

CRABS OF THE FAMILY HOMOLODROMIIDAE, III. FIRST RECORD OF THE LARVAE

Joel W. Martin

A B S T R A C T

The first known larval stage of a species of the crab family Homolodromiidae is described from advanced embryos of a preserved *Dicranodromia felderi* Martin. The larvae are in some ways similar to those few larvae known for the other two dromiacean families, Dromiidae and Dynomenidae, and therefore are similar to anomuran and thalassinidean larvae in general, but differ in lacking a hairlike second telson process. The larvae are embryologically advanced in that the pereopods and maxillipeds are well developed and the abdomen has large pleopods on somites 2 through 5. Despite this apparently advanced developmental state at eclosion, the larvae do not possess uropods, a marked difference between them and all other known late-stage larvae of the Dromiacea, perhaps slightly closing the gap between anomuran and brachyuran larval morphology.

Morphology of the larval stages of crabs of the section Dromiacea has been a source of considerable confusion to students of decapod systematics. Although adult dromiaceans are crablike, the few known larvae of the Dromiacea, most studies of which have been on members of the family Dromiidae (see Table 1), are decidedly anomuran-like (see reviews in Rice, 1980, 1981a-c; Williamson, 1982, 1988a, b). Several workers (e.g., Williamson, 1976) suggested that the other two dromiacean families, Dynomenidae and Homolodromiidae, might have larvae that show somewhat intermediate characters between anomurans and primitive brachyurans, specifically the homolids. However, it is now known that larvae of at least one dynomenid species (*Acanthodromia erinacea* A. Milne Edwards) are also anomuran-like (Rice, 1981b). Larvae of the third family, the Homolodromiidae, have not been described previously, with the exception of a brief note by Cautier (1895) that lacked illustrations. The absence of any description of larvae in the Homolodromiidae is unfortunate. Many workers, such as Guinot (1978), feel that the homolodromiids are the most primitive of the three families (Dromiidae, Dynomenidae, and Homolodromiidae) constituting the Dromiacea, and indeed constitute a separate superfamily, the Homolodromioidea; they are therefore the most primitive of all the "true" crab families, if indeed dromiaceans belong in the Brachyura and not the Anomura, a point of much contro-

versy in the past. Knowledge of homolodromiid larvae might shed light on relationships both within the Dromiacea and between dromiaceans and the anomurans or brachyurans.

While visiting the National Museum of Natural History in July 1989, I removed 14 orange white, oval eggs, measuring on the average 2.4×1.9 mm ($N = 5$), from a large (32.0-mm carapace length) homolodromiid that later became a paratype (USNM 221961) of a new species, *Dicranodromia felderi* Martin, 1990, a deep-sea species from the western Atlantic (Martin, 1990). The developing embryos were removed from the outer egg membrane and partially cleared in 5% lactic acid. Although the embryos appeared to be well developed, and were probably close to hatching, many of the details could not be confirmed because of a lack of clear segmentation and poorly developed setation (see Fig. 1). Nevertheless, certain phylogenetically important characters can be discerned, allowing at least brief and rather speculative comments to be made concerning the relationships of the homolodromiids to other dromiacean crabs.

DESCRIPTION OF THE FIRST ZOEAE

The larvae are well developed, with chelipeds, maxillipeds, and pleopods obvious, therefore being more or less equivalent to late stage (at least third or fourth zoeal) larvae as described, for example, by Rice and Provenzano (1966) for *Dromidia antillensis*, Lang and Young (1980) for *Hypoconcha*

Table 1. Descriptions of dromiacean larvae subsequent to Gurney's (1939) bibliography. PZ = prezoa stage. An asterisk (*) indicates that the described material was taken from the plankton; all other material was laboratory-reared. Accounts marked (†) are taken from other literature sources and were not seen by the present author.

Family and species	Stage(s) described	Reference
Dromiidae		
<i>Conchoecetes artificiosus</i> (Fabricius)	PZ, Zoea 1, 2, Megalopa*	Sankolli and Shenoy, 1967† Terada, 1987
<i>Cryptodromia pileifera</i> Alcock	Zoea 1, Megalopa	Tan <i>et al.</i> , 1986
<i>Dromia personata</i> Linnaeus	Zoea 1-4, Megalopa	Rice <i>et al.</i> , 1970
<i>Dromia personata</i> Linnaeus	Zoea 1, 2, 5, Megalopa*	Pike and Williamson, 1960†
<i>Dromia dehaani</i> (Rathbun)	Zoea 1-3*	Terada, 1983†
<i>Dromia erythropus</i> (George Edwards)	Zoea 1-5, Megalopa	Laughlin <i>et al.</i> , 1982
<i>Dromidia antillensis</i> Stimpson	Zoea 1-6, Megalopa	Rice and Provenzano, 1966
<i>Hypoconcha arcuata</i> Stimpson	Zoea 1-3, Megalopa	Kircher, 1970
<i>Hypoconcha parasitica</i> (Linnaeus) (as <i>H. sabulosa</i> (Herbst))	Zoea 1-3, Megalopa	Lang and Young, 1980
<i>Petalomera japonica</i> (Henderson)	Zoea 1, 2	Terada, 1983†
<i>Petalomera japonica</i> (Henderson)	PZ, Zoea 1, 2, Megalopa	Hong and Williamson, 1986
<i>Petalomera wilsoni</i> (Fulton and Grant)	PZ, Zoea 1-3 Megalopa*	Wear, 1970 Wear, 1977
	Zoea 1, 2 Zoea 1, Megalopa*	Terada, 1983† Wear and Fielder, 1985
Dynomenidae		
<i>Acanthodromia erinacea</i> A. Milne Edwards	Zoea 1 (late embryo)	Rice, 1981b
Homolodromiidae		
<i>Dicranodromia felderi</i> Martin	Zoea 1 (late embryo)	This study

parasitica (as *H. sabulosa*), Laughlin *et al.* (1982) for *Dromia erythropus*, and others (see Table 1).

The carapace (Fig. 1a, b) is globular, nearly spherical, with no evidence of any lateral or dorsal spines. The rostrum extends ventrally between the eyestalks and is weakly tridentate. The eyes are well formed and lightly pigmented.

The antennule (Fig. 1c, right side) is biramous, with both rami weakly segmented and with the protopod bearing setae at each segmentation line. The antenna (Fig. 1c, left side) has a 3-segmented peduncle and a weakly segmented flagellum almost as long as the antennal scale. The antennal scale is broad and flat, with about 20 setae along the inner margin and about 10 setae on the outer margin, with the outer setae covering only the distal half of the scale border.

The maxilla (Fig. 1d) bears numerous setae (or setal precursors) along the scaphognathite blade. The endopod is unsegmented, and the bilobed basal and coxal lobes bear few setae distally. The maxillule was tightly curled, and I could not discern any of its shape or setation.

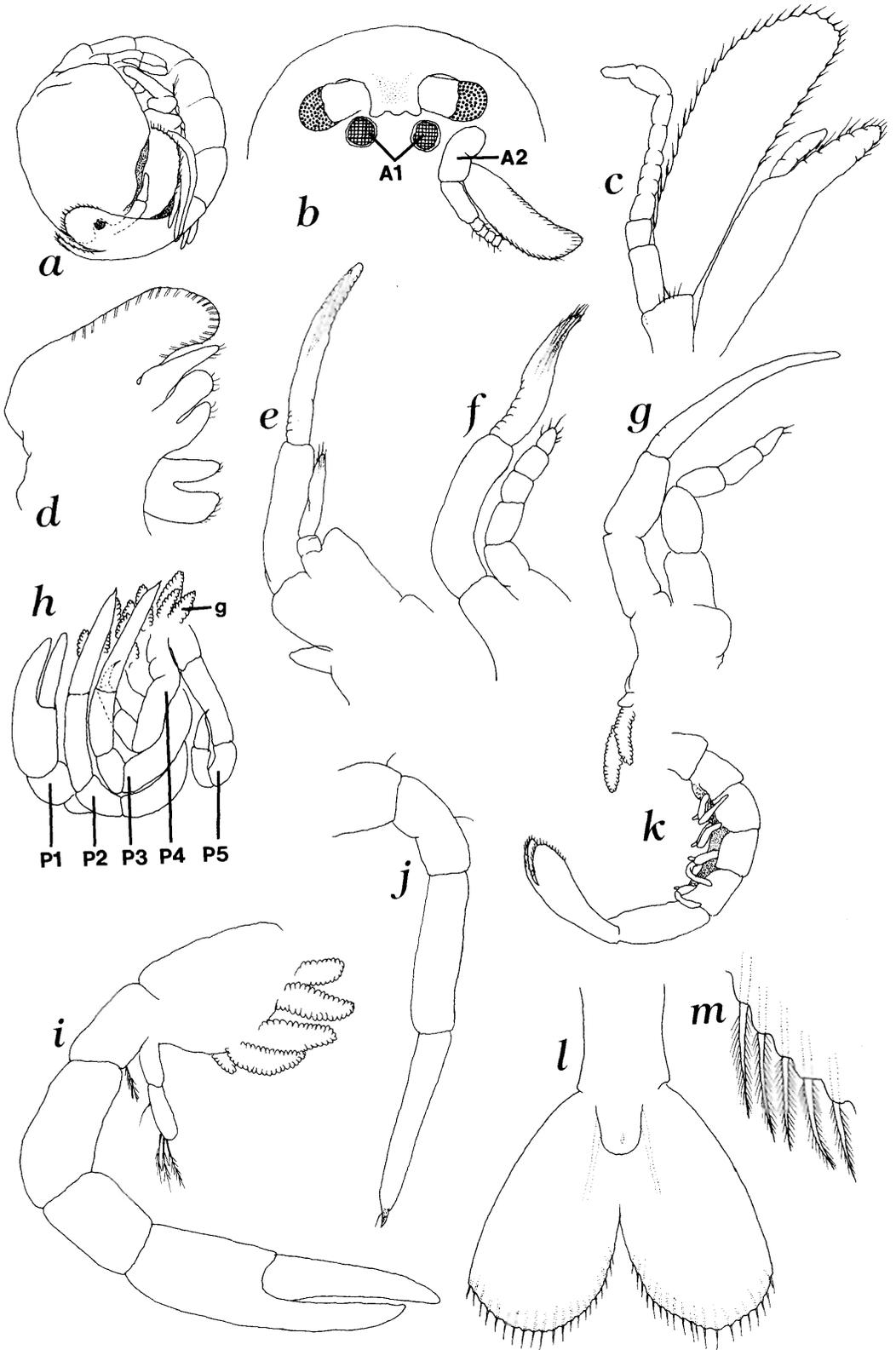
The maxillipeds are biramous, the external branch bearing signs of multisegmentation

and distal setae. Segmentation of the endopod is just discernible; there are 2 or 3 segments on maxilliped 1, 5 on maxilliped 2, and 5 on maxilliped 3 (Fig. 1e-g).

The pereopods (Fig. 1h) are all well developed, each bearing at least 2 branchiae. The cheliped bears a short 2-segmented exopod on the basi-ischium and up to 5 branchiae, all of which appear to be arthrobranch in location (Fig. 1i). Pereopods 2 and 3 terminate in a sharp, sclerotized spine and a small subterminal seta (Fig. 1j). Pereopods 4 and 5, which are greatly reduced in the adult, are about half the length of pereopods 2 and 3 and bear a similar sclerotized spine and seta at the tip of the dactylus but have not yet developed the subchelate terminal process seen in adults.

The abdomen (Fig. 1k) consists of 6 distinct somites plus the telson. There are no apparent spines or tubercles on any of the abdominal somites. Somites 2 through 5 bear biramous, 3-segmented pleopods, the distal portion of which curves dorsally over the lateral margin of each pleuron. The pleopodal endopod is small, 2-segmented, and bears few distal setae.

The telson (Fig. 1l, m) is large and broad, with a deep medial cleft. Approximately 20



plumose setae are present on the rounded posterior border of each branch. The second telson process (counting from the external-most seta) does not differ from any of the others; all terminal processes are short, plumose setae (Fig. 1m).

DISCUSSION

Of the three extant dromiacean families, larvae are best known for the Dromiidae (Table 1). Many of the early descriptions (listed in Gurney, 1939, 1942) of larvae in this section were based on plankton-caught specimens, which were therefore of somewhat questionable parentage. Some of the studies cited by Gurney were of larvae of the Homolidae or Latreillidae, then considered to belong to the Dromiacea. However, there were several studies, notably that of Lebour (1934), that focused on larvae that could be reliably attributed to the Dromiidae; these larvae are decidedly anomuran in their morphology. There have been a number of descriptions of dromiacean larvae subsequent to Gurney's monograph (Table 1). I have not been able to examine all of the larval descriptions listed in Table 1, but it is clear from those that I have seen, and from reading the more extensive works of Rice (1980, 1981a-c) and Williamson (1982, 1988a, b), that, without exception, these dromiid larvae are, for all intents and purposes, anomuran. The same can be said for larvae of the family Dynomenidae, based on the description of a zoeal stage of *Acanthodromia erinacea* given by Rice (1981b).

One salient feature of anomuran (and many thalassinidean) larvae is the possession of a hairlike second process on the posterior border of the telson. This feature, so common in anomuran larvae that it has been referred to in the past as the "anomuran hair," is lacking in the larvae of *Dicranodromia felderi*. Although the absence of this feature could be taken as evidence that the homolodromiids are less like anomurans than are other dromiacean families, and therefore are candidates for bridging the an-

omuran-homoloid "gap," there are other explanations. The "anomuran hair" depends, in at least some anomuran and thalassinidean species, on the developmental stage of the larvae. For example, Konishi (1989) documented that this seta is present in early zoeal stages of *Upogebia major* (de Haan) but has disappeared, or more accurately has become a fixed spine rather than a hairlike seta, by the third zoeal stage. The loss of the hairlike second telson process during anomuran ontogeny was noted also by Shenoy (1967) and Ngoc-Ho (1977, 1981). It is possible that, because of the relatively advanced stage of the homolodromiid hatchling, the second telson process in *D. felderi* has been lost during development. This is also apparently the case in at least one dromiid, *Cryptodromia pileifera* Alcock, a species having only one zoeal stage, which also lacks this hairlike seta and has instead a "vestigial knob" (Tan *et al.*, 1986: 111). In addition, several dromiid species lack the zoeal stage altogether, hatching as a megalopa, so that the group, as a whole, shows a tendency toward abbreviated development, with the number of zoeal stages ranging from 0-6 (see Tan *et al.*, 1986, table 1). All other characters, such as the broad antennal scale and more or less spatulate telson, would seem to argue for anomuran rather than brachyuran affinity.

A problem arises when the absence of uropods is considered. Uropods are usually absent in early stage dromiacean larvae, and so their absence in the prezoal stage of the dynomenid *Acanthodromia erinacea* necessitated no explanation by Rice (1981b). Uropods always appear by the third zoeal stage in those species having at least three zoeal stages. If the larvae of *Dicranodromia felderi* are indeed in a rather advanced stage of development, as seems to be indicated by the condition of the pleopods, pereopods, maxillipeds, and unfused abdomen, the absence of uropods is puzzling. If the absence of uropods is taken to imply that homolodromiids are more allied to brachy-

←
Fig. 1. *Dicranodromia felderi* Martin, 1990, late embryo removed from USNM 221961 (female paratype). *a*, Lateral view, embryo removed from egg membrane; *b*, frontal view of eyes, rostrum, and antenna 2; antenna 1 removed (hatched areas); *c*, first antenna (at right) and second antenna, left side, dorsal view; *d*, maxilla; *e-g*, first through third maxillipeds, respectively; *h*, pereopods in situ; *i*, cheliped; *j*, pereopod 3; *k*, abdomen and telson, lateral view showing pleopods; *l*, telson, ventral view; *m*, higher magnification of setae on inner margin of telson showing plumose nature. A1 = first antenna (antennule); A2 = second antenna; P1-5 = pereopods 1 through 5; *g* = gill. Not drawn to scale.

uran crabs than are dromiids or dynome-nids, there are problems in explaining the similarity of the adult morphologies of the three families and in explaining zoeal similarities such as the presence of an anomuran-like antennal scale in all three. On the other hand, it is possible that some characters in these late-stage zoeal hatchlings have not developed ontogenetically at the same pace as have other features. Hong and Williamson (1986: 1273), in their discussion of development in *Petalomera japonica* (Henderson), a species having only two zoeal stages, both of which lack uropods, noted that "asynchronous progress in different appendages of an individual larva is not uncommon in the decapod moult cycle, and morphogenesis of uropods appears to precede other morphological changes . . ." (cited by Hong and Williamson as personal communication from K. Anger). The description of the larval development of *Cryptodromia pileifera* by Tan *et al.* (1986) would question the significance of the absence of uropods. In that species, there is a single zoeal stage that lacks uropods, but that metamorphoses to the uropod-bearing megalopa.

As has been discussed often in the past, the apparent contradiction between dromiacean adult and larval morphology has caused various workers to suggest that the Dromiacea might be in some ways intermediate between the Anomura and Brachyura, and that the larvae of other dromiacean families might, when fully known, display characters intermediate between anomurans and "lower" brachyurans such as the homolids. It is also possible that dromiaceans are simply true anomurans, not intermediate in any way, but displaying remarkable convergent evolution in the attainment of a crablike body. This seems very possible, especially in light of the other groups of brachyuran-like anomurans, such as lithodid and porcellanid crabs and the Lomisidae. This scenario has been suggested by many previous students of larval morphology (e.g., Williamson, 1976). The problem with this explanation is that students of adult morphology (e.g., Guinot, 1978, 1979) feel that dromiacean adults are not at all anomuran, but are true (albeit primitive) brachyurans, a view that persists in many current classifications of the Decapoda (e.g., Bowman and Abele, 1982).

Another, more recent, hypothesis championed by Williamson (1988a, b) is that the dromiaceans are not an intermediate group but rather are true brachyurans. The attainment of anomuran larvae is then credited to genetic transfer of material as a result of past cross-fertilization between a true brachyuran and a true anomuran (see Williamson, 1988a, b). While not qualified to comment on the possibility of such an occurrence in the group's history, I feel that the earlier hypothesis, that dromiaceans are true anomurans with crablike adult morphology, is the more likely. This is especially so in light of recent molecular work (which of course was not available to Williamson or earlier workers) suggesting that, on the basis of 18S ribosomal RNA, the dromiids are more similar to anomurans than to brachyurans (Spears and Abele, 1988). Unfortunately, because the larvae of the Homolodromiidae hatch in an advanced stage (assuming that larvae of *D. felderi* are representative of the family), some characters typically found on dromiacean larvae can not be compared. Thus the description of the zoea of *D. felderi* adds little to our understanding of dromiacean affinities.

ACKNOWLEDGEMENTS

This paper is the third in a series on homolodromiid crabs that was facilitated by a Smithsonian Institution Short-Term Visitor Award in July 1989 (Báez and Martin, 1989; Martin, 1990). I thank R. B. Manning, B. Kensley, A. B. Williams, G. and S. Graves, and the Crustacea Section of the National Museum of Natural History for assistance during my stay. I especially thank Gary and Sid Graves for their friendship, generosity, and counsel during that visit.

LITERATURE CITED

- Báez R., P., and J. W. Martin. 1989. Crabs of the family Homolodromiidae, I. Description of the male of *Homolodromia robertsi* Garth, 1973, based on specimens from deep waters off the coast of Chile.—*Journal of Crustacean Biology* 9: 492–500.
- Bowman, T. E., and L. G. Abele. 1982. Classification of the Recent Crustacea.—*In*: L. G. Abele, ed., *The biology of Crustacea*. Vol. 1. Systematics, the fossil record, and biogeography. Academic Press, New York, New York. Pp. i–xx, 1–319.
- Caustier, E. 1895. Sur le développement embryonnaire d'un Dromiacé du genre *Dicranodromia*.—*Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, Paris 120: 573–575.
- Guinot, D. 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyours.—*Bulletin Biologique de la France et de la Belgique* 112: 211–292.
- . 1979. Données nouvelles sur la morphologie,

- la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. — Mémoires du Muséum National d'Histoire Naturelle, Zoologie 112: 1-354.
- Gurney, R. 1939. Bibliography of the larvae of decapod Crustacea. — Pp. 1-123. Ray Society, London, England.
- . 1942. Larvae of decapod Crustacea. Ray Society, London, England. Publication no. 129, pp. 1-306.
- Hong, S. Y., and D. I. Williamson. 1986. The larval development of *Petalomera japonica* (Henderson) (Decapoda, Dromiidae) reared in the laboratory. — Journal of Natural History 20: 1259-1278.
- Kircher, A. B. 1970. The zoeal stages and glaucothoe of *Hypoconcha arcuata* Stimpson (Decapoda: Dromiidae) reared in the laboratory. — Bulletin of Marine Science 20: 769-792.
- Konishi, K. 1989. Larval development of the mud shrimp *Upogebia (Upogebia) major* (De Haan) (Crustacea: Thalassinidea: Upogebiidae) under laboratory conditions, with comments on larval characters of thalassinid families. — Bulletin of the National Research Institute of Aquaculture, Nansei, Mei 15: 1-17.
- Lang, W. V., and A. M. Young. 1980. Larval development of *Hypoconcha sabulosa* (Herbst) (Crustacea: Decapoda: Dromiidae) reared in the laboratory, and a review of the systematic position of the family Dromiidae. — Fishery Bulletin, United States 78: 851-863.
- Laughlin, R. A., P. B. Rodriguez, and J. A. Marval. 1982. The complete larval development of the sponge crab *Dromia erythropus* (George Edwards, 1771) (Brachyura: Dromiidae) from the Archipelago de los Roques, Venezuela. — Journal of Crustacean Biology 2: 342-359.
- Lebour, M. V. 1934. The life history of *Dromia vulgaris*. — Proceedings of the Zoological Society of London 1934: 241-249.
- Martin, J. W. 1990. Crabs of the family Homolodromiidae, II. *Dicranodromia felderi*, a new species from the western Atlantic, with notes on the holotype of *D. ovata* A. Milne Edwards, 1880. — Journal of Crustacean Biology 10: 708-720.
- Ngoc-Ho, N. 1977. The larval development of *Upogebia darwini* (Crustacea, Thalassinidea) reared in the laboratory, with a redescription of the adult. — Journal of Zoology 181: 439-464.
- . 1981. A taxonomic study of the larvae of four thalassinid species (Decapoda, Thalassinidea) from the Gulf of Mexico. — Bulletin of the British Museum (Natural History), Zoology 40: 237-273.
- Pike, R. B., and D. I. Williamson. 1960. Larvae of decapod Crustacea of the families Dromiidae and Homolidae from the Bay of Naples. — Pubblicazioni della Stazione Zoologica di Napoli 31: 553-563.
- Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. — Transactions of the Zoological Society of London 35: 271-424.
- . 1981a. Crab zoeae and brachyuran classification: a reappraisal. — Bulletin of the British Museum (Natural History), Zoology 40: 287-296.
- . 1981b. The zoea of *Acanthodromia erinacea* A. Milne Edwards; the first description of a dromioid larva (Decapoda, Dromioidea). — Journal of Crustacean Biology 1: 174-176.
- . 1981c. The megalopa stage in brachyuran crabs. The Podotremata Guinot. — Journal of Natural History 15: 1003-1011.
- , R. W. Ingle, and E. Allen. 1970. The larval development of the sponge crab, *Dromia personata* (L.) (Crustacea, Decapoda, Dromiidae), reared in the laboratory. — Vie et Milieu, Series A, Biologie Marine 21: 223-240.
- , and A. J. Provenzano. 1966. The larval development of the West Indian sponge crab *Dromidia antillensis* (Decapoda: Dromiidae). — Journal of Zoology 149: 297-319.
- Sankolli, K. N., and S. Shenoy. 1967. Larval development of a dromiid crab, *Conchoecetes artificiosus* (Fabr.) (Decapoda, Crustacea) in the laboratory. — Journal of the Marine Biological Association of India 9: 96-101.
- Shenoy, S. 1967. Studies on larval development in Anomura (Crustacea, Decapoda). II. — Proceedings of the Symposium on Crustacea, Ernakulam, Part II, pp. 777-804, Marine Biological Association of India.
- Spears, T., and L. G. Abele. 1988. Molecular phylogeny of brachyuran crustaceans based on 18S rRNA nucleotide sequences. — American Zoologist 28: 2A (abstract).
- Tan, L. W. H., S. S. L. Lim, and P. K. L. Ng. 1986. Larval development of the dromiid crab *Cryptodromia pileifera* Alcock, 1899 (Decapoda: Dromiidae) in the laboratory. — Journal of Crustacean Biology 6: 111-118.
- Terada, M. 1983. Zoea larvae of three crabs in the family Dromiidae. — Zoological Magazine 92: 361-370.
- . 1987. Zoeal forms of 14 species of crabs from the Enshunada. — Researches on Crustacea 16: 93-120.
- Wear, R. G. 1970. Some larval stages of *Petalomera wilsoni* (Fulton and Grant, 1902) (Decapoda, Dromiidae). — Crustaceana 18: 1-12.
- . 1977. A large megalopa attributed to *Petalomera wilsoni* (Fulton & Grant, 1902) (Decapoda, Dromiidae). — Bulletin of Marine Science 27: 572-577.
- , and D. Fielder. 1985. The marine fauna of New Zealand: larvae of the Brachyura (Crustacea, Decapoda). — New Zealand Oceanographic Institute Memoir 92: 1-90.
- Williamson, D. I. 1976. Larval characters and the origin of crabs (Crustacea, Decapoda, Brachyura). — Thalassia Jugoslavica 10: 401-414.
- . 1982. Larval morphology and diversity. — In: L. G. Abele, ed., The biology of Crustacea, Vol. 2. Embryology, morphology, and genetics. Pp. 43-110. Academic Press, New York. Pp. i-xx, 1-319.
- . 1988a. Evolutionary trends in larval form. — Symposium of the Zoological Society of London 59: 11-25.
- . 1988b. Incongruous larvae and the origin of some invertebrate life-histories. — Progress in Oceanography 19: 87-116.

RECEIVED: 14 May 1990.

ACCEPTED: 8 June 1990.

Address: Life Sciences Division, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.