

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

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

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

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

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

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

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

Last pair of legs greatly reduced; surface granular but not spinous; basis-ischium and merus fused, lying along posterolateral border of carapace, reaching only as far as half-way along meral article of preceding limb. Subchelate, sexually dimorphic: female with well developed distal extension of propodus which opposes dactyl, male

without a propodal extension. Female propodal extension bearing 14-16, unequal, stout, hooked, spines with a ridged, concave inner surface and marginal rows of 7-12 tiny flattened teeth proximally. These teeth are directed laterally. Female dactyl as long as propodal extension, bearing 15-16 unequal, stout, hooked spines (arranged asymmetrically around perimeter of dactyl) whose concave inner surface is devoid of tiny teeth. Distal margin of male propodus not produced (as illustrated by GUINOT, 1993, fig. 1), but bearing five unequal curved spines without teeth. Male dactyl largely withdrawn into propodus and ending in a single acute claw which has a tiny subterminal spine on its dorsal margin.

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

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

COLOUR. — Pale brown. Tips of dactyli black.

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

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

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

DISCUSSION. — The description of *Paradynomene tuberculata* given here differs somewhat from that of SAKAI (1963). In the original description SAKAI stated that the lateral carapace borders are armed with six principal teeth, of which the third is somewhat dorsal in position and the last located on the posterolateral border, with several additional small teeth between the principal teeth. It is debatable whether the third tooth mentioned above should

be regarded as being marginal or not. In my description I have not treated it as being part of the anterolateral margin and I have treated the last two teeth as being on the posterolateral border because the carapace margin begins to curve inwards posteriorly. Exact enumeration of the anterolateral teeth is made difficult by the fact that there are a variable number of small teeth/tubercles following the first lacinated tooth. SAKAI also stated that the dactyli of second to fourth pereopods are unarmed, but 4-5 very small spines are present.

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

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

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

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

In both *Paradynomene tuberculata* and *Acanthodromia erinacea* the basis-ischium and merus articles of the fifth pereopods are fused to make a single bent or curved article. GUINOT (1993) examined closely the last pair of legs in *P. tuberculata*, noting the coxal extension which conducts sperm to the base of the male insemination organs, a feature unique to all dynomenids, and the extreme reduction of the dactyl, which is almost totally withdrawn inside the end of the propodus. However this is only true of the male. In the female the propodal extension, and opposing dactyl, are better developed (see figs 10b-d, 32f) and equipped with 14-16 hooked spines, amongst the



largest number of such spines found in any dynomenid. In the male the propodal extension is absent but still bears five spines (as found in most other dynomenid males) while the very small dactylus has a spine on its dorsal margin. This kind of dactyl spine is only found in males and besides *P. tuberculata*, only found in *Dynomene filholi* and *Metadynomene tanensis* (see these species for further discussion). However in the latter two species the spine, although similar in shape, is not on the dorsal margin but on the lateral margin of the dactylus. The dactylar spines are reminiscent of those found in both males and females of dromiids such as *Dromidiopsis* Borradaile, 1900, *Tunedromia* McLay, 1993, and *Lauridromia* McLay, 1993 where they are used, along with other spines, to assist in securing the sponge carried by the last two pairs of legs over the crab. However, in the dynomenids the spines are closely flattened against the surface of the dactyl so that they could not presently function in the same way as in the dromiids. These spines indicate a common ancestral relationship.

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

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

## DISCUSSION

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

**DIET.** — Guts of nine dynomenid species, *Dynomene hispida*, *D. praedator*, *D. filholi*, *D. pilumnoides*, *Hirsutodynomene spinosa*, *H. ursula*, *Metadynomene tanensis*, *M. devaneyi*, and *Paradynomene tuberculata*, were examined (usually only one or two specimens for each species). The most common material found was sand grains along with soft unidentifiable particulate organic material and, in some species, chopped chitinous fragments which could have come from hydroids or perhaps other crustaceans. It seems likely that most of their food was obtained by sieving organic fragments from the substrate, or in the case of coral inhabiting crabs, perhaps from coral mucous. This is consistent with the presence of a well developed screen of stiff setae in the hollowed out interior of the cheliped fingers and the setose palps of the third maxillipeds. The chopped chitinous fragments suggest that some food might be also obtained by direct grazing. Based on the shape of the chelae, BALSS (1938)

suggested that dynomenids consume coral polyps in the same way as, for example the xanthids, *Chlorodiella* and *Chlorodopsis*, but this is not supported by the stomach contents. Feeding behaviour has only been observed for *D. praedator* which seems to obtain most of its food by deposit feeding in sand. The gut contents of the other dynomenids would be consistent with feeding behaviour similar to that of *D. praedator*.

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

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

**DEPTH DISTRIBUTION.** — The greatest diversity of dynomenids occurs in the 0-50 m depth range. Seven species from three of the genera, *Dynomene* (4), *Hirsutodynomene* (2) and *Paradynomene* (1) are shallow water

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

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

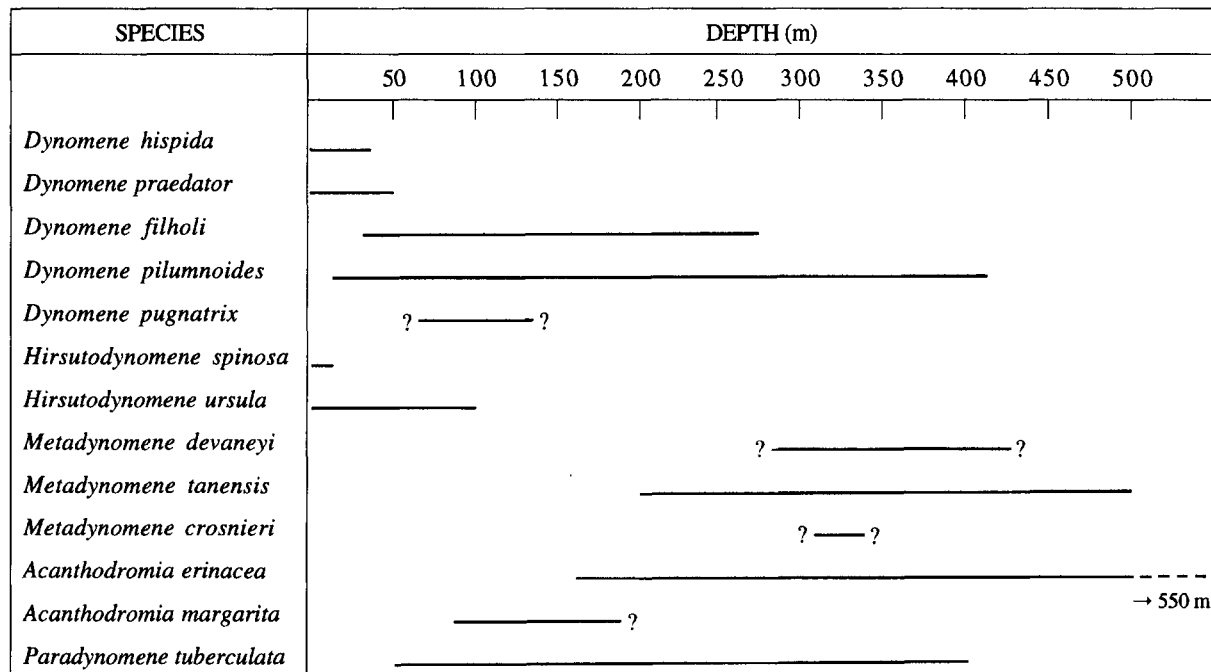


FIG. 33. — Depth distribution of dynomenid species. The "?" indicates an uncertain depth range because of a very small sample size.

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

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

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

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

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

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

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

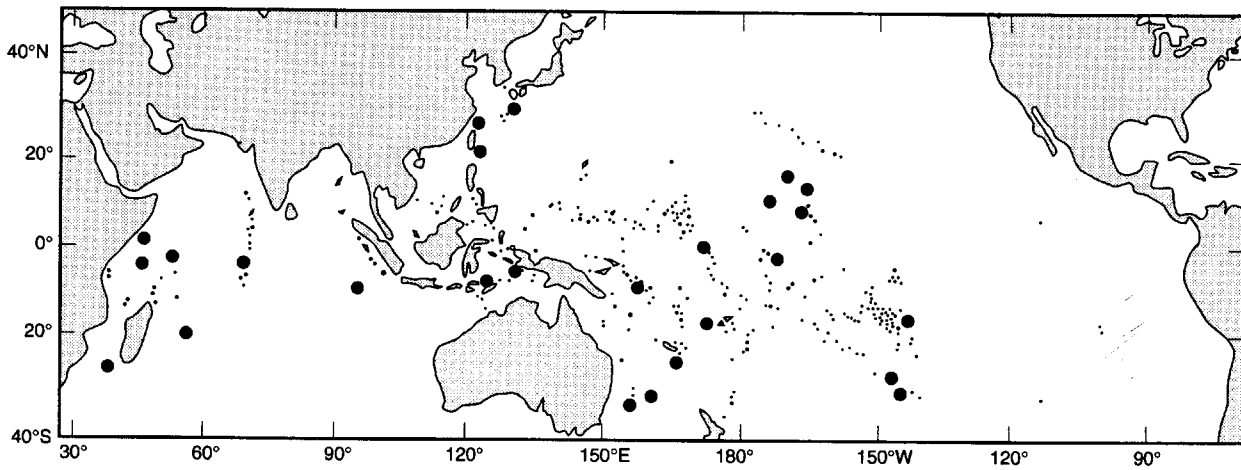


FIG. 34. — Geographic distribution of *Dynomene hispida* Guérin-Méneville, 1832.

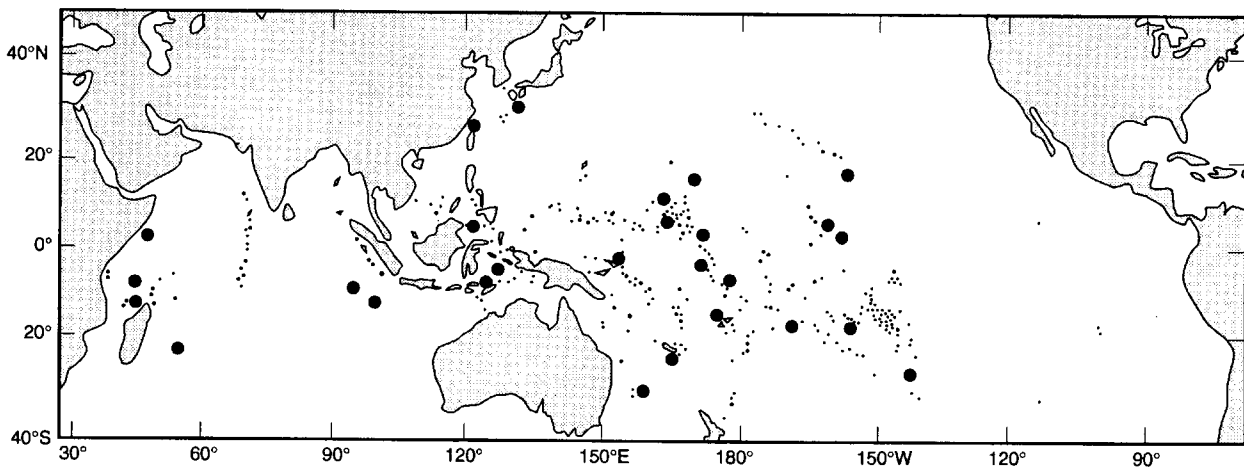


FIG. 35. — Geographic distribution of *Dynomene praedator* A. Milne Edwards, 1879.

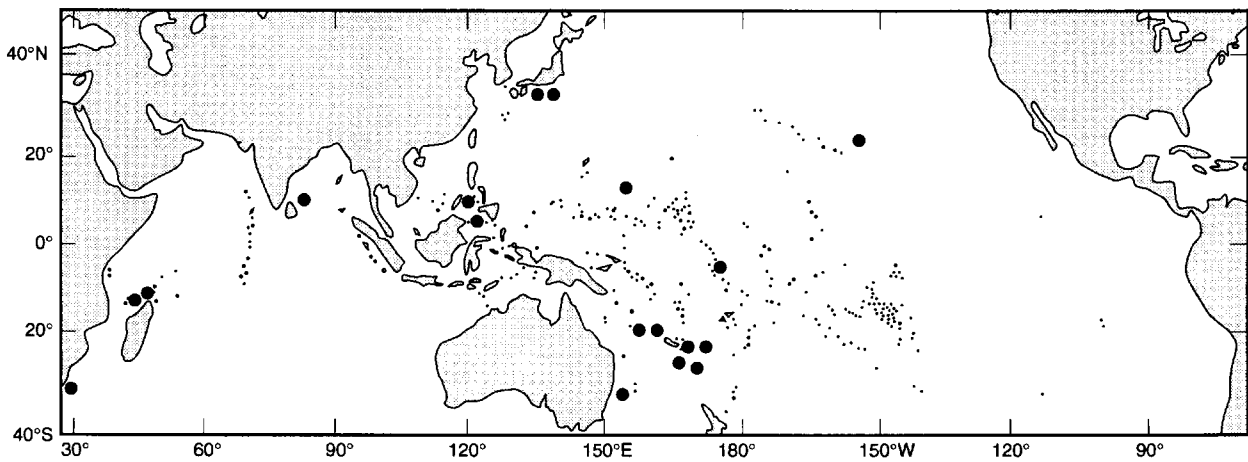


FIG. 36. — Geographic distribution of *Dynomene pilumnoides* Alcock, 1900.

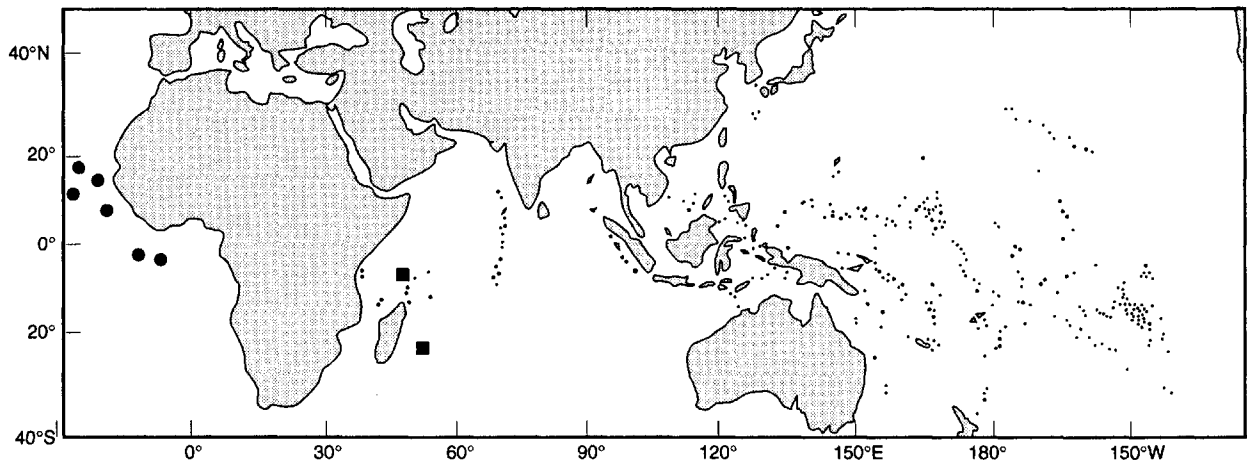


FIG. 37. — Geographic distribution of *Dynomene pugnatrix* de Man, 1889 (■), and *D. filholi* Bouvier, 1894 (●).

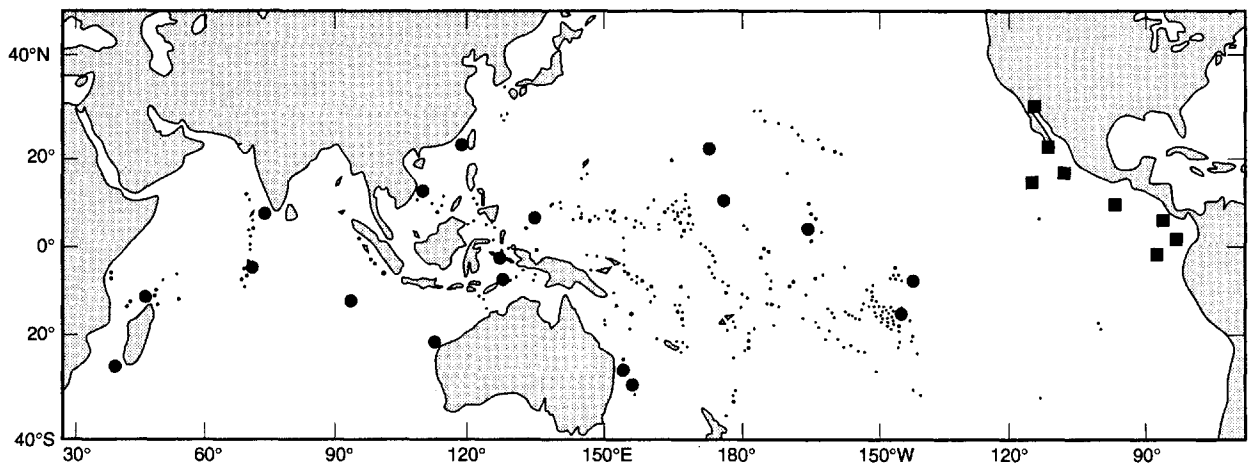


FIG. 38. — Geographic distribution of *Hirsutodynomene ursula* (Stimpson, 1860) (■) and *H. spinosa* (Rathbun, 1911) (●).

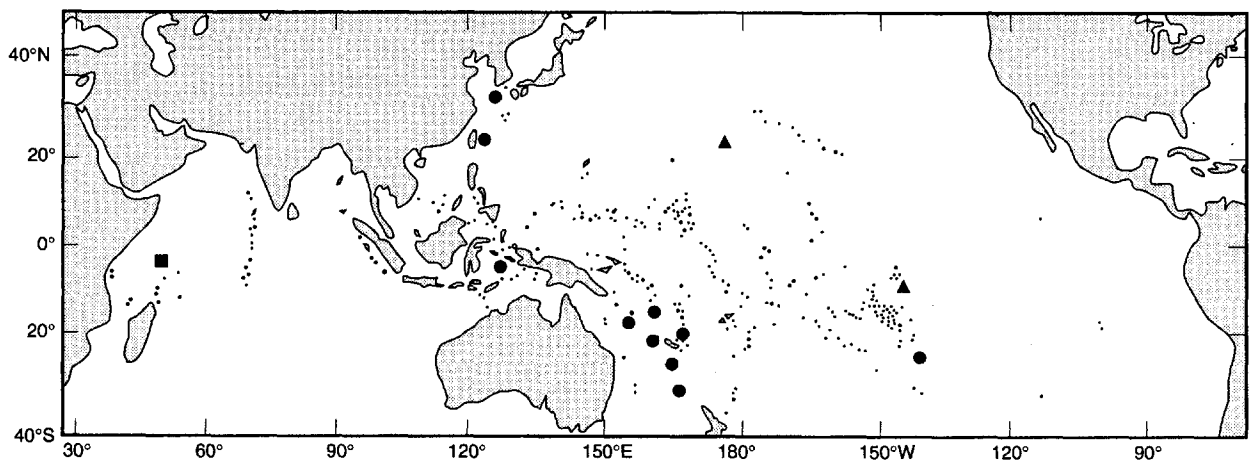


FIG. 39. — Geographic distribution of *Metadynomene devaneyi* (Takeda, 1977) (▲), *M. tanensis* (Yokoya, 1933) (●), and *M. crosnieri* sp. nov. (■).



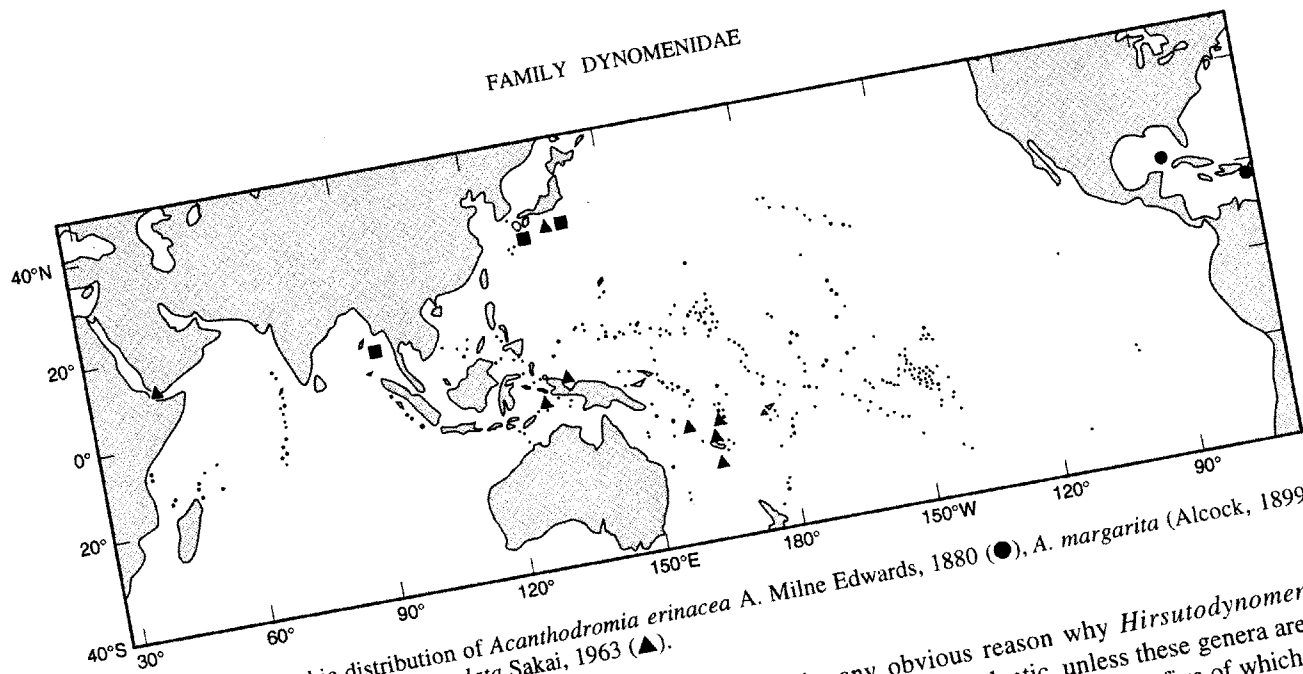


FIG. 40. — Geographic distribution of *Acanthodromia erinacea* A. Milne Edwards, 1880 (●), *A. margarita* (Alcock, 1899) (■), and *Paradynomene tuberculata* Sakai, 1963 (▲).

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

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

FIG. 41. — Longitudinal distribution of the Dynomenidae.

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

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

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