CRUSTACEA DECAPODA:
Revision of the Family Dynomenidae

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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

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.
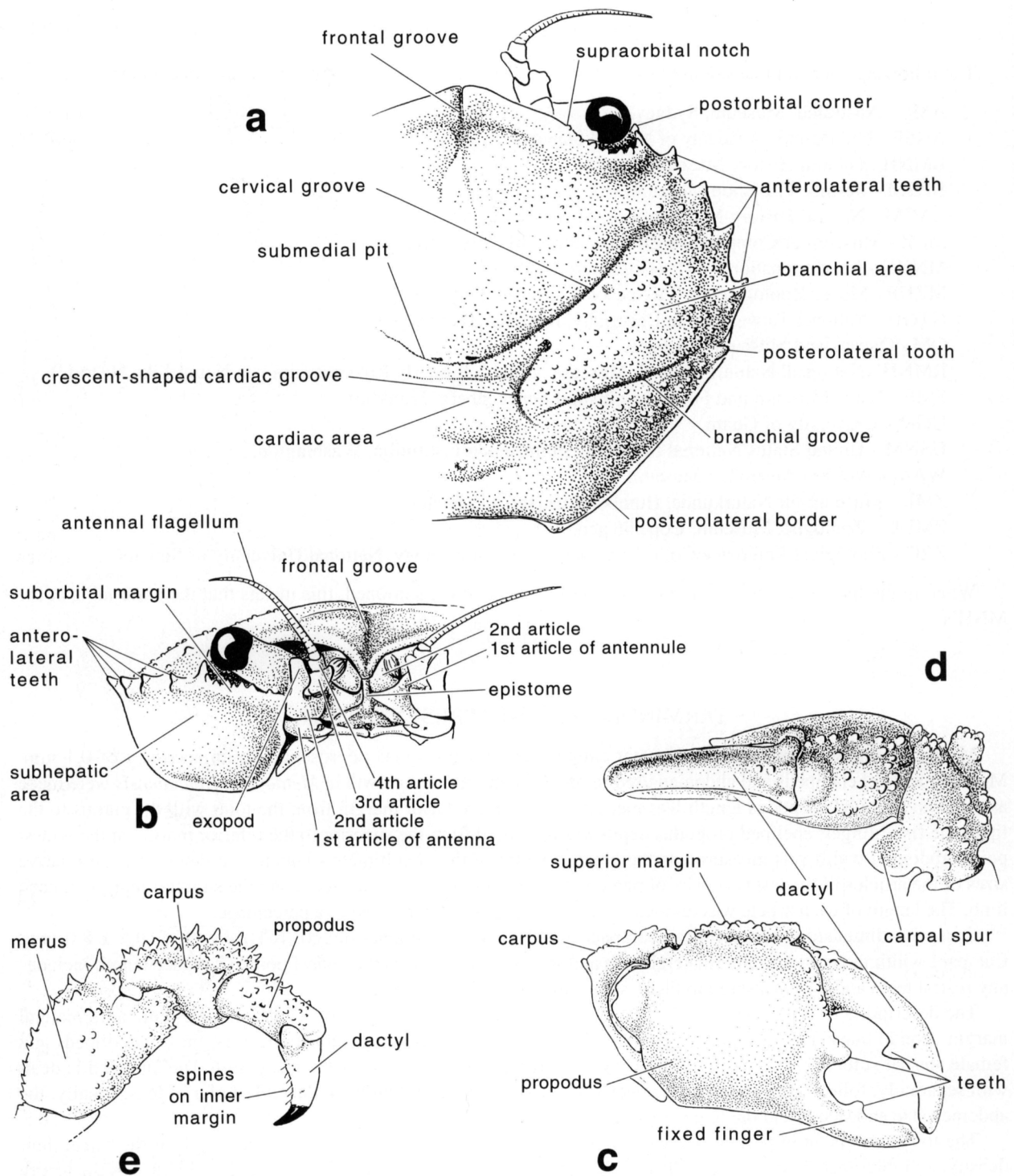
C. L. McLAY

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.
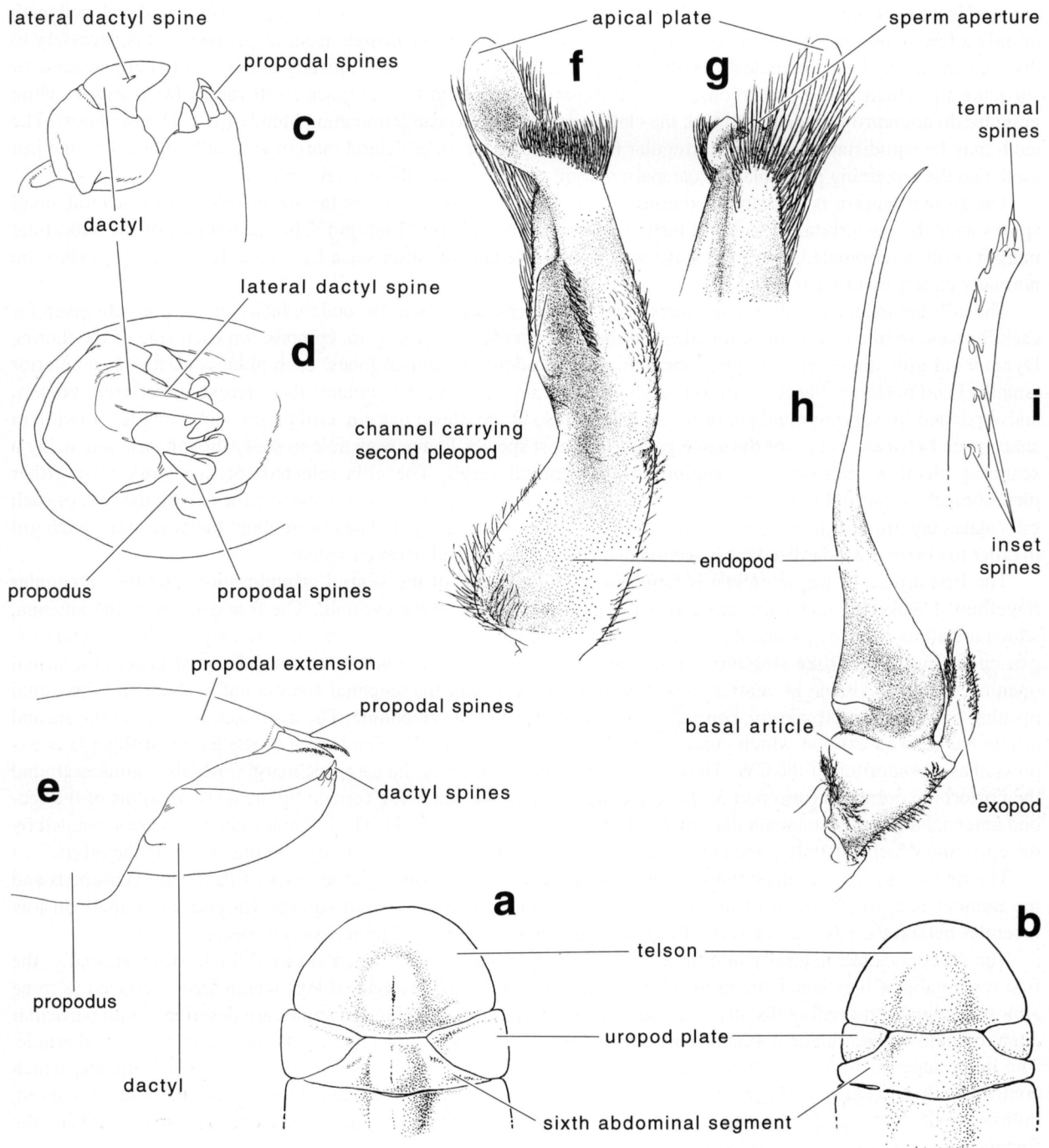
FIG. 2. — Selected figures illustrating the terminology used to describe crabs of the family Dynomenidae : a based on *Dynomene hispida*, b based on *D. filholi*; c-e based on *Metadynomene tanensis*, f-h based on *M. devaneyi* (reprinted from TAKEDA, 1977, *Pacific Science*, vol. 31 (1) by permission 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.