* the basis-ischium and merus articles of the fifth pereopods are fused to make a single bent or curved article.

BOUVIER (1896) compared the chelate nature of the last legs of *Acanthodromia erinacea* with that found in *Dicranodromia ovata* A. Milne Edwards, 1880 and *Homolodromia paradoxa* A. Milne Edwards, 1880. He noted that in the sequence *D. ovata* - *H. paradoxa* - *A. erinacea* the propodus becomes more developed so that a subchelate limb becomes a "..pince parfaitement caracterisée". He argued that *A. erinacea* was probably derived from a very primitive form in which the last pair of legs were similar to that found in *H. paradoxa.* This idea about the origin of dynomenids may well be correct but BOUVIER could not have known that there are considerable differences in the fine structure of the limbs between dynomenids and homolodromiids. His intuitive idea ignores the fact that the propodal and dactyl spines of *A. erinacea* are constructed on a different plan, and the dactyl itself is also very different from that found in any brachyuran crab: at least in females, it is more like a blunt, flattened, articulated plate, with the spines arranged around the margins, rather than an articulated claw with a single row of medial spines. Considerable evolutionary change is required to transform a camouflage-carrying homolodromiid limb into what may have been some kind of cleaning appendage.

The branchial formula of *Acanthodromia erinacea* is summarized in the table at the top of the next page.

The branchial formula given by A. MILNE EDWARDS and BOUVIER (1902) for this species is 19 gills + 7 epipods. However there seem to some errors in this interpretation. Firstly, they omitted the podobranch of the second maxilliped and secondly, they indicated that the third maxilliped had two arthrobranchs. It seems likely that

Somite	VII (Mxp1)	VIII (Mxp2)	IX (Mxp3)	X (P1)	XI (P2)	XII (P3)	XIII (P4)	XIV (P5)
Pleurobranchiae	-	-	-	-	1	1	1	-
Arthrobranchiae	-	1	1	2	2	2	2	-
Podobranchiae	-	1	1	1	1	1	1	-
Epipods	1	1	1	1	1	1	1	-

the correct number is only one arthrobranch, as found in all other dynomenids which have been examined. Thus the total number of gills is still 19, but for different reasons. The gill structure of *A. erinacea* is very different from other dynomenid species: there are no epibranchial lobes and the gills consist of paired plates surrounding the gill axis. A. MILNE EDWARDS and BOUVIER (1902, pl. 4, fig 4) show a small epibranchial projection between these plates, but I could not find this. The anterior and posterior margins of each plate are slightly notched. The gill structure of *A. erinacea* most closely resembles that found in *Dynomene hispida* and *D. praedator*. The gill structure of *Acanthodromia margarita* is virtually identical. A. MILNE EDWARDS and BOUVIER (1902, pl. 3, fig 7) show three long setae on the posterior margin of the scaphognathite. This number of setae is only found in *Dynomene filholi* and *D. pilumnoides*. All the other dynomenid species only have two such setae.

The mature female *Acanthodromia erinacea* has spinous coxal projections on the third maxillipeds and the first three pereopods which appear to help hold the abdomen in place. In order to release the abdomen, it would be necessary for these pereopods to move posteriorly. In other dynomenids, neither males nor females, have any really effective abdominal locking mechanism, and the abdomen is only held loosely against the sternum. In immature dromiids both sexes have an abdominal locking mechanism, usually involving pereopodal coxae and the uropods, which only persists in mature males. Therefore *A. erinacea* is unusual in having a locking mechanism in mature females. Unfortunately the male of this species is unknown but presumably it also has a similar mechanism.

For two species inhabiting widely separated regions (Indo-West Pacific and Caribbean Sea), *Acanthodromia margarita* and *A. erinacea* are extraordinarily similar: the only differences are in the shape of the supraorbital spines, and the pearl-like lobes on the fourth and fifth abdominal segments. A likely scenario for the origins of these two species might be as follows: species of *Acanthodromia* originated in the Tethys Sea and spread to seas that eventually became the Atlantic and Caribbean, perhaps as early as the Upper Jurassic (145 mybp). This dispersal could have been as late as the Middle Miocene (25 mybp), when connections between these two oceans was severed, but an earlier date seems more likely because even by Palaeocene times (65 mybp) the Atlantic was already well formed and the Caribbean isolated. Therefore these two species could have been separated at least since the Palaeocene (or at latest the Middle Miocene), but there has scarcely been any divergence in their morphology. Both are deeper water species although *A. erinacea* extends to a greater depth (540 m). They grow to a similar maximum size and inhabit muddy coral bottoms. *A. erinacea* appears to be a relict Tethyan species.

Acanthodromia margarita (Alcock, 1899)

Fig. 31

Dynomene margarita Alcock, 1899: 19, pl. 2, fig 3.
Acanthodromia margarita - ALCOCK, 1900: 134; 1901: 36, pl. 1, fig. 3, 3a. — IHLE, 1913: 92 (list). — SAKAI, 1965b: 43; 1976: 31, pl. 7, fig 2. — SERÈNE, 1968: 37 (list). — MIYAKE, 1983: 196 (list). — NAGAI, 1989: 43.

MATERIAL EXAMINED. — **Japan**. Wakayama, 120 m, 1989, S. NAGAI coll.: 1 ♀ 12.0 X 13.0 mm (see NAGAI, 1989).

TYPES. — *Dynomene margarita* Alcock, 1899: holotype is a male 4.5 x 5.0 mm, collected by the *"Investigator"*, from 13°16.00'N, 93°08.00'E, Andaman Sea, 135 m, held by the Indian Museum, Calcutta, registration number 2690/10.

DESCRIPTION. — Carapace longer than wide, ratio of CW/CL = 0.92, ovoid in outline; surface evenly convex, with a dense cover of acute spines and spinules with occasional long setae. Microscopic details of setae not investigated. Density of spines completely obscures body surface. Frontal, cervical, and post-cervical grooves not evident, crescentic lateral cardiac grooves and branchial groove faint, posterior cardiac area not defined. Anterolateral carapace margin poorly defined, begins below level of postorbital corner, subparallel and adorned with longer spines but these are not arranged in a well-defined row. Posterolateral border convergent alongside which lies the reduced last leg. Posterior carapace margin recessed in order to accommodate first segment of abdomen which is visible dorsally.

Frontal margin V-shaped, spinous, ventrally-directed, joined to epistome. Supraorbital margin projecting, continuous above orbits, eave-like, not interrupted by a notch, adorned with long spines which become smaller and blunter near postorbital corner and are not curved posteriorly. Suborbital margin concave, adorned by small spines with a larger spine at inner corner. Cornea of eye and suborbital margin clearly exposed dorsally.

First article of antennule large, filling a large part of ventral orbital region, prominent spine mid-way along length; distal margin spinous, obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. First article of antenna moveable, wider than long, bearing a row of spines, not medially beaked, opening of antennal gland is on medial margin and concealed against base of antennule. Second article spinous, longer than wide, medial margin longest produced as a spine, to which is fixed the third article. Exopod short, spinous, blunt extending behind third antennal article and curving over base of eyestalk. Remaining antennal articles absent from specimen. Eyestalk can be completely folded into orbit, outer surface spinous; cornea light brown, well developed, occupying all of tip. Epistome triangular, surface slightly concave; dorsal arm joined to tip of carapace margins bearing spines; lateral arms shorter. Joint between epistome and carapace marked by a narrow suture.

Subhepatic area inflated, covered with tubercles. A groove (pleural suture or linea dromica) begins near base of antenna, curving round under branchial region and on to carapace to meet faint branchial groove. A short groove branches off, ascending and curving towards postorbital corner marking posterior margin of inflated subhepatic area. Third maxillipeds operculiform, bases widely separated by tip of sternum. Female sternal sutures 7/8 short, ending wide apart under an overhanging lip immediately below female gonopores.

Branchial formula unknown. In cross section gills consist of pairs plates, one on each side of the gill axis, with epibranchial tips of each plate ending in a blunt thickened lobe. Lateral margins of each plate are faintly notched about mid-way along their length.

Cheliped stouter and longer than first leg. Merus trigonal, inner face roughened with rounded tubercles and fitting closely against pterygostomial region of carapace; borders spinous, superior border has a faint subterminal restriction which separates a thickened distal ridge, on which there are several spines, from a row of five or six similar spines on the superior border. Outer face of carpus convex with small blunt tubercles interspersed among longer, sharper spines; inner superior border lacks a flattened, distomedially directed, spur restricting closure of cheliped. Instead, both superior and inferior inner margins are spinous like the outer face. Entire surface of propodus covered with spines which are longer on superior and outer faces. Outer surface of fingers covered with small spines. Dactyl strongly downcurved, margin sinuous but not interrupted by teeth except at tip where there are two blunt teeth, roof of finger strongly concave. Fixed finger almost straight with three evenly spaced blunt teeth on the outer margin, three further teeth on tip (interlocking with pair of teeth on dactyl), inner margin without teeth and floor strongly concave. Small groups of long stiff setae, inserted near base of dactyl and fixed finger, are directed across the space between the two fingers. Spoon-shaped fingers gape proximally on internal face but there is no gape externally.

First three pairs of walking legs decreasing in length posteriorly. Meri elongate, both faces of meri of first two legs and anterior face third leg merus covered with low rounded tubercles, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of second to fourth pereopods with numerous long spines, length of merus of third pereopod about 2.0 x width and equal to about one quarter of CL. Dorsal margins of carpi bearing several long spines, and produced distally to overhang base of propodi. Propodi bearing numerous long spines. Dactyli curved, bearing numerous shorter spines; inferior margin armed with four small spines similar to tip which is dark brown and subacute.

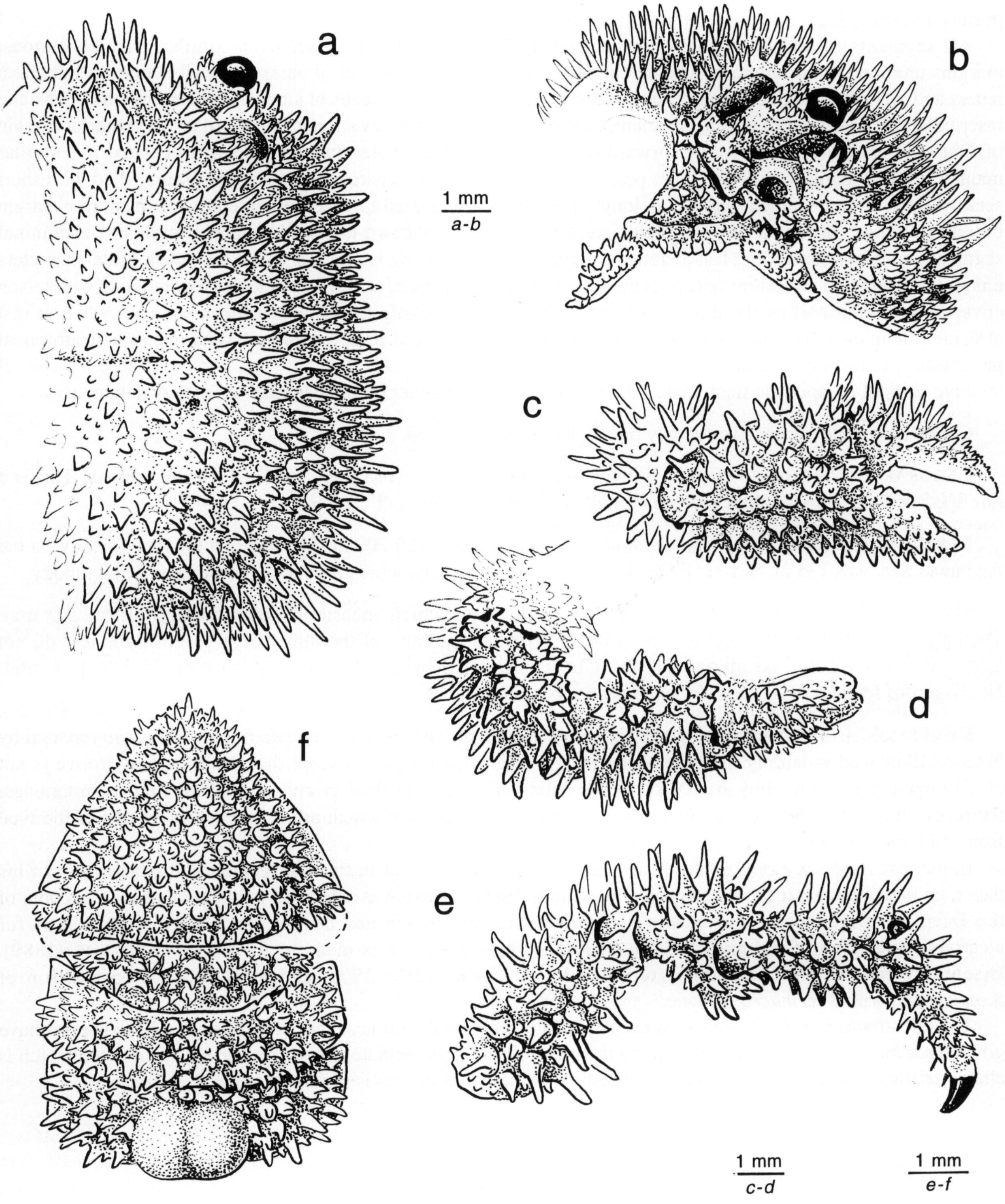

FIG. 31. — *Acanthodromia margarita* (Alcock, 1899): **a-f**, ♀ 12.0 x 13.0 mm, Wakayama, Japan, 120 m: **a**, dorsal view of right half of carapace; **b**, ventral view of left orbital area (note that most of antenna is missing) ; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, ventral view of telson and terminal segments of female abdomen (note that uropod plates are missing).

Last pair of legs greatly reduced; articles spinous, lying along posterolateral carapace border above bases of posterior walking legs. Structural details of subchelate mechanism not available.

All segments of abdomen freely moveable, length and breadth of all segments similar, surface spinous, margins unarmed. First segment partially concealed under posterior border of carapace, visible portion fits into a recess and articulates with carapace margin, anterior margin of second segment sinuous, medial region convex and inserted under margin of preceding segment, lateral margins produced as a flange which fits over posterior margin of first segment thereby preventing forward slippage of abdomen. Subsequent segments articulated in a similar manner. Fourth segment with two large pearl-like medial tubercles separated by a narrow fissure filled with short setae. Telson spinous, much wider than long; anterior margin angled to accommodate uropod; posterior margin broadly rounded. In female uropod plates are large, filling about two-thirds of space between last abdominal segment and telson, excluding last abdominal segment from reaching lateral margin of abdomen. Male characters unknown. Abdomen of mature female occupies all of ventral surface, covering coxae of all pereopods with telson covering proximal half of the third maxillipeds. Abdominal locking mechanism well developed: when at rest abdomen of mature female lies between bordering flanges on first three pereopods with telson beneath coxal projections of third maxillipeds.

Five pairs of pleopods in the female, first pair vestigial, remainder biramous. Male characters unknown.

COLOUR. — Pale cream. Eyes deeply pigmented when preserved.

GEOGRAPHIC DISTRIBUTION. — Andaman Sea, Indian Ocean, Tosa Bay, and Kii Peninsula, Japan. This is a rare species: there are only three records of *Acanthodromia margarita* (1 ♂, 2 ♀).

DEPTH. — The depth range for *Acanthodromia margarita* is 120-200 m. The depth at the type locality, in the Andaman Sea, was 135 m. SAKAI (1976) describes the bottom from which his specimen came as being muddy.

SIZE. — The only male specimen known is the type which measured approximately 4.5 x 5.0 mm. The largest female has been reported by SAKAI (1976) but the ratio of the dimensions given in the text do not agree with his figure: assuming that the CL is correct, then the dimensions must be 15.5 x 17.0 mm. No ovigerous females of *Acanthodromia margarita* are known.

DISCUSSION. — The description given above is based on the specimen of *Acanthodromia margarita* reported by NAGAI (1989) and is largely in agreement with the original description except that the branchial groove is not clearly evident as claimed by ALCOCK (1899). Admittedly the branchial groove is difficult to discern amongst the forest of spines. There are no features of the Japanese specimen which are different from those of the type from the Indian Ocean.

In the text ALCOCK (1899) placed this species in *Dynomene*, but in the Corrigenda, at the beginning of his paper, he indicated that it should be placed in *Acanthodromia*. There was a delay in publication of the "Account of the Deep-Sea Brachyura..."and meanwhile the generic designation had been corrected in his "Materials for a carcinological fauna of India" (ALCOCK, 1900) where reference is made to A. MILNE EDWARDS (1880). Essentially the same description is repeated by ALCOCK (1899, 1900, and 1901) but no comparison of *A. margarita* with *A. erinacea* is made.

The gill structure of *Acanthodromia margarita* is essentially the same as that of *A. erinacea*. Both species have gills which lack epibranchial lobes, making them almost phyllobranchiate, except for the marginal notch which is characteristic of dynomenid gills. The relationships of these two species is discussed under *A. erinacea*.

Genus ***PARADYNOMENE*** Sakai, 1963

Paradynomene Sakai, 1963: 230; 1965a: 13. — GUINOT, 1993: 1226.

DIAGNOSIS. — Carapace subquadrangular in shape, slightly longer than wide; surface convex, granulate, well areolated; individual areolae each having one or two low conical tubercles. Lateral carapace margins well defined, subparallel and armed with irregular teeth. Narrow frontal groove split in two posteriorly; cervical, postcervical grooves evident. Frontal carapace margin well produced anteriorly, cut into three teeth; median tooth small; lateral teeth broad and cristate; eyestalks short; eyes protected by well defined orbits. Sternal sutures 7/8 of female end well apart on low tubercles behind bases of second walking legs.

Antennule can be concealed inside orbit at base of eyestalk. Antennal flagella shorter than half of carapace width. All articles of antenna moveable; first article (urinal) beaked medially and second article has an exopod firmly fixed. Third maxillipeds opercular, completely covering buccal cavern, separated at their bases by a plate at the same level as the sternum; basis and ischium of endopod fused but joint always marked by a shallow groove. Crista dentata present. Chelipeds robust, equal, stouter than walking legs. Last pair of legs very reduced; dactyl rudimentary, forming an obsolete chelate mechanism with an extension of propodus only in female. Branchial formula 19 gills + 7 epipods.

Abdomen of six segments and telson folded loosely under thorax; uropods comparatively small; effective abdominal locking mechanism absent. Both sexes have five pairs of pleopods, first pair vestigial in female, last three pairs rudimentary in male. First pair of male pleopods consist of a stout, setose semi-rolled tube with an apical plate; second pair needle-like bearing a linear row of tiny inset spines along anterior surface (modified from SAKAI, 1963).

TYPE SPECIES. — *Paradynomene tuberculata* Sakai, 1963 by original designation and monotypy.

DISCUSSION. — *Paradynomene* Sakai, 1963, collected from Sagami Bay, Japan, was the third extant genus of dynomenids to be discovered. As with *Acanthodromia*, this genus is radically different from the type genus of the family (*Dynomene*). While both have a carapace which is longer than wide, in *Paradynomene* the carapace is subquadrangular with tuberculate areolae and in *Acanthodromia* it is ovoid and densely covered with spines. However, all three genera share the distinctive characters associated with the last pereopods. The characters of the second male pleopod are also similar to those found in *Metadynomene* and *Dynomene*. It is intriguing to make the same kind of comparison between members of the Dromiidae: the genus *Epigodromia* McLay, 1993 is to *Dromia* or *Cryptodromia*, what *Paradynomene* is to *Dynomene*. *Epigodromia* has a highly areolate carapace and obsolete last two pairs of legs, while *Dromia* and *Cryptodromia* have a smooth setose carapace and functional last two pairs of legs. Perhaps this tendency to evolve a thickened, ornamented carapace has occurred independently in the two families (see Discussion below). Also SAKAI (1963) noted that the general features of the front, thoracic appendages and the external maxillipeds of *Paradynomene* resemble those of the family Dromiidae, rather than those of *Dynomene* or *Acanthodromia*.

GUINOT (1993) suggested that there are certain resemblances between *Paradynomene* and the fossil genera *Rathbunopon* Stenzel, 1945 and *Mithracites* Gould, 1859. The similarities relate to the ornamentation of the carapace.

Paradynomene tuberculata Sakai, 1963

Figs 4 e-f, 6 e-f, 7 c, e, 10 b-d, 14 a, 25 d, 32

Paradynomene tuberculata Sakai, 1963: 231, fig. 8; 1965a: 13, pl. 6, fig. 1; 1976: 31, pl. 7, fig. 1. — SERÈNE, 1968: 37 (list). — MIYAKE, 1983: 196 (list). — NAGAI, 1989: 43. — GUINOT, 1993: 1227, figs 1-2.

MATERIAL EXAMINED. — **Gulf of Aden.** *"Meteor"*: stn Mc 5/230-KD2, 12°43.5'N, 43°14.8'E, 214-277 m, 5.03.1987: 1 ♂ 7.8 x 8.6 mm (SMF).

Indonesia. KARUBAR: stn DW 18, Kai Ids, 5°18'S, 133°01'E, 205-212 m, 24.10.1991: 1 ♀ ovig. 13.8 x 14.5 mm. — Stn DW 49, Tanimbar Ids, 8°00'S, 132°59'E, 210-206 m, 29.10.1991: 1 ♂ 11.2 x 12.5 mm.

Chesterfield Islands. CORAIL 2: stn DW 159, 19°46.04'S, 158°19.98'E, 52 m, 1.09.1988: 1 ♀ 18.5 x 18.3 mm.

New Caledonia. LAGON: stn 444, 18°15.3'S, 162°58.8'E, 300-350 m, 28.02.1985: 1 ♂ 17.0 x 17.2 mm.

SMIB 3: stn DW 14, 23°40.1'S, 167°59.7'E, 246 m, 22.05.1987: 1 ♂ 22.0 x 22.8 mm.

SMIB 4: stn DW 44, 24°46.0'S, 168°8.2'E, 300 m, 8.03.1989: 1 ♂ 17.0 x 17.8 mm.

SMIB 8: stn DW 184, 23°18'S, 168°05'E, 305-320 m, 31.01.1993: 1 ♂ 19.2 x 19.0 mm. — Stn DW 189, 23°18'S, 168°05'E, 400-402 m, 31.01.1993: 2 ♂ 12.2 x 13.1, 21.0 x 21.9 mm.

BATHUS 3: stn DW 830, 23°19'S, 168°01'E, 361-365 m, 23.11.1993: 1 ♂ 14.7 x 15.8 mm.

BATHUS 4: stn DW 931, 18°55'S, 163°24'E, 360-377 m, 7.08.1994: 1 ♂ 23.7 x 23.0 mm.

HALICAL 1: stn DW 02, 18°54'S, 163°24'E, 352-397 m, 23.11.1994: 1 ♀ 23.2 x 24.0 mm.

Loyalty Islands. MUSORSTOM 6: DW 406, 20°40.65'S, 167°06.80'E, 373 m, 15.02.1989: 1 ♂ 21.5 x 22.3 mm; 1 ♀ 21.5 x 21.2 mm; 1 ♀ ovig. 20.6 x 21.4 mm.

Guam (H. T. CONLEY coll.). Piti Lagoon, 13°27'N, 144°47'E, 1.2-7.5 m deep in dead coral, 26.05.1994: 1 ♂ 21.7 x 20.0 mm (UGM). — *Ibidem*, 4-8 m, among dead coral, 5.06.1994: 1 ♂ 17.2 x 16.4 mm (UGM). — *Ibidem*, 1.5-5 m, in coral rubble, 12.05.1997: 1 ♀ ovig. 20.5 x 19.4 mm (UGM).

TYPES. — The holotype is a male 9.5 x 10.5 mm, collected by His Majesty the Emperor of Japan, from 35°08.00'N, 139°37.00'E, west of Jogashima Misaki, Sagami Bay, Japan, 85 m, deposited in His Majesty's Museum at the Imperial Palace.

DESCRIPTION. — Carapace sparsely setose, longer than wide, ratio of CW/CL approx. 0.95, oblong in outline; posterior margin truncate; surface convex, areolate and granulate. There are about eighteen to nineteen swellings each marked by a subacute tubercle carrying three or four long (0.11 x CW), stiff serrate setae, and whole surface is covered in evenly distributed, rounded granules. Largest tubercles on inner branchial area. Pereopods also carry a few stiff setae, and abdomen margins and bases of third maxillipeds are densely covered with long, soft serrate setae. General body surface thickly covered with short setae, although these are only evident under high magnification. Structure of short and long setae are different. In short setae the proximal 40% of shaft is erect and lacks ornamentation, then the setae bend at about 45° and bear two opposite rows of fine setules decreasing in size distally. These setae are feather-like, lack an acute smooth tip, and are especially common in areas between carapace swellings. In long setae the proximal 50% of shaft is covered with small setules, then next 45% bears longer setules, projecting at right angles, increasing distally in size and finally last 5% is smooth, narrowing to an acute tip. Distal 50% of each setae curved, forming a U-shape, so that tip of setae is directed towards body.

A narrow frontal carapace groove separates a pair of small tubercles behind frontal margin, and then divides into separate grooves which terminate beside a similar median tubercle. Just in front of cardiac region two laterally-directed grooves originate: first groove (cervical) arises separately (but close together) from small gastric pits and runs directly anterolateral just in front of the largest tubercles on to branchial region. Second, shallower groove extends across mid-line and joins two deep, longitudinal pits bordering anterior cardiac region. Cardiac area is defined by grooves and adorned by two large tubercles. Branchial groove not evident. A row of four large tubercles curve across posterior region of carapace. Anterolateral carapace margin begins below level of postorbital corner, is slightly convex and bears six rather irregular, laterally directed, subacute teeth or tubercles. First, fourth and sixth teeth largest, and about equidistant, while second, third and fifth are mere tubercles in between. Posterolateral margin bears two teeth which are much larger than any of preceding anterolateral teeth. Posterior carapace margin is recessed in order to accommodate first segment of abdomen part of which is visible dorsally.

Frontal margin projecting, tridentate, ventrally-directed, joined to epistome (which separates orbits). Median tooth on a lower level, lateral teeth lie above on beginning of the orbital margin. Supraorbital margin has two small tubercles followed by a small notch closer to postorbital corner, which is granulated; suborbital margin with similar granules followed by a subacute tooth (visible dorsally) and then notched before inner corner. Orbits obliquely arranged, clearly exposed dorsally.

First article of antennule large, granulated, filling a large part of ventral orbital region; distal margin obliquely angled and not continuous with distal margin of second antennal article. Remainder of antennule folded into orbit. Antennal articles granulated; first article moveable, wider than long, medially beaked; inferior tooth well developed, blunt; superior tooth above opening of antennal gland is much smaller. Second article wider than long; distal margin widest, to which exopod is fixed, curving over base of eyestalk and becoming broader and terminating bluntly. Third antennal article longer than wide, and attached to remaining distal border of second article, slotting in behind exopod, and along with fourth article just surpassing length of exopod. Fourth antennal article smaller, as long as wide; remaining antennal articles directed laterally, extending well beyond postorbital corner, and can be partially folded under supra-orbital margin. Ratio of length of antennal flagella to CW = 0.35. Eyestalk can be completely folded into orbit, and cornea is well developed, occupying all of tip. Epistome broadly triangular, surface granulate and concave; dorsal arm, joined to tip of carapace, is very elongate and narrow; lateral arms shorter and thicker. Joint between epistome and carapace is marked by a faint suture.

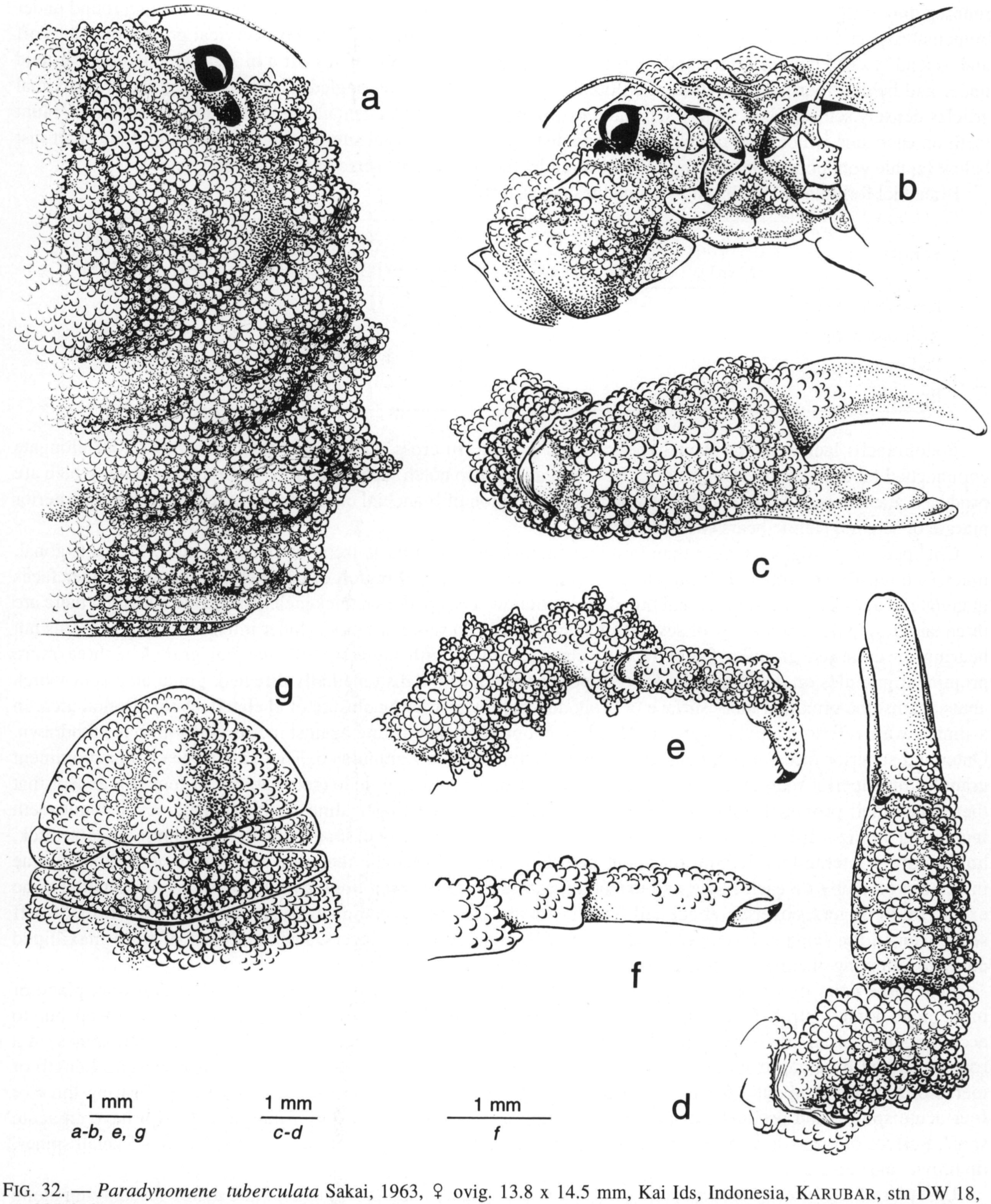

FIG. 32. — *Paradynomene tuberculata* Sakai, 1963, ♀ ovig. 13.8 x 14.5 mm, Kai Ids, Indonesia, KARUBAR, stn DW 18, 205-212 m: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view of terminal articles of right fourth pereopod; **f**, posterior view of terminal articles of right fifth pereopod; **g**, ventral view of telson and terminal segments of female abdomen.

Subhepatic area granulate, very inflated to an acute angle which is adorned with two or three larger granules running diagonally down from first anterolateral tooth. A groove begins near base of antenna, curving round under branchial region and meeting lateral carapace margin just behind fifth tooth. A short cervical groove branches off and ascends to gap between third and fourth anterolateral teeth and also gives off a branch which curves around under and behind fourth tooth. Third maxillipeds operculiform, sharply angled, distal articles granular, proximal articles densely setose, bases widely separated by tip of sternum. Crista dentata has twelve or thirteen small, blunt teeth on each side which tend to increase in size distally. Female sternal sutures 7/8 short, ending wide apart just below female gonopore, almost completely covered by the coxa and its setae of third walking legs.

Branchial formula is 19 gills and 7 epipodites on each side:

Somite	VII (Mxp1)	VIII (Mxp2)	IX (Mxp3)	X (P1)	XI (P2)	XII (P3)	XIII (P4)	XIV (P5)
Pleurobranchiae	-	-	-	-	1	1	1	-
Arthrobranchiae	-	-	2	2	2	2	2	-
Podobranchiae	-	1	1	1	1	1	1	-
Epipods	1	1	1	1	1	1	1	-

Podobranchs lack setae on their hypobranchial margin. In cross section, gill structure shows four elongate epibranchial lobes radiating from the afferent vessel and a deep notch separating off hypobranchial plates which are produced at corners. Hypobranchial setae in posterior region of branchial chamber very well developed. Posterior margin of scaphognathite bears two long setae.

Cheliped stout, slightly longer than first leg; anterior border of basis-ischium densely setose. Merus trigonal, inner face mostly smooth and fitting closely against pterygostomial region of carapace; borders and other faces granulate; outer face has a subterminal broad, restriction which separates a thickened distal ridge on which there are three larger granules from a row of several smaller granules on superior border. Inner inferior margin of merus not bearing an enlarged granule. Outer face of carpus convex with many small, unequal granules, three more prominent granules on distal margin; inner superior border with a distomedially directed, granulated spur which abuts against the proximal inner surface of propodus thereby restricting closure of cheliped against frontal area. In a similar way, inferior carpal margin produced as an obtuse, flange fitting against merus when limb is withdrawn. Outer and superior faces of propodus and base of dactylus densely granulated. There are three or four prominent granules on superior margin, inner face smooth and densely setose in male (setae absent in female), except that there is a small proximal granule on inner propodal face. Fixed finger almost straight with seven blunt teeth increasing in size distally; moveable finger not strongly curved, two small apical teeth, both fingers thick, hollowed out internally, touching for about half their length. In female there are small tufts of long stiff setae inserted proximally on each finger and extending across space between fingers. In male long soft propodal setae extend on to fingers, covering about half length of both fixed finger and dactyl, and embedding the tufts of stiff setae seen in the female. Externally these setae fill angle between fingers. Proximal half of third maxilliped concave, allowing chelipeds to fold tightly away beneath them.

First three pairs of walking legs decreasing in length posteriorly, articles granular. Meri elongate, plane of movement dorsoventral, faces of meri of first three legs granulate, inferior distal margin hollowed out to accommodate carpal article. Superior border of meri of these legs with four to six prominent, blunt spines, in a row, separated by a gap from two similar distal spines, and three or four spines on posterior margin. Length of merus of second leg about 1.6 x its width and equal to about 0.4 x CL. Dorsal surface of carpi bearing three or four acute spines, and produced distally to overhang base of propodi. Posterior margins of carpi have an acute spine. Surface of propodi with several similar spines. Dactyli curved, inferior margin armed with 4-5 small spines, tip brown and subacute.

Last pair of legs greatly reduced; surface granular but not spinous; basis-ischium and merus fused, lying along posterolateral border of carapace, reaching only as far as half-way along meral article of preceding limb. Subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male without a propodal extension. Female propodal extension bearing 14-16, unequal, stout, hooked, spines with a ridged, concave inner surface and marginal rows of 7-12 tiny flattened teeth proximally. These teeth are directed laterally. Female dactyl as long as propodal extension, bearing 15-16 unequal, stout, hooked spines (arranged asymmetrically around perimeter of dactyl) whose concave inner surface is devoid of tiny teeth. Distal margin of male propodus not produced (as illustrated by GUINOT, 1993, fig. 1), but bearing five unequal curved spines without teeth. Male dactyl largely withdrawn into propodus and ending in a single acute claw which has a tiny subterminal spine on its dorsal margin.

All segments of abdomen freely moveable; surface granular except for central area of telson which is smooth: margins unarmed but fringed with short setae. Medial area of abdomen convex and clearly marked. First segment divided into two parts: first part hidden, narrower and longer inserted under posterior margin of carapace; second part, bearing four tubercles, wider and shorter with its anterior margin abutting against posterior carapace margin preventing forward slippage of abdomen. Second segment narrowest, anterior margin sinuous, medial region convex, lateral margins produced as a flange which fits over posterior margin of first segment; third segment wider; both segments have a lateral tubercle on each side. Subsequent segments gradually increasing in length and breadth distally, not overlapping with preceding segments. Telson much wider than long, anterior margin slightly angled to accommodate uropod, posterior margin broadly rounded. A row of granules follows entire border of telson, surrounding central smooth area. In both male and female uropod plates comparatively small, filling about half of space between last abdominal segment and telson, so that part of last abdominal segment reaches lateral margin of abdomen. No effective abdominal locking mechanism: abdomen only loosely held against sternum in both sexes. Margins of the abdomen are neatly surrounded by many coxal granules which restrict sideways movement. In mature female abdomen occupies all of ventral surface, covering coxae of all pereopods with telson reaching to base of third maxillipeds. In male, abdomen not quite so broad and again, telson only extends as far as base of third maxillipeds.

Five pairs of pleopods in female, first pair vestigial, remainder biramous. First male pleopod a semi-rolled tube with a small apical plate surrounded by long setae. Second male pleopod with an exopod on basis, needle-like distally, armed with a series of fourteen tiny, straight, acute, inset spines and ending in two very short straight spines. Subterminal spines evenly spaced. Third to fifth male pleopods rudimentary and biramous, exopod articulated.

COLOUR. — Pale brown. Tips of dactyli black.

GEOGRAPHIC DISTRIBUTION. — *Paradynomene tuberculata* was previously known from Japan and New Caledonia (including the Chesterfield Ids, Loyalty Ids, Ride de Norfolk). The material examined includes specimens from Guam, Mariana Ids, Indonesia and the Gulf of Aden and these provide a large extension of the range of this species.

DEPTH. — The depth range of the material examined in this study was 1.5-402 m with most of the specimens coming from greater depths than previously reported. The depth at the type locality was 85 m and SAKAI (1976) gives a depth range of 35-85 m for his Japanese material. Their habitat includes dead coral and rocky bottoms. The specimens of *Paradynomene tuberculata* from Guam were collected from very shallow depths: only 1.5 - 8 m.

SIZE. — The maximum size for males is 22.0 x 22.8 mm and for females 20.6 x 21.4 mm. Only three ovigerous females have been collected: a female 13.8 x 14.5 mm carried 400 eggs, another female 20.5 x 19.4 mm carried 840 eggs, while the female 20.6 x 21.4 mm was damaged with most of the abdomen and brood missing. The mean egg diameter was 0.5 mm which is similar to the other dynomenids and indicates the existence of a planktotrophic stage. Two females, carrying newly laid eggs, were collected during October and February and one female was collected in May carrying eggs almost ready to hatch.

DISCUSSION. — The description of *Paradynomene tuberculata* given here differs somewhat from that of SAKAI (1963). In the original description SAKAI stated that the lateral carapace borders are armed with six principal teeth, of which the third is somewhat dorsal in position and the last located on the posterolateral border, with several additional small teeth between the principal teeth. It is debatable whether the third tooth mentioned above should be regarded as being marginal or not. In my description I have not treated it as being part of the anterolateral margin and I have treated the last two teeth as being on the posterolateral border because the carapace margin begins to curve inwards posteriorly. Exact enumeration of the anterolateral teeth is made difficult by the fact that there are a variable number of small teeth/tubercles following the first lacinated tooth. SAKAI also stated that the dactyli of second to fourth pereopods are unarmed, but 4-5 very small spines are present.

As found in all the other genera of the Dynomenidae, there are two sizes of setae and as in most species (except for *Dynomene hispida* and *D. praedator*) there are morphological differences between the two types of setae in *Paradynomene tuberculata*. While the long setae are similar to those found in other species, the short setae are very different. They are feather-like, lack an acute tip, and because they are bent, form a dense mat over the body surface. The only other dynomenid with feather-like setae is *Dynomene pugnatrix* as described by DE MAN (1889). The rarity of this species prevents a comparative microscopic study to confirm this similarity. The unusual short setae of *D. filholi* have a subterminal brush of fine setules, but in other respects they are quite different from the setae of *P. tuberculata*.

The gills of *Paradynomene tuberculata* have the typical dynomenid structure: there are four epibranchial lobes separated from the hypobranchial plate by a notch. This similar to that found in *Dynomene pilumnoides* and the species of *Metadynomene*. The posterior margin of the scaphognathite bears two long setae and there are no cleaning setae on the hypobranchial margin of the podobranchs. *P. tuberculata* is the only dynomenid in which these podobranch setae are absent. Particularly noteworthy is the extensive development of hypobranchial setae on the wall at the back of the gill chamber. These tufts of setae have also been reported from some dromiids.

In his original description, SAKAI (1963) did not include a description of the male pleopods. Although *Paradynomene tuberculata* is, in many respects, very different from the other dynomenids, its pleopods are clearly built on the same plan. The first pleopod has an apical oval lobe surrounded by a dense fringe of long setae and the second pleopod has an exopod at its base and is armed with a row of small inset distal spines. The terminal spines are reduced making the tip almost blunt as is found in dromiids such as *Stimdromia lamellata* (Ortmann, 1894) and *Epigodromia gilesii* (Alcock, 1899) (unpublished photos). The second male pleopods in these species lack spines of any description.

Several authors have commented upon the similarities between *Paradynomene* and certain dromiids. JAMIESON *et al.* (1993) described the structure of *Paradynomene* sperm and listed four or five synapomorphies with the sperm of some dromiids. With respect to the general features of the carapace front, thoracic appendages, and external maxillipeds, SAKAI (1963) noted the resemblance of *Paradynomene* to some dromiids rather than to *Dynomene* or *Acanthodromia*. The front or "face" of *Paradynomene* is different to the other dynomenids and remarkably similar to some dromiids like *Epigodromia* spp. In both these genera the rostrum is clearly tridentate, a feature seen only in *Paradynomene* and no other dynomenids. Also the "face" in these two genera is much flatter because the rostrum, inflated pterygostomial areas, and third maxillipeds all extend further forward compared to *Dynomene* spp. The longer coxa of the third maxilliped results in the whole of the endopod extending more anteriorly. In *Paradynomene* the merus of the third maxilliped forms almost a right angle with the preceding basis-ischium article whereas it forms a much greater angle in *Dynomene* with all of the articles lying more or less in the same plane. In both *Paradynomene* and *Epigodromia* the third maxilliped is much more strongly operculiform and fits more closely against the epistome so that there is a much narrower gap. Furthermore the chelipeds of these two genera are modified so as to fit compactly against the body and the bases of the third maxillipeds. In *Epigodromia* the anterior surface of the cheliped basis-ischium and merus is flattened so that the remainder of the cheliped can be folded tightly away. In *Paradynomene* the modification goes even further because the basis-ischium is sculptured so that the inferior surface of the cheliped propodus fits closely against a raised ridge (see also GUINOT, 1993). These two genera are also similar in having strongly calcified, areolate and tuberculate exteriors.

In both *Paradynomene tuberculata* and *Acanthodromia erinacea* the basis-ischium and merus articles of the fifth pereopods are fused to make a single bent or curved article. GUINOT (1993) examined closely the last pair of legs in *P. tuberculata*, noting the coxal extension which conducts sperm to the base of the male insemination organs, a feature unique to all dynomenids, and the extreme reduction of the dactyl, which is almost totally withdrawn inside the end of the propodus. However this is only true of the male. In the female the propodal extension, and opposing dactyl, are better developed (see figs 10b-d, 32f) and equipped with 14-16 hooked spines, amongst the largest number of such spines found in any dynomenid. In the male the propodal extension is absent but still bears five spines (as found in most other dynomenid males) while the very small dactylus has a spine on its dorsal margin. This kind of dactyl spine is only found in males and besides *P. tuberculata*, only found in *Dynomene filholi* and *Metadynomene tanensis* (see these species for further discussion). However in the latter two species the spine, although similar in shape, is not on the dorsal margin but on the lateral margin of the dactylus. The dactylar spines are reminiscent of those found in both males and females of dromiids such as *Dromidiopsis* Borradaile, 1900, *Tunedromia* McLay, 1993, and *Lauridromia* McLay, 1993 where they are used, along with other spines, to assist in securing the sponge carried by the last two pairs of legs over the crab. However, in the dynomenids the spines are closely flattened against the surface of the dactyl so that they could not presently function in the same way as in the dromiids. These spines indicate a common ancestral relationship.

All these characters seem to indicate evolutionary convergence in *Paradynomene* and *Epigodromia*. It may be that the species of both these genera normally live partially buried in the surface coral fragments and that by tightly folding away their pereopods they resemble their surroundings because the rugose subquadrangular carapace resembles a piece of coral. It should be noted that *P. tuberculata* and *E. areolata* (Ihle, 1913), for example, have a similar depth range and specimens of both species have been collected from similar depths during the New Caledonia Lagoon survey, 1985 and the MUSORSTOM 6, 1989, expedition to the Loyalty Ids (see McLAY, 1993). *Epigodromia* has the last two pairs of pereopods very reduced, carried subdorsal and they are not used for carrying camouflage as seen in many other dromiids. *Paradynomene*, like all the other dynomenids, has only the last pair of pereopods reduced but they are held horizontally. Thus while the reduced limbs may be an adaptation to a cryptic way of life in *Epigodromia*, the reduced limb in *Paradynomene* is an ancestral character. Observation of living specimens in natural surroundings would allow the hypothesis of cryptic convergence to be tested.

Examination of the stomach contents of a large male 21.0 x 21.9 mm (SMIB, 8 stn DW 189, 400-402 m) showed sand grains, soft unidentifiable organic material and chopped fragments of a hydroid coenosarc. One specimen of *Paradynomene tuberculata* was associated with the stylasterine hydrocoral *Stylaster* (New Caledonia, LAGON, stn 444, 300-350 m).

DISCUSSION

HABITAT. — In most collections, dynomenid crabs are usually comparatively rare (RICHER DE FORGES, pers. comm.). The habitat of the shallow water dynomenids (maximum depth < 100 m) , i.e. *Dynomene hispida*, *D. praedator*, *Hirsutodynomene spinosa* and *H. ursula*, seems to be rocky substrates and corals such as *Acropora* spp., *Pocillopora damicornis*, *P. elegans*, *Seriatopora hystrix*, *Goniastrea retiformis*, *Favia stelligera*, *Oulophyllia crispa*, *Porites* sp. and crustose alga such as *Amphiora foliacea* (EDMONDSON, 1946; PEYROT-CLAUSADE, 1977, 1981; RIBES, 1978; NAIM, 1980; ODINETZ, 1983, and HIGHSMITH, 1981). They seem to occur more often in dead than in live coral. Dynomenids living in deeper water (maximum depth > 100 m), such as *D. filholi*, *D. pilumnoides*, *Metadynomene* spp., *Acanthodromia* spp., and *Paradynomene tuberculata*, seem to live on lithothamnion algae, red coral, precious coral (e.g. *Corallium* sp.) as well as rock and sand. The deepest living dynomenids are *M. tanensis* (520 m) and *A. erinacea* (540 m). Thus most dynomenids show some association with corals but this link does not appear to be obligatory.

DIET. — Guts of nine dynomenid species, *Dynomene hispida*, *D. praedator*, *D. filholi*, *D. pilumnoides*, *Hirsutodynomene spinosa*, *H. ursula*, *Metadynomene tanensis*, *M. devaneyi*, and *Paradynomene tuberculata*, were examined (usually only one or two specimens for each species). The most common material found was sand grains along with soft unidentifiable particulate organic material and, in some species, chopped chitinous fragments which could have come from hydroids or perhaps other crustaceans. It seems likely that most of their food was obtained by sieving organic fragments from the substrate, or in the case of coral inhabiting crabs, perhaps from coral mucous. This is consistent with the presence of a well developed screen of stiff setae in the hollowed out interior of the cheliped fingers and the setose palps of the third maxillipeds. The chopped chitinous fragments suggest that some food might be also obtained by direct grazing. Based on the shape of the chelae, BALSS (1938) suggested that dynomenids consume coral polyps in the same way as, for example the xanthids, *Chlorodiella* and *Chlorodopsis*, but this is not supported by the stomach contents. Feeding behaviour has only been observed for *D. praedator* which seems to obtain most of its food by deposit feeding in sand. The gut contents of the other dynomenids would be consistent with feeding behaviour similar to that of *D. praedator.*

REPRODUCTIVE STRATEGY. — The concept of reproductive strategy includes size at sexual maturity, maximum size, relationship of egg numbers to female size, egg size, and extent of the reproductive season. The extremes of this strategy are brooding or broadcasting progeny. Some information about these characteristics are available for all the dynomenid species except *Metadynomene crosnieri*, and *Acanthodromia margarita.* Egg size is a useful indicator of whether the species has direct or indirect development. In terms of maximum body size the dynomenids fall into two groups: small species whose maximum CW is less than 20 mm (*D. hispida*, *D. praedator*, *D. filholi*, *D. pugnatrix*, *Acanthodromia erinacea* and *A. margarita*), and larger species whose maximum CW is greater than 20 mm (*D. pilumnoides*, *Hirsutodynomene spinosa*, *H. ursula*, *M. devaneyi*, *M. tanensis*, *M. crosnieri*, and *Paradynomene tuberculata*). For all species males have on average a CW 19% larger. Size at sexual maturity is roughly related to maximum size: for the small species sexual maturity occurs at 5.8 - 8.0 mm CW while for the large species it is at 9.5 - 13.0 mm CW. Egg numbers increase logarithmically with CW with a brood size of 30 to 900 eggs for small species and 120 to 3800 for large species. Mean egg diameter for the small species is 0.46 mm, for large species 0.51 mm and for all species together it is 0.49 mm. These egg sizes suggest that all dynomenids have indirect development with planktonic larvae, i.e. a broadcast strategy. The only larvae reported are from *Acanthodromia erinacea* but these were dissected from eggs (RICE, 1981). No dynomenid larvae have ever been reported from plankton collections. Only a limited amount of information about the timing of reproduction is available. Despite the fact that dynomenids are tropical crabs all of the species for which there are adequate sample sizes have their reproduction confined to only part of the year. *D. hispida* and *D. praedator* (from the Indo-Pacific) are ovigerous from January to July, *D. filholi* (from the Atlantic) is ovigerous from May until December, *D. pilumnoides* from February to September, *H. ursula* from April to December, and *P. tuberculata* from October to February (all Indo-Pacific species). Therefore larvae could be expected in the plankton in any month, but the average reproductive period for all species is only 6.7 months.

Amongst the dynomenids we do not find species which have unusually large eggs, such as are seen in homolodromiids (see GUINOT, 1995), and a small number of dromiids (see McLAY, 1993). The modal size class for dromiid eggs is within 0.7-0.8 mm diameter, and direct development (brooding) has been found in *Dromidiopsis globosa* (Lamarck, 1818), *Austrodromidia octodentata* (Haswell, 1882), and *Stimdromia lateralis* (Gray, 1931) all of which have eggs >1.0 mm diameter. Homolodromiids have large eggs which are 2.0-2.5 mm diameter and brooding is known in *Dicranodromia nagaii* Guinot, 1995. When we examine these features in relation to the hypothesized sister group relationships of these families (see Fig. 15), it becomes obvious that the ancestral condition must have been females carrying small numbers of very large eggs (probably brooding the young), as in the homolodromiids, and the derived condition must be females carrying much larger numbers of smaller eggs (broadcasting the young). Viewed in this way, the dynomenids are the most derived group, having the smallest eggs with indirect development, and the dromiids are intermediate. Judging by their egg size, most dromiids must have indirect development (the development of more than ten species is known) with only a few retaining the ancestral condition of large eggs. One Australian dromiid, *Haledromia bicavernosa* (Zietz, 1887) has the largest eggs known for any brachyuran i.e. 2.8 mm diameter. It is interesting to note that all dromiids known to have direct development live in Australian waters. Also the endemic dromiid genera, *Dromidia* Stimpson, 1858, *Exodromidia* Stebbing, 1905, *Pseudodromia* Stimpson, 1858, and *Speodromia* Barnard, 1947, from South Africa all have large eggs, implying direct development, although their mode of development is unknown (McLAY, 1993: 159). Therefore we could hypothesize that the common ancestor shared by the dynomenids and dromiids also had a reproductive strategy of a small number of large eggs. If this is true then the broadcast strategy, seen in dynomenids and most dromiids, must have evolved independently. This interpretation is no doubt contrary to accepted wisdom, but it is the most parsimonious conclusion.

DEPTH DISTRIBUTION. — The greatest diversity of dynomenids occurs in the 0-50 m depth range. Seven species from three of the genera, *Dynomene* (4), *Hirsutodynomene* (2) and *Paradynomene* (1) are shallow water inhabitants (see Fig. 33). Four species (*D. hispida*, *D. praedator*, *H. spinosa*, and *H. ursula*) have been collected from the lower intertidal range, and between 25 and 50 m, six species are known. Between 50 and 400 m all five genera are represented with no more than five species at any one depth interval. Below 400 m the number of species begins to decline with two species at 500 m and none at 550 m. The species of *Dynomene* and *Paradynomene* occur from 0-400 m, those of *Hirsutodynomene* are shallow water inhabitants (<100 m), and species of *Metadynomene* and *Acanthodromia* all inhabit deeper waters down to a maximum depth of 540 m. *D. pugnatrix*, *M. devaneyi* and *M. crosnieri* are only known from a few specimens and so their depth range is uncertain. The average depth range (maximum - minimum) for all the more common species (n = 10) is 196 m.

The bathymetric distribution of dynomenids is very similar to that of the dromiids (see McLAY, 1993) where the majority of species are found in shallow waters from 0 to 150 m, with a maximum of around 500 m. By contrast most of the homolodromiids are found in depths of 300 to 900 m, with a maximum of 1330 m (see GUINOT, 1995), and the homolids are mostly found in depths from 200 to 1500 m, with a maximum of 2200 m (see GUINOT & RICHER DE FORGES, 1995). So we have a depth "zonation" of these three families with dynomenids + dromiids in shallow water, followed by homolodromiids and lastly the homolids at the greatest depths. Thus the hypothesized sister group relationship of dynomenids and dromiids is supported by the depth distribution data which shows that these two families share the same "habitat". Furthermore, if these two families shared a common ancestor with the homolodromiids, as is hypothesized above for the Dromiacea, then it would seem that dynomenids and dromiids evolved from ancestors which must have lived in deep waters (approx. 300-900 m). Similarly, if the Dromiacea and Archaeobrachyura shared a common ancestor then it must also have lived in deep water, perhaps at even greater depths than the dynomenid - dromiid ancestor, with descendants radiating into very deep water. Thus, the dynomenids and dromiids are families of the continental shelves while the homolodromiids and archaeobrachyurans are inhabitants of the continental slopes.

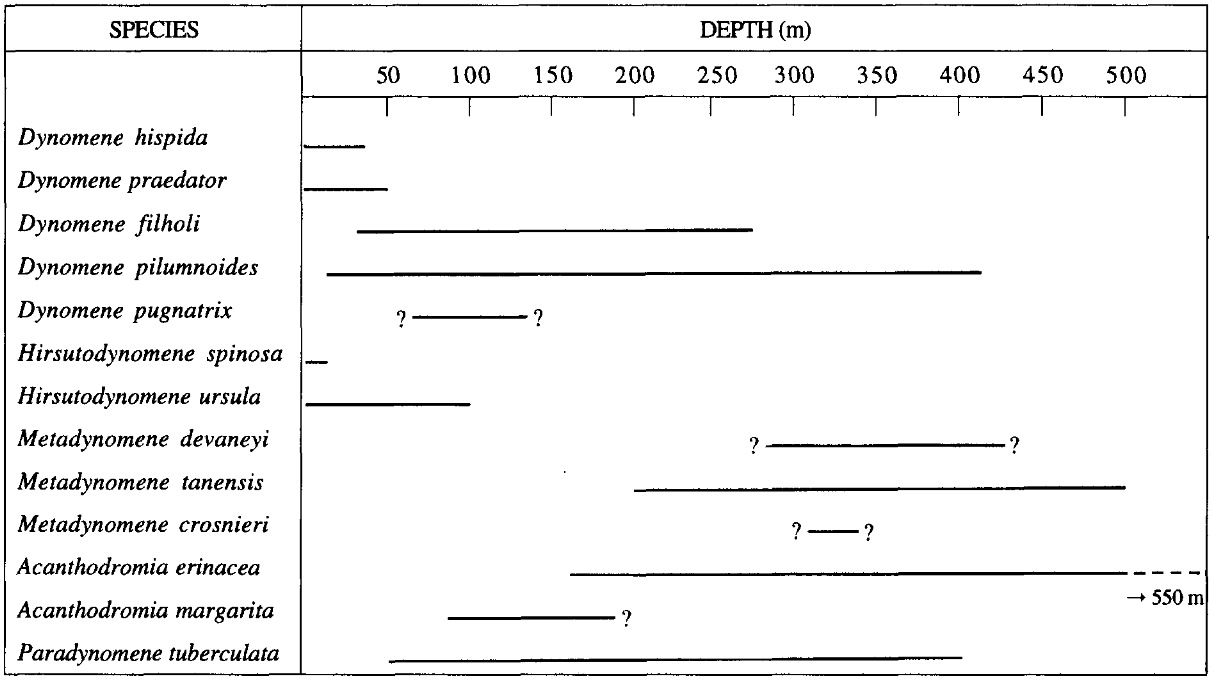

FIG. 33. — Depth distribution of dynomenid species. The "?" indicates an uncertain depth range because of a very small sample size.

The hypothesis that dynomenids and dromiids represent shallow-water evolutionary radiations from ancestors living in deeper water is similar to the hypothesis put forward by GEORGE and MAIN (1967) to explain the Cretaceous evolutionary radiation of the Palinuridae which is supported by an analysis of phyllosoma characters of the whole Palinuroidea by BAISTRE (1994).

BIOGEOGRAPHY. — Only two dynomenid species, representing two genera, are known from the Atlantic Ocean: *Dynomene filholi* and *Acanthodromia erinacea*. Both of these are insular species (Figs 37, 40). *A. erinacea* is restricted to the Caribbean area and *D. filholi* to the South Atlantic. In overall appearance, their obvious Indo-Pacific counterparts are *A. margarita* and *D. pilumnoides* respectively.

The species of *Acanthodromia* no doubt originated from a tethyan ancestor and spread to seas that eventually became the Atlantic and Caribbean, perhaps as early as the Upper Jurassic (145 mybp). This dispersal could have been as late as the Middle Miocene (25 mybp), when connections between these two oceans were severed, but an earlier date seems more likely because even by Palaeocene times (65 mybp) the Atlantic was already well formed and the Caribbean isolated (HOWARTH, 1981). Therefore these two species could have been separated at least since the Palaeocene (or at latest the Middle Miocene). The remarkable thing about *A. erinacea* and *A. margarita* is how similar they are because there has scarcely been any divergence in their morphology (see Discussion under *A. erinacea*).

Similarly, it seems to be a reasonable assumption that the ancestor of *Dynomene filholi* was a Tethyan crab which also gave rise to *D. pilumnoides*. A southern colonization route for these crabs could have been open as early as the Upper Cretaceous (90-80 mybp) or sometime later. At present there does not seem to be a dispersal route via the Cape because it is blocked by the local Agulhas oceanic circulation pattern. This self-contained circulation pattern seems to have been in existence for a considerable time because there is a suite of endemic South African dromiid genera and species (see McLAY, 1993) which have been isolated perhaps since the Upper Cretaceous or Palaeocene (65 mybp). This interpretation would imply that colonization of the Atlantic by *Dynomene* must have been during the late Mesozoic or very Early Tertiary. Again there are many features in common between *D. filholi* and *D. pilumnoides* (see Discussion under *D. pilumnoides*).

Eleven species, representing all five genera, are known from the Indo-Pacific region. These species vary in the extent of their distribution, but all of them lie within the limits of 40°N and 40°S. Within the genus *Dynomene* two species (*D. hispida*, and *D. praedator*) are very widespread occurring from the coast of Africa to French Polynesia in the east (Figs 34 & 35). *D. pilumnoides* is distributed over almost the same region except that it only extends as far east as Hawaii (Fig. 36). The other species, *D. pugnatrix*, has a very limited distribution restricted to the vicinity of Madagascar (Fig. 37). In the genus *Hirsutodynomene* one species, *H. spinosa*, has a similar distribution to *D. hispida* and *D. praedator* while the other species, *H. ursula*, is restricted to the Pacific side of Central America (Fig. 38). The distributions of these two sister species do not overlap. It may well be that *H. ursula* is of quite recent origin, perhaps not colonizing the eastern Pacific until after the formation of the isthmus of Panama, because otherwise it would be reasonable to expect it to occur in the Caribbean as well as the Pacific. Two of the species of *Metadynomene* are very rare: *M. crosnieri* is only known from the type locality, north of Madagascar and *M. devaneyi* is only known from Hawaii and the Marquesas Islands. The third species, *M. tanensis*, is common in the eastern Pacific and also occurs in French Polynesia (Fig. 39). While one species of *Acanthodromia*, *A. erinacea*, lives in the Caribbean region, the other, *A. margarita*, has been recorded from the Andaman Sea and Japan (Fig. 40). The last genus, *Paradynomene*, has until now been known only from the eastern Pacific but I report herein a record of a specimen of *P. tuberculata* from the Gulf of Aden. Thus *Paradynomene* is an Indo West Pacific genus (Fig. 40). Given the reproductive strategies outlined above, the large geographic ranges of dynomenids is not unexpected. All dynomenids probably have planktonic larval stages.

The dynomenid fauna of insular Indo-Pacific localities is drawn from a suite of species which includes (in decreasing order of frequency of occurrence): *Dynomene praedator*, *D. hispida*, *Hirsutodynomene spinosa*, *D. pilumnoides*, *Metadynomene tanensis*, *Paradynomene tuberculata*, *H. ursula*, and *M. devaneyi*. Almost without exception wherever *D. praedator* is found, so is *D. hispida*. The largest number of species is found in Japanese waters (6), followed by New Caledonia, Madagascar and French Polynesia (5), and Hawaii (4), while Mauritius, Taiwan, Mariana Ids, Cocos Keeling Ids, Marshall Ids (Eniwetak) have 3 species. All other localities have only 1 or 2 species, usually *D. praedator* and/or *D. hispida*.

Although there are two shared genera (*Dynomene* and *Acanthodromia*) in the Atlantic, there are no dynomenid species which occur in both the Atlantic and Indo-Pacific regions. It can be safely assumed that the two Atlantic species are derived from Indo-Pacific stocks and that their origin could have been as late as about 25 mybp before the destruction of the Tethyan connection between these two oceans (ADAMS, 1981), although they could have

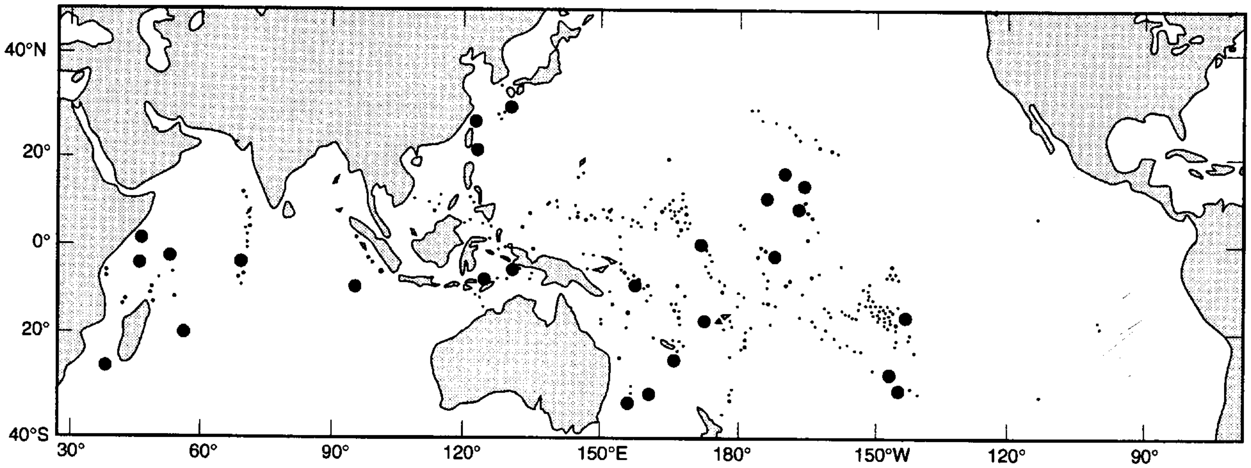

FIG. 34. — Geographic distribution of *Dynomene hispida* Guérin-Méneville, 1832.

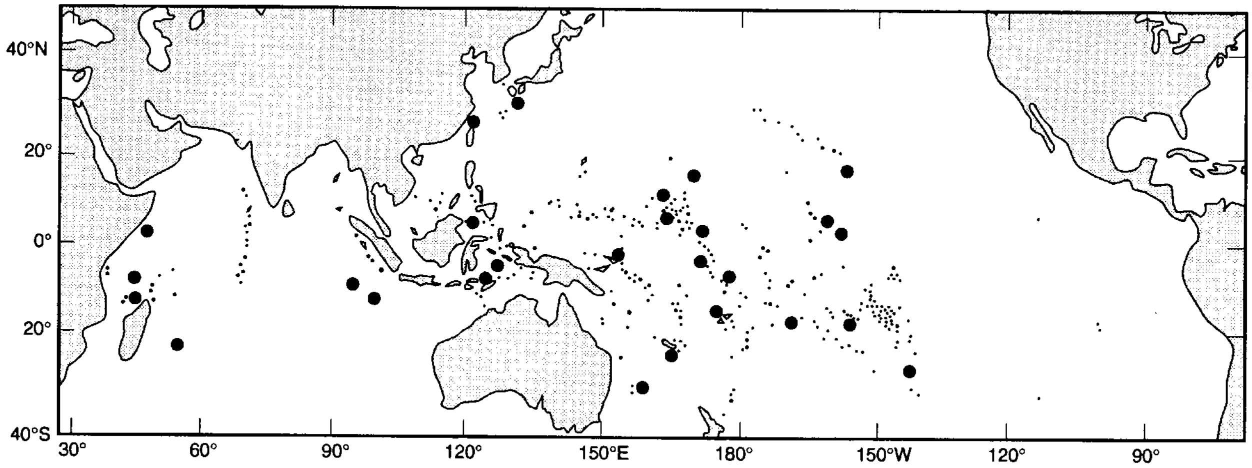

FIG. 35. — Geographic distribution of *Dynomene praedator* A. Milne Edwards, 1879.

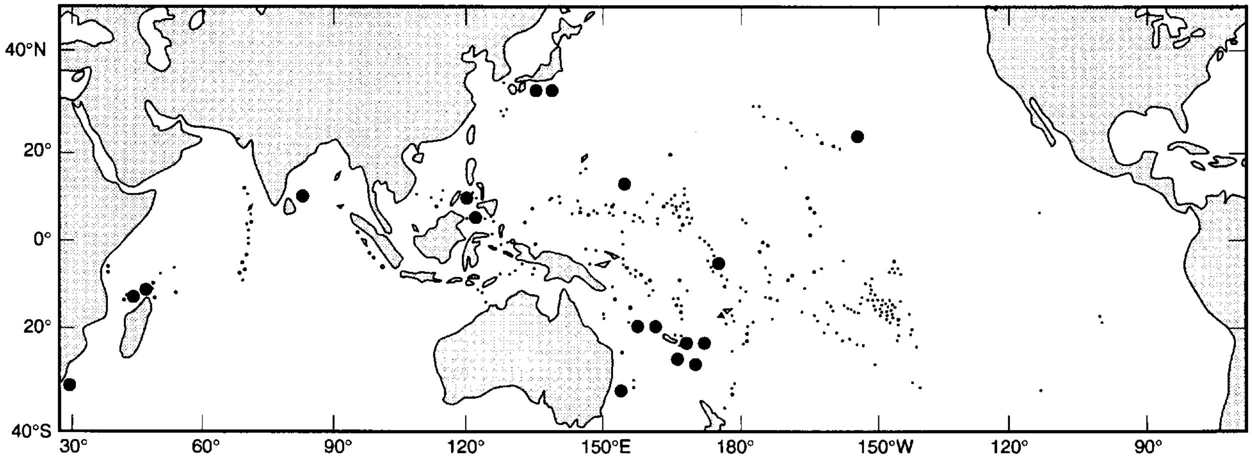

FIG. 36. — Geographic distribution of *Dynomene pilumnoides* Alcock, 1900.

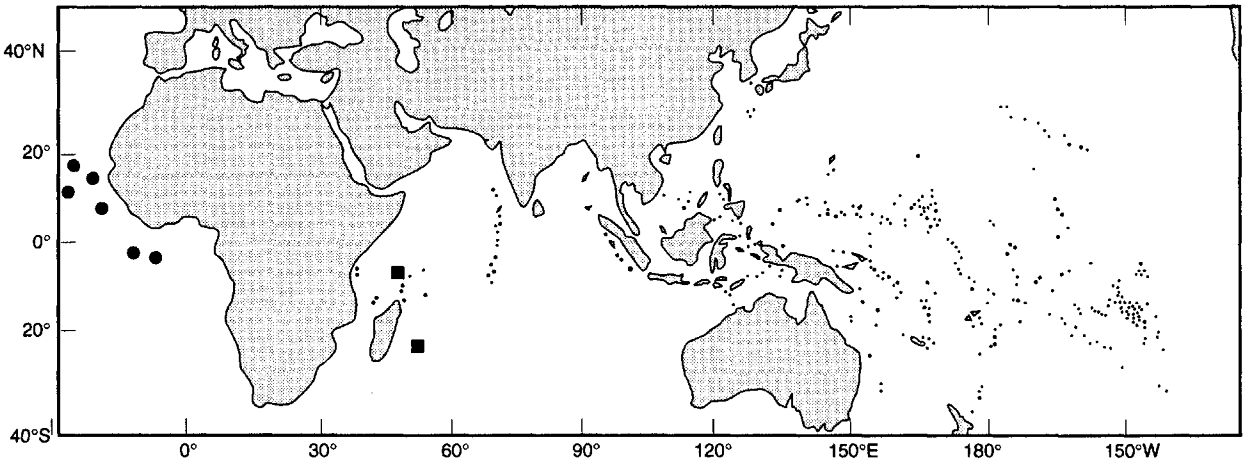

FIG. 37. — Geographic distribution of *Dynomene pugnatrix* de Man, 1889 (■), and *D. filholi* Bouvier, 1894 (●).

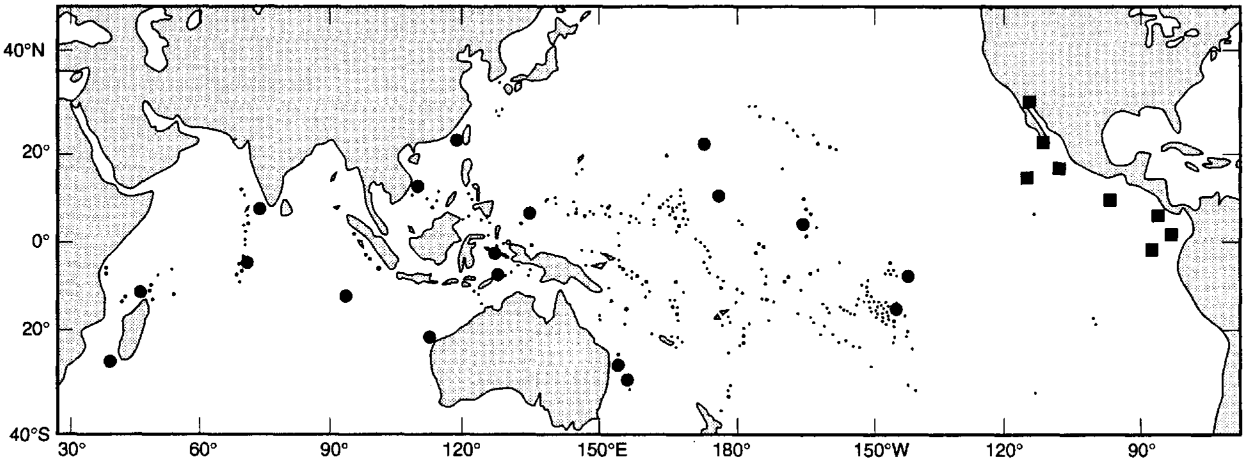

FIG. 38. — Geographic distribution of *Hirsutodynomene ursula* (Stimpson, 1860) (■) and *H. spinosa* (Rathbun, 1911) (●).

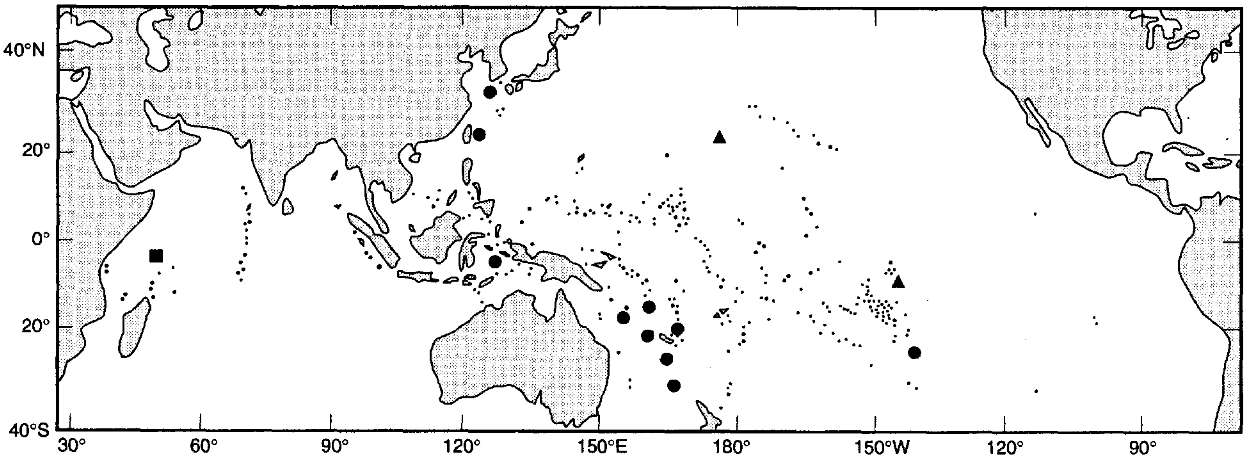

FIG. 39. — Geographic distribution of *Metadynomene devaneyi* (Takeda, 1977) (▲), *M. tanensis* (Yokoya, 1933) (●), and *M. crosnieri* sp. nov. (■).

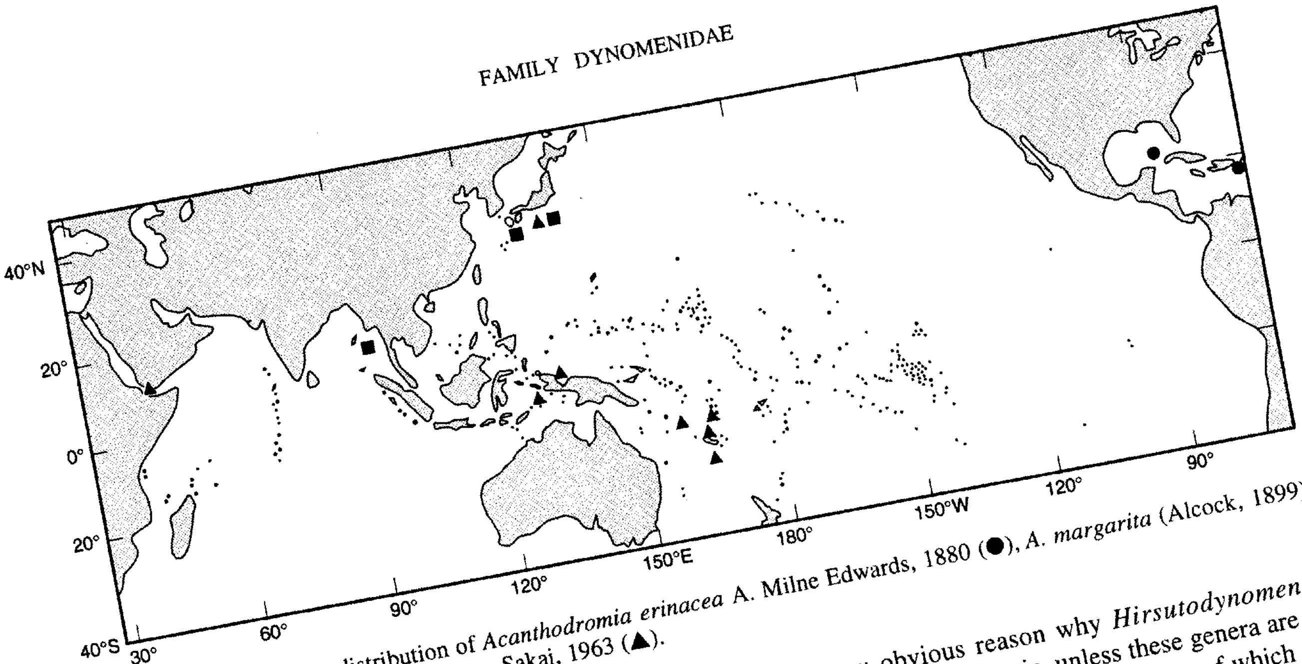

FIG. 40. — Geographic distribution of *Acanthodromia erinacea* A. Milne Edwards, 1880 (●), *A. margarita* (Alcock, 1899) (■), and *Paradynomene tuberculata* Sakai, 1963 (▲).

been separate species much earlier. There does not seem to be any obvious reason why *Hirsutodynomene*, *Metadynomene* and *Paradynomene* should not have become established in the Atlantic, unless these genera are of more recent origin. In the Indian and Pacific Oceans there are eight and nine species respectively, five of which are shared. All five genera have representatives in both oceans. Dynomenids are undoubtedly an ancient group of crabs.

	East Atlantic: 0-29°E	East Africa: 30-59°E	India: 60-98°E	Southeast Asia: 90-119°E	Japan-Philippines: 120-149°E	New Caledonia: 150-179°E	Hawaii: 180-151°E	French Polynesia: 150-121°E	Mexico:120-91°W	Central America: 90-61°W	South America: 60-31°W	Cape Verde: 30-0°W
D. hispida	-	+	+	+	+	+	+	+	-	-	-	-
D. praedator	-	+	-	+	+	+	+	+	-	-	-	-
D. pilumnoides	-	+	+	-	+	+	+	-	-	-	-	-
D. pugnatrix	-	+	-	-	-	-	-	-	-	-	-	-
D. filholi	-	-	-	-	-	-	-	-	-	-	-	+
H. spinosa	-	+	+	+	+	+	-	+	-	-	-	-
H. ursula	-	-	-	-	-	-	-	-	+	+	-	-
M. devaneyi	-	-	-	-	-	-	+	+	-	-	-	-
M. crosnieri	-	+	-	-	-	-	-	-	-	-	-	-
M. tanensis	-	-	-	-	+	+	-	+	-	-	-	-
A. erinacea	-	-	-	-	-	-	-	-	-	+	-	-
A. margarita	-	-	-	+	+	-	-	-	-	-	-	-
P. tuberculata	-	+	-	-	+	+	-	-	-	-	-	-
No. species	0	7	3	4	7	6	4	5	1	2	0	1

FIG. 41. — Longitudinal distribution of the Dynomenidae.

A similar picture emerges from our limited knowledge of the distribution of the Homolodromiidae (GUINOT, 1995) and the Homolidae (GUINOT & RICHER DE FORGES, 1995). The Atlantic and Indo-Pacific share genera but not species. However, the species of both *Homolodromia* and *Dicranodromia* have quite localized distributions which may be a consequence of their tendency to have direct development. Dynomenid distribution is more like that of the Homolidae where some genera are restricted to the Indo-Pacific and the species are widely distributed. A similar pattern is found amongst the Dromiidae, although this family is a mixture of widespread genera along with groups of genera endemic to a relatively small area. e.g. South Africa, or Australia (see McLAY, 1993).

The relationship between dynomenid diversity and longitude shows that the highest diversity is found in the Indo-West Pacific (Fig. 41). Diversity is lowest (0-2 species) in the Eastern Pacific and the Atlantic, and highest (6-7 species) in East African and Japan/Philippines/New Caledonian latitudes. To some extent, this pattern probably reflects the amount of collecting that has been done.

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Family and genus names are given in capital letters, species names in italics. Bold family, genus and species names indicate that the taxa are treated in detail.

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