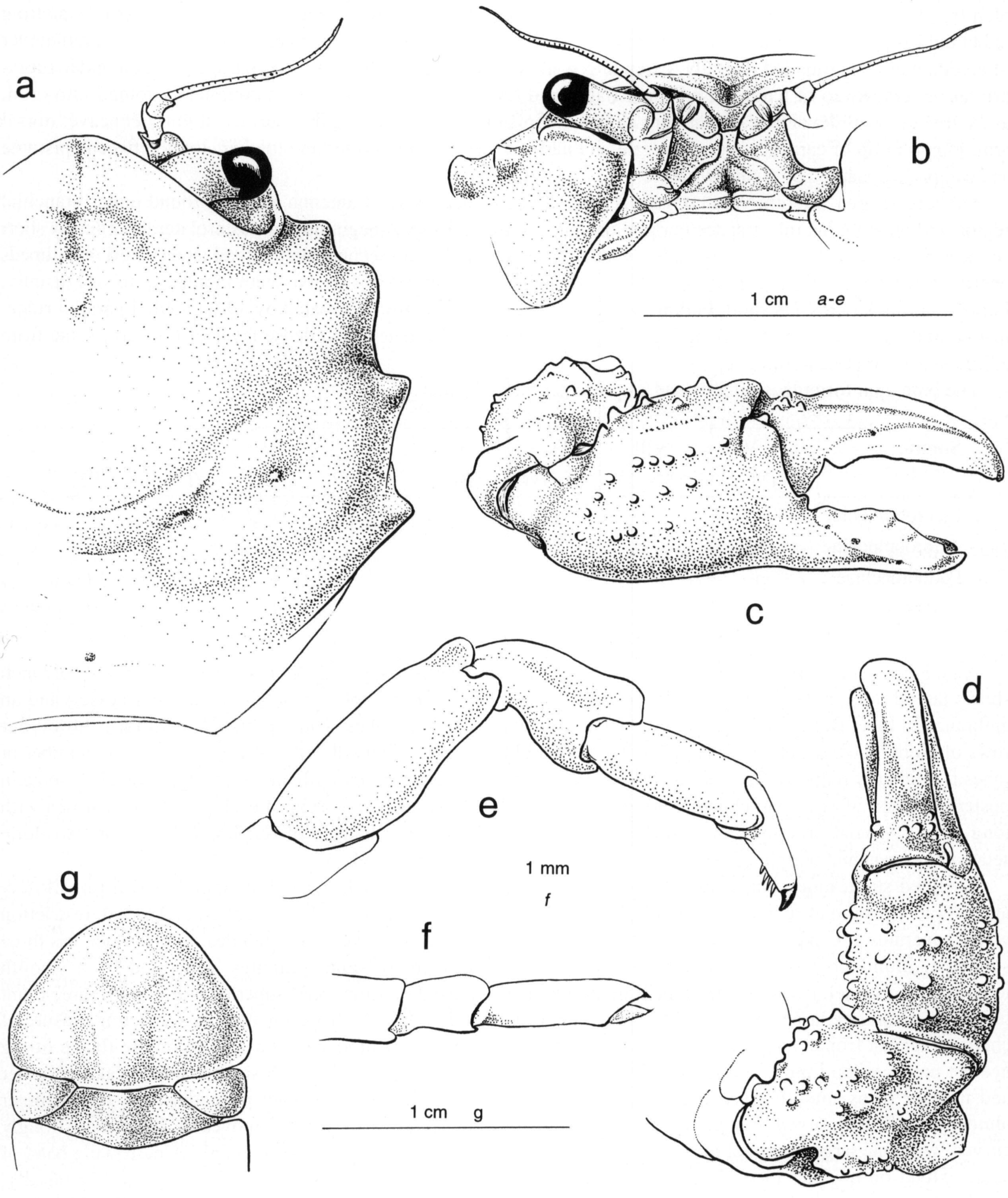

FIG. 27. — *Metadynomene tanensis* (Yokoya, 1933), ♀ 19.2 x 18.9 mm, New Caledonia, MUSORSTOM 4, stn 215, 485-520 m: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of right cheliped; **d**, dorsal view of right cheliped; **e**, posterior view 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 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 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 (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	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

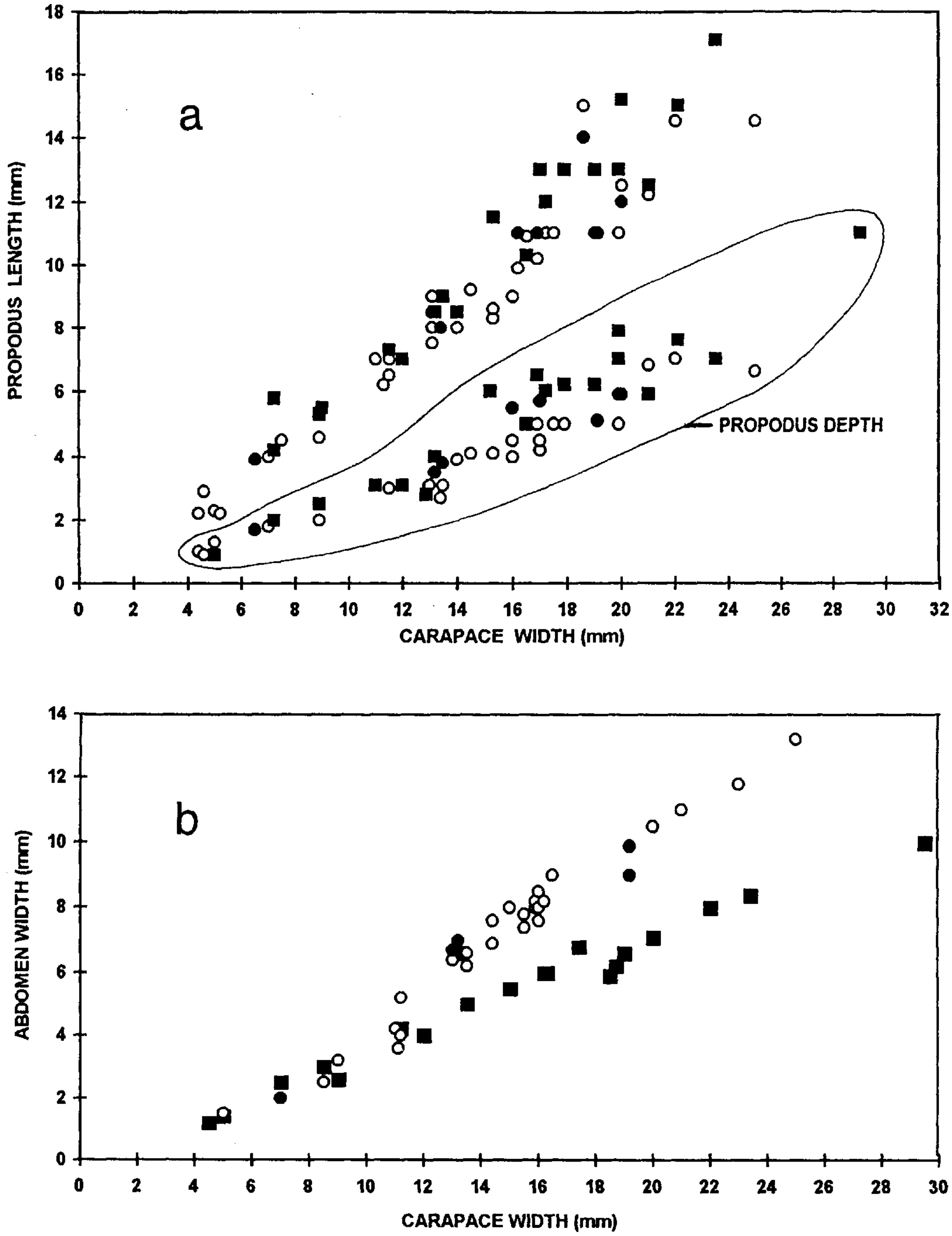

FIG. 28. — Relative growth of *Metadynomene tanensis* (Yokoya, 1933): **a**, cheliped propodus length and depth plotted against carapace width; **b**, width of penultimate abdominal segment plotted against carapace width (mm). Open circles are for males, closed circles are for females, and triangles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

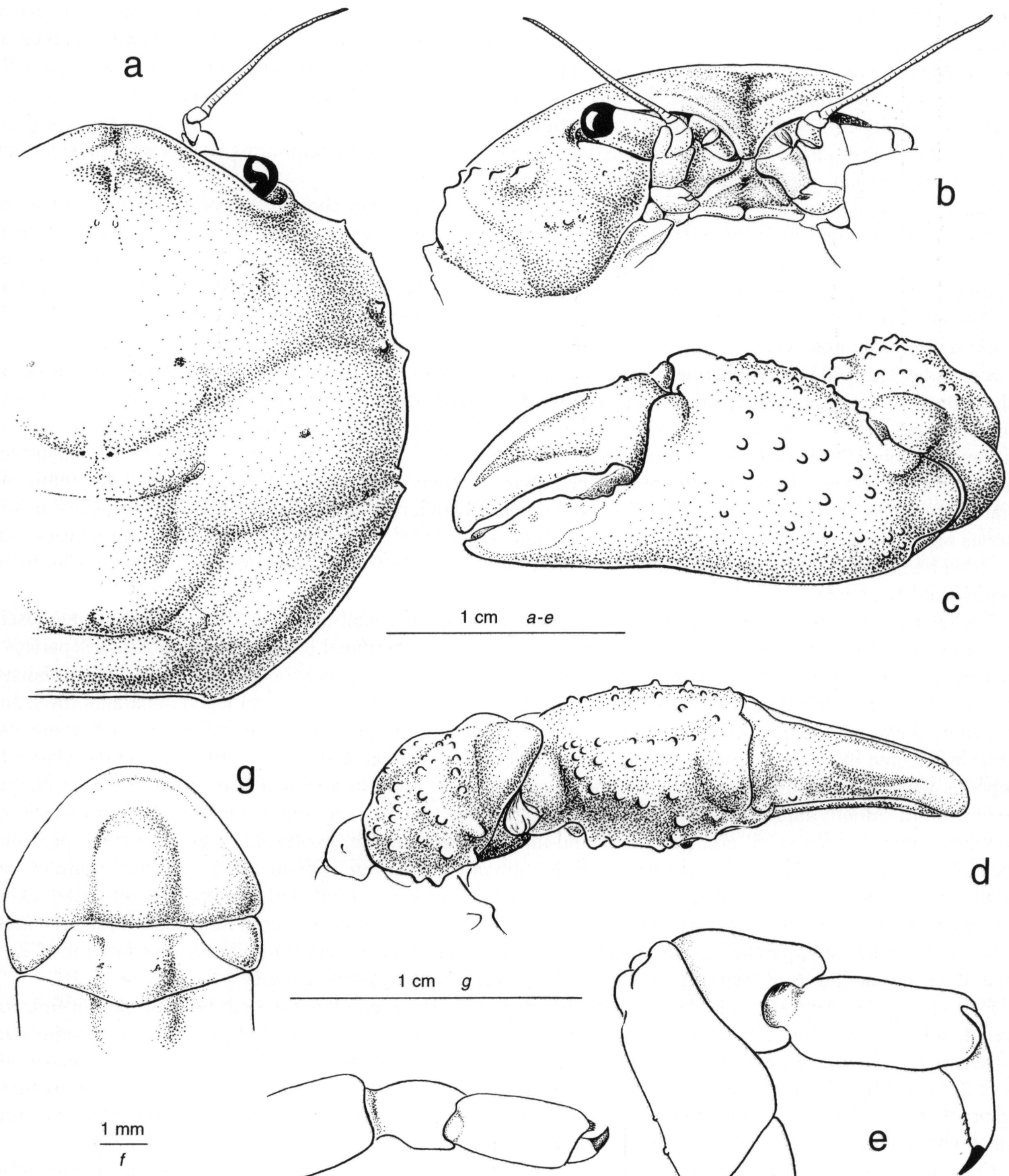

FIG. 29. — *Metadynomene crosnieri* sp. nov., ♂ 23.2 x 22.7 mm, holotype, Glorieuses Ids, BENTHEDI, 330-440 m: **a**, dorsal view of right half of carapace; **b**, ventral view of right orbital area; **c**, outer face of left cheliped; **d**, dorsal view of left cheliped; **e**, posterior view of terminal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