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.
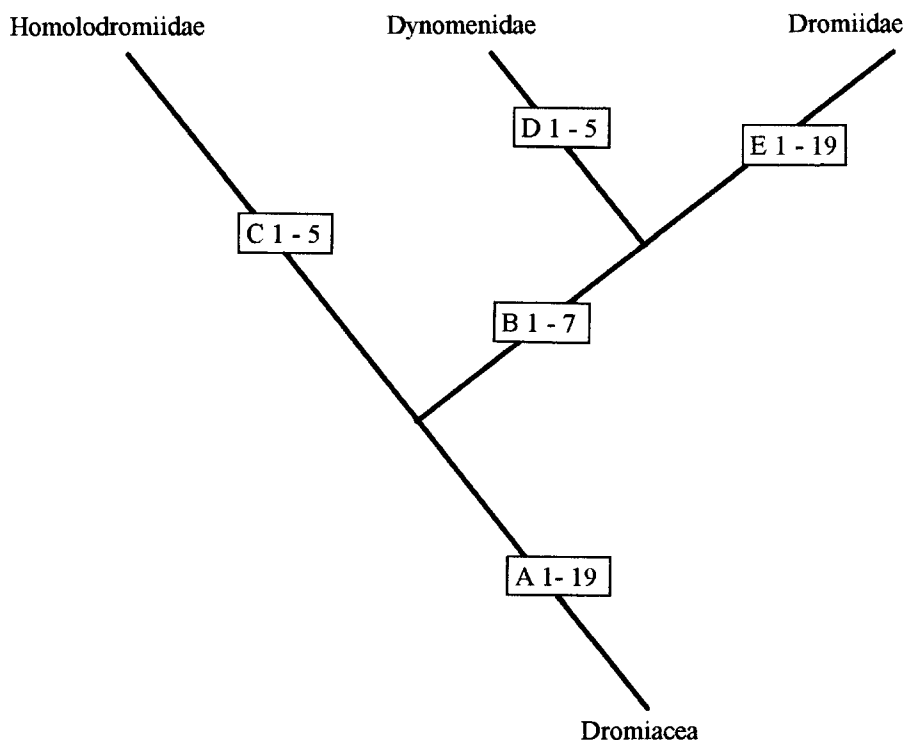

FIG. 15. — Cladogram showing the assumed relationships between the families of the Dromiacea. Numbers refer to apomorphic and plesiomorphic characters mapped on to this hypothesis (see text).

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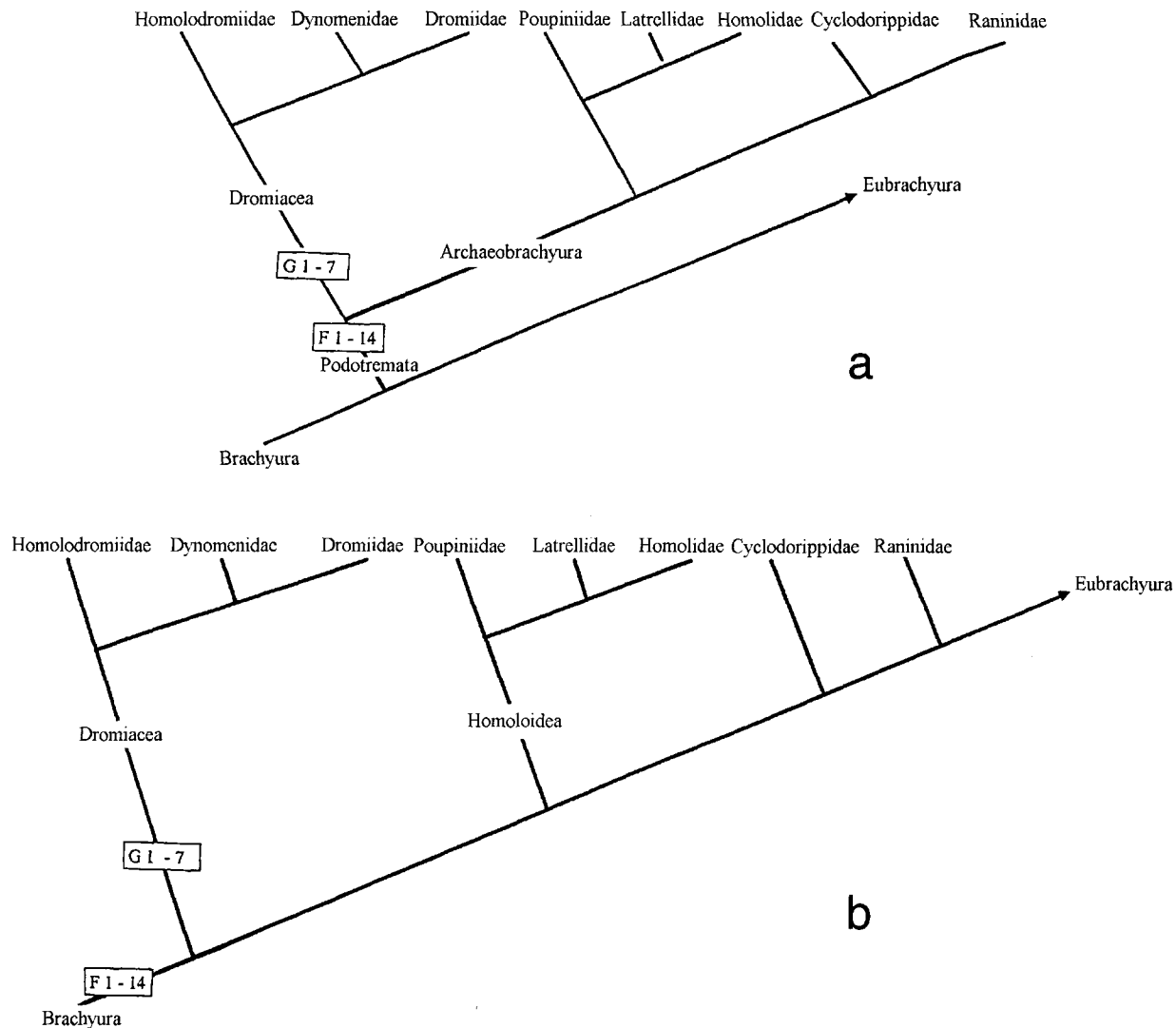
FIG. 16. — Cladogram showing two different relationships between the families of the Podotremata: **a**, the Podotremata are assumed to be monophyletic (modified after GUINOT *et al.*, 1994); **b**, the Podotremata are assumed to be paraphyletic (modified after SCHOLTZ & RICHTER, 1995). Numbers refer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