

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

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ABSTRACT

Several large adults of *Homolodromia robertsi* Garth, 1973, previously known from 2 females collected off the coast of Peru, were collected from deep waters off the coast of Chile. The male of the species is described. In general, characters of the male are similar to those of the female; little sexual dimorphism exists. The first gonopod is 3-segmented, robust, and similar to that of other genera in the Dromiacea and to an earlier description of the pleopods of *Homolodromia paradoxa*. Data on the biology of the species (occurrence of ovigerous females, geographic range, and morphometry) are included. The range of the species is extended more than 2,600 km south.

The brachyuran crab family Homolodromiidae was erected by Alcock (1899b) (as Homolodromidae, corrected to Homolodromiidae by Stebbing, 1905: 58) to accommodate the genera *Homolodromia* A. Milne Edwards, 1880, *Dicranodromia* A. Milne Edwards, 1880, and *Arachnodromia* Alcock, 1899a (later synonymized). The primitive nature of the homolodromiids (see Discussion) has resulted in their historical alignment with the anomuran-like crabs of the superfamily Dromioidea in the section Dromiacea (e.g., Rathbun, 1937; Balss, 1957). More recently, Guinot (1978) recognized additional characters separating homolodromiids from other dromioids and consequently elevated the Homolodromiidae to the rank of superfamily, thereby establishing the Homolodromioidea Alcock as the second superfamily of the Dromiacea. This arrangement has not been followed by all workers. The genus *Homolodromia*, originally erected for a male specimen of *H. paradoxa* A. Milne Edwards collected at a depth of 356 fathoms (651 m) "off Nevis" in the Leeward Islands of the Caribbean (see Milne Edwards, 1880, 1883; Bouvier, 1896; Milne Edwards and Bouvier, 1902; Rathbun, 1937), now additionally contains *H. bouvieri* Doflein, known from East Africa (Doflein, 1904), and *H. robertsi* Garth, known from two females taken off the coast of Peru (Garth, 1973). Very little is known

about the systematic relationships, morphology, and biogeography of the family.

In 1980 and 1981, collections of a large species of homolodromiid crab were made from deep waters off the coast of Chile by the vessels RV *Itzumi* and RV *Tiberiades*. These crabs appear to be conspecific with *Homolodromia robertsi* Garth, 1973. Below we describe the male of the species for the first time and provide additional observations on the morphology and biology of the female.

MATERIALS AND METHODS

Material of *Homolodromia robertsi* Garth was obtained through a project entitled "Exploración y prospección de recursos pesqueros del Talud Continental de Chile," a systematic fishery survey of the continental slopes of Chile. The survey was carried out by the IFOP (Instituto de Fomento Pesquero de Chile) and the Museo Nacional de Historia Natural de Santiago, Chile, and was supported by a grant from CORFO-CHILE (Anonymous, 1981; Henríquez *et al.*, 1981). The cruises covered the area between Arica and Isla Mocha at depths of 500-1,000 m (Cruise 1, RV *Itzumi*, 1980: 83 stations; Cruise 2, RV *Tiberiades*, 1981: 90 stations). Illustrations were made with a Wild M-5APO stereoscope with camera lucida. Specimens of both sexes of *H. robertsi* have been deposited in the Natural History Museum of Los Angeles County and in the Museo Nacional de Historia Natural de Santiago de Chile.

*Homolodromia robertsi* Garth, 1973

*Homolodromia robertsi* Garth, 1973, pp. 1-3, Fig. 1A-F.

Description of Male (Figs. 1-3, Table 1)

Fig. 1. *Homolodromia robertsi* Garth, largest male (carapace length = 32.3 mm). a, dorsal view; b, ventral view.



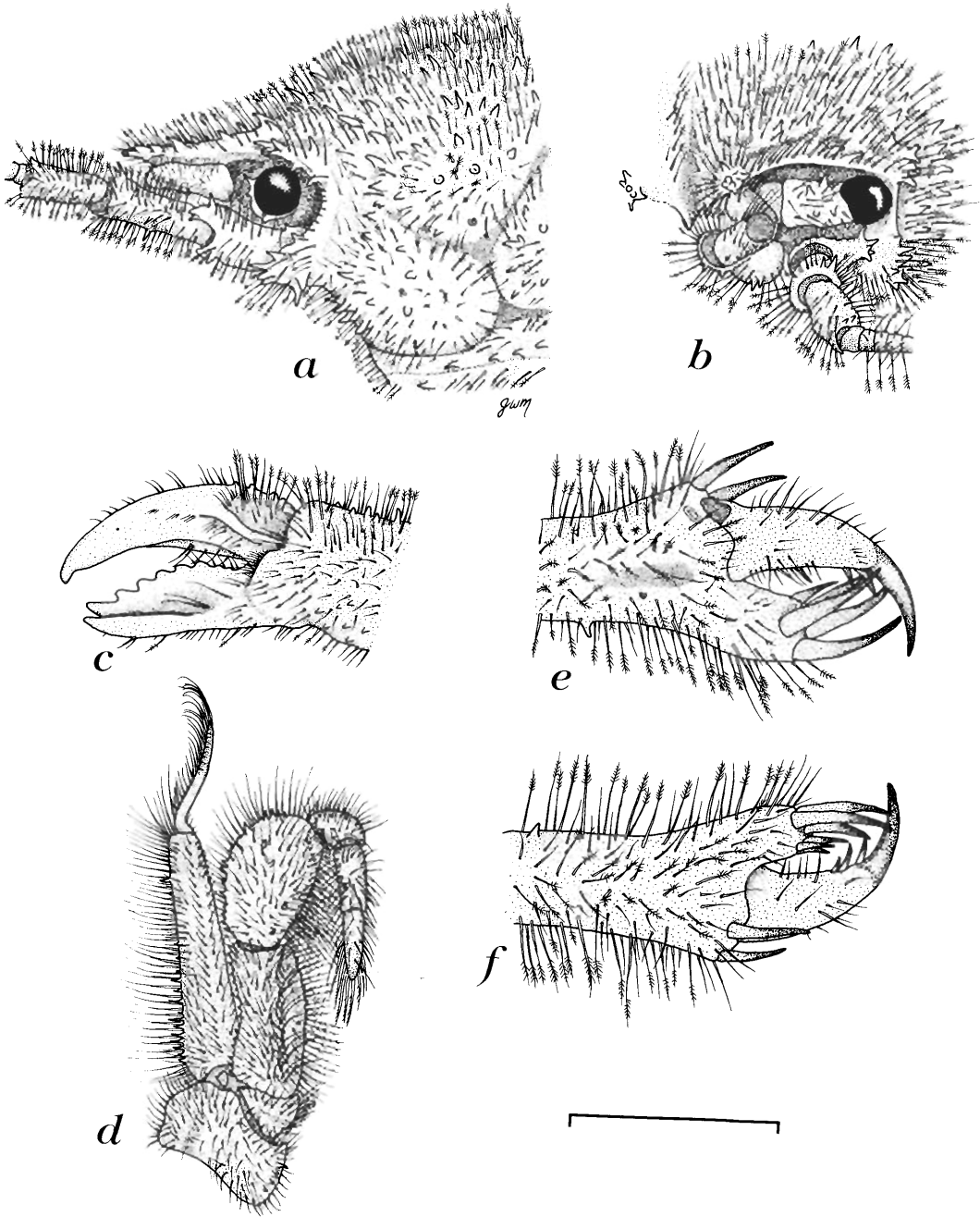


Fig. 2. *Homolodromia robertsi* Garth, selected characters of smallest male (carapace length = 20.2 mm). *a*, lateral view of left orbital region of carapace; *b*, frontal view of left orbital region; *c*, "inner" view of right chela showing bifid, grooved propodus and interdigitating fingers; *d*, external face of left third maxilliped; *e*, posterior (functional dorsal) surface of chela of pereopod 4; *f*, posterior (dorsal) surface of chela of pereopod 5. Scale bar = 5.0 mm for *a-d*, 2.5 mm for *e, f*.

Fig. 3. Male pleopods of *Homolodromia robertsi* Garth. *a*, male first and second pleopods in situ, showing position of pleopod 2 within anteromedial groove of pleopod 1; *b*, male first pleopod; *c*, male second pleopod. P2 = second pereopod, P3 = third pereopod, pl1 = male first pleopod, pl2 = male second pleopod. Scale bar = 5.0 mm for *b* and *c*; *a* not drawn to scale.

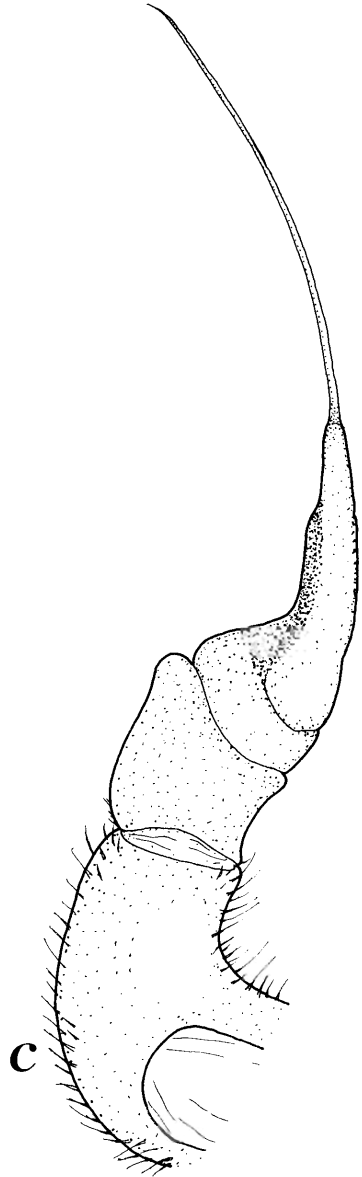
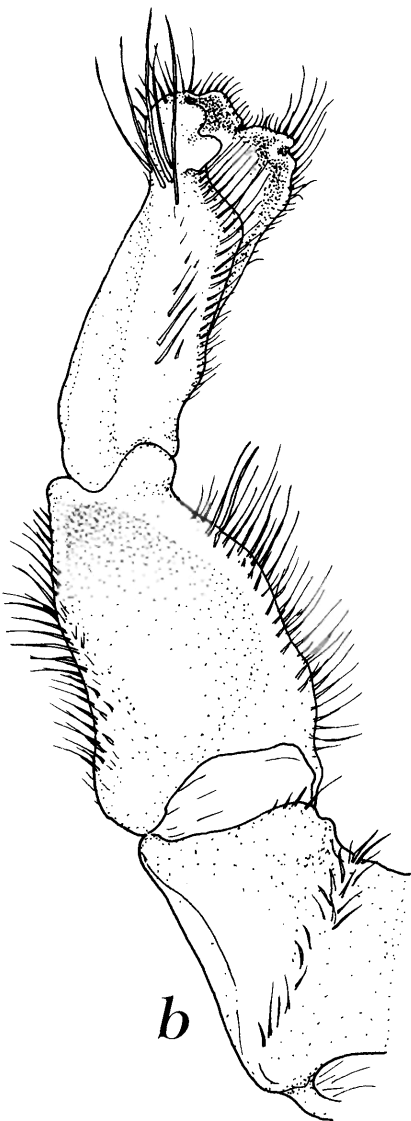
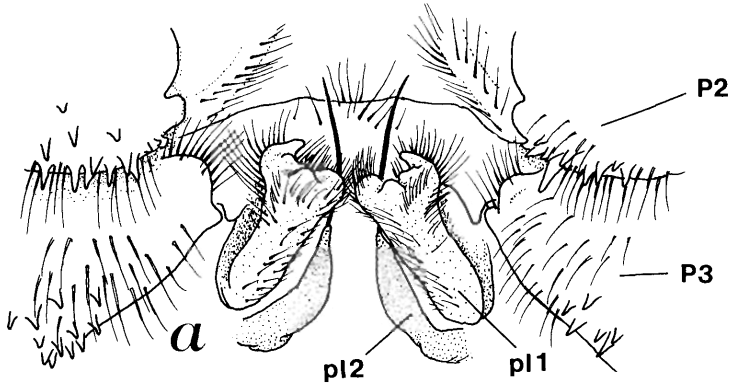


Table 1. Collection and morphometric data for 13 Chilean specimens of *Homolodromia robertsi* Garth, 1973. Body measurements in mm. (\*) = approximated, (\*\*) = in regeneration.

| Specimen number                        | 1         | 2         | 3          | 4         | 5         |
|--|-----------|-----------|------------|-----------|-----------|
| Latitude (S)                           | 32°06'    | 32°06'    | 28°26'     | 28°26'    | 28°26'    |
| Longitude (W)                          | 71°46'    | 71°46'    | 71°23'     | 71°23'    | 71°23'    |
| Depth (m)                              | 850       | 850       | 560        | 560       | 560       |
| Date                                   | 04 Sep 80 | 04 Sep 80 | 16 Jan 81  | 16 Jan 81 | 16 Jan 81 |
| Cruise and Trawl                       | 80068     | 80068     | 81013      | 81013     | 81013     |
| Sex                                    | female    | female    | male       | male      | female    |
| Carapace length                        | 43.2      | 26.7      | 25.6       | 20.2      | 37.2      |
| Rostrum length and width (l./w.)       | 4.1/3.7   | 2.2/2.6   | 2.0/2.2    | 0.9/2.6   | 3.6/3.5   |
| Carapace width                         | 37.8      | 22.2      | 21.7       | 16.4      | 30.8      |
| Cheliped: (coxa-ischium-merus)         | 35.5      | 22.5      | —          | 18.1      | 29.8      |
| (carpus-propodus)                      | 39.1      | 23.5      | —          | 20.1      | 32.3      |
| Right chela length                     | —         | 16.9      | —          | 14.1      | 23.3      |
| height of palm                         | —         | 4.5       | —          | 3.8       | 6.1       |
| length of dactylus                     | —         | 7.9       | —          | 6.4       | 11.2      |
| Left chela length                      | 28.2      | 16.9      | 18.7       | 13.9      | 22.9      |
| height of palm                         | 7.6       | 4.6       | 4.6        | 3.8       | 6.1       |
| length of dactylus                     | 12.8      | 7.9       | 9.4        | 6.1       | 11.4      |
| Length of first ambulatory leg         | —         | 73.6      | —          | —         | —         |
| Length of second ambulatory leg        | —         | 74.1      | —          | 63.1      | —         |
| Length of third ambulatory leg         | —         | 32.8      | 35.3       | 26.9      | 42.8      |
| Length of fourth ambulatory leg        | 42.6      | 31.9      | 35.7       | 27.5      | 43.1      |
| Abdomen length/width                   | 78.4/27.1 | 30.1/13.8 | 34.7/9.8   | 26.2/7.8  | 64.6/22.2 |
| Telson length/width                    | 42.8/26.9 | 15.6/13.8 | 10.7/8.5   | 9.9/6.1   | 28.6/22.3 |
| Length of male pleopods (first/second) | —         | —         | 9.8/11.9   | 9.5/12.9  | —         |
| penultimate/terminal segments          | —         | —         | (*)8.5/9.4 | 7.1/11.1  | —         |

*Material Examined.*—Specimens of *Homolodromia* were collected off the coast of Chile in both 1980 and 1981. These collections yielded 13 adult or subadult specimens (5 males, 8 females) of *Homolodromia robertsi* (see Table 1). The female holotype (AHF No. 719; see Garth, 1973) of *H. robertsi* was also examined. Specimens of *Homolodromia paradoxa* were borrowed from the Museum of Comparative Zoology, Harvard University (male holotype, MCZ 6512), and from the National Museum of Natural History (USNM), Smithsonian Institution (uncatalogued specimens). Specimens of *Dicranodromia ovata* and *D. baffini* (uncatalogued material) were also borrowed from the National Museum.

**Carapace** (Figs. 1, 2*a, b*).—Similar to that described for females (Garth, 1973); extremely convex, with distinct subparallel grooves (apparently cervical groove and postcervical groove) that divide carapace roughly into thirds, distinct branchial sutures, large inflated branchial regions, and bifid rostrum ("rostral horns" of Garth, 1973). Entire carapace covered with short, blunt spines and short, distinctive, distally plumose setae.

**Size.**—Carapace length (including rostrum) and width of smallest 20.2 by 16.4 mm, respectively; largest 32.3 by 25.9 mm (see Table 1).

**Third maxillipeds** (Figs. 1*b, 2d*).—More

or less pediform, but with expanded merus shielding other mouthparts. Borders of segments of endopod and exopod spinose and setose.

**Chelipeds** (Figs. 1*a, b, 2c*).—Right and left chelipeds equal in length, chelae (dactylus plus propodus) approximately three-fourths length of carapace. Chelae as described for females, with dentate fingers and with dactylus fitting into grooved and fork-tipped propodal finger. Dorsal surface of dactylus with proximal flattened area bearing several plumose and simple setae; dorsal border becoming ridgelike toward distal terminus of dactylus. Entire appendage with numerous short spines and distally plumose setae.

**First and second ambulatory pereopods.**—Similar in length (Table 1) (note that male in Fig. 1 has lost the last three segments of the left second walking leg and is regenerating the right second walking leg; normal condition similar to female illustrated in Garth, 1973: 2, fig. 1A); both pereopods spinose, setose, and nearly twice length of cheliped and with recurving dactylus.

**Third and fourth ambulatory pereopods**

Table 1. Extended.

| 6         | 7         | 8         | 9         | 10               | 11        | 12        | 13               |
|-----------|-----------|-----------|-----------|------------------|-----------|-----------|------------------|
| 28°26'    | 28°26'    | 26°55'    | 27°50'    | 27°50'           | 25°06'    | 19°03'    | 21°08'           |
| 71°23'    | 71°23'    | 70°59'    | 71°18'    | 71°00'           | 70°35'    | 70°25'    | 70°26'           |
| 560       | 560       | 805       | 720       | 720              | 740       | 820       | 880              |
| 16 Jan 81 | 16 Jan 81 | 21 Jan 81 | 21 Jan 81 | 21 Jan 81        | 23 Jan 81 | 18 Feb 81 | 22 Feb 81        |
| 81013     | 81013     | 81026     | 81027     | 81027            | 81037     | 81056     | 81075            |
| female    | female    | male      | female    | ovigerous female | male      | male      | ovigerous female |
| 35.4      | 42.6      | 26.1      | 38.4      | 31.6             | 22.9      | 32.3      | 39.0             |
| 3.4/3.4   | 4.0/4.9   | 3.0/3.0   | 4.2/3.4   | 3.1/2.5          | 2.8/2.7   | 2.9/4.0   | 2.0/4.2          |
| 29.5      | 36.0      | 24.2      | 30.9      | 28.6             | 19.9      | 25.9      | 34.6             |
| 30.2      | 36.7      | 28.1      | 31.7      | 28.4             | 24.9      | 29.7      | 33.9             |
| 31.2      | 38.4      | 28.9      | 33.2      | 31.4             | 25.1      | 32.2      | —                |
| 22.1      | 27.6      | 20.9      | 24.0      | 22.1             | 18.1      | 22.4      | —                |
| 6.0       | 7.1       | 6.1       | 6.6       | 7.0              | 5.8       | 5.8       | —                |
| 10.5      | 12.3      | 9.1       | 11.7      | 9.8              | 9.2       | 10.2      | —                |
| 22.1      | 27.5      | 21.2      | 24.1      | 22.3             | 18.5      | 22.3      | —                |
| 6.1       | 7.3       | 6.1       | 6.5       | 7.0              | 5.6       | 5.6       | —                |
| 10.7      | 12.2      | 9.4       | 11.7      | 10.4             | 8.6       | 10.7      | —                |
| (*90.7    | —         | 89.1      | —         | —                | 89.3      | 101.2     | 101.4            |
| (*87.6    | —         | 90.3      | —         | —                | (*91.0    | (**)55.2  | 108.2            |
| 40.9      | 48.7      | 38.9      | 43.9      | 40.5             | 33.1      | 41.4      | 46.2             |
| 41.1      | 44.3      | 36.4      | 42.6      | 41.1             | 36.1      | 41.0      | 44.4             |
| 59.5/20.6 | 75.5/27.2 | 37.6/11.3 | 65.9/25.1 | 59.9/20.3        | 32.5/9.2  | 35.6/12.1 | 68.4/23.2        |
| 32.2/20.5 | 39.4/27.1 | 13.5/9.2  | 36.8/25.1 | 30.9/19.8        | 11.2/8.0  | 14.1/9.4  | 34.7/22.4        |
| —         | —         | 13.6/16.6 | —         | —                | 10.9/13.9 | 13.0/16.7 | —                |
| —         | —         | 10.5/14.6 | —         | —                | 8.6/12.1  | 10.5/15.0 | —                |

(Fig. 2e, f).—Chelate, similar in length, less than half length of ambulatory legs 1 and 2, directed posteriorly (pereopod 4) and anteriorly (pereopod 5), with propodus extended to form blunt spine-tipped finger opposing hooklike sclerotized dactylus.

Abdomen.—Seven-segmented, with all segments loosely articulated and with seventh (telson) one-third to one-half length of other segments combined. Vestigial pleopods present on ventral surface of segments 3 through 6, most obvious on segment 6 where previously termed uropods.

First pleopods (Fig. 3a, b).—Extremely large and heavy, 3-segmented, arising from calcified sternal bridge on ventral surface of abdomen. Tip produced into several irregular setose lobes surrounding mesial groove accommodating distal part of second pleopod. Middle segment broader than either first or third segment.

Second pleopods (Fig. 3a, c).—Long, 3-segmented; distal segment tapering to sclerotized filamentous projection in life inserted along groove of first pleopod and extending well beyond distal tip of first pleopod (Fig. 3a). Distal segment indistinctly segmented basally. Basal segment lightly se-

tose, other segments lacking setae or with very sparse setae.

Sexual dimorphism.—Males tending to be smaller than females (carapace lengths of the five males ranged from 20.2 to 32.3 mm, averaging 25.4 mm, compared to a range of 26.7 to 43.2, average 36.7 mm, for females) but otherwise two sexes similar in size and bodily proportions.

#### Natural History

Of the eight females collected off Chile, two were ovigerous. The larger ovigerous female, taken at 880 m in February 1981, carried 332 ovoid to nearly spherical eggs, averaging 2.53 mm in length and 2.27 mm in width ( $N = 35$ ). The second ovigerous female of the Chilean specimens, taken in January 1981, carried 251 eggs of about the same size. The holotype female, also ovigerous, was taken off the coast of Peru in 800 m in January 1971 (Garth, 1973). Because of the relatively small size of the eggs, we suggest that eclosion is probably zoeal rather than in a more advanced state as is the case for many other deep-water decapods (e.g., see Martin, 1986).

None of the known specimens were car-

rying anything in the chelate fourth and fifth pereopods. Carrying behavior is well known in the Dromiacea, especially in the Dromiidae, where some genera carry sponges or bivalve shells that completely cover the carapace. Crabs of the family Homolidae, which bear a subchelate fifth (but not fourth) pereopod, are known to carry pieces of sponges and cnidarians above the posterior portion of the carapace, but, in contrast to dromiids, they do not carry any "permanent" protective covering (see Wicksten, 1985; Guinot, 1978). It is possible that homolodromiids exhibit a type of carrying behavior similar to that known for the homolids. Guinot (1978: 226) noted that, in homolodromiids, the fourth and fifth pereopods probably are not employed in carrying any "permanent" protective covering because they carry these appendages in much the same way as the homolids. This difference between facultative grasping (e.g., homolids, dorippids, and probably homolodromiids) and reliance on a protective covering (e.g., dromiids) was used by Guinot (1978) as a character separating the homolodromiids from the dromiids.

The collection of *Homolodromia robertsi* from deep waters off the coast of Chile provides the first record of this species and of the family Homolodromiidae for Chile and extends the range of *H. robertsi* south about 2,666 km.

#### DISCUSSION

Brachyuran crabs of the section Dromiacea, which is presently comprised of the families Dromiidae De Haan, Dynomenidae Ortmann, and Homolodromiidae Alcock (after Bowman and Abele, 1982), are thought by most workers to be relatively primitive (e.g., see Gordon, 1950, 1963; Rice, 1980; Abele and Felgenhauer, 1982). The morphology of adult dromiaceans differs markedly from that seen in the majority of "true" crabs (the Eubrachyura of de Saint Laurent, 1980a) and many authors have argued for their removal from the Brachyura (e.g., see Guinot, 1977, 1978, 1979; de Saint Laurent, 1979, 1980a, b). Dromiacean larval stages, where known, are also unusual and unlike those of the Eubrachyura, causing some workers to suggest that dromiaceans have closer affinities with the Ano-

mura than with the true crabs (see Williamson, 1976, 1988).

The family *Homolodromiidae* has additional characters that set it off from the other dromiaceans, causing some workers to suggest that this family is the most primitive of all of the Brachyura. Guinot (1978: 226) placed this family in a separate superfamily, the Homolodromioidea, stating that "Les Homolodromioidea representent sans doute les plus primitifs des Brachyours s.l. actuels: ils seraient les plus primitifs des Podotremata, les plus primitifs des Dromiacea." The characters of the homolodromiids that might be considered primitive (see Bouvier, 1896; Milne Edwards and Bouvier, 1902; Balss, 1957; Guinot, 1978, 1979) are (1) the weakly calcified carapace with poorly defined lateral margins, (2) an absence of lineae on the carapace (see Martin and Abele, 1988), (3) the reduced and subchelate fourth and fifth pereopods, (4) a more or less pediform third maxilliped (although obviously expanded beyond the natantian condition), (5) the relatively long second and third pereopods, (6) a spermatheca separated from the oviducts, (7) the weakly formed orbito-antennular fossa, (8) numerous trichobranchiate gills, (9) incompletely fused segments of the male abdomen, (10) the presence of vestigial abdominal uropods, and (11) the stout 3-segmented male pleopod as described herein. We do not agree with the treatment of all of the above characters as primitive (note, for example, the apparent contradiction of numbers 3 and 5), but we do agree with the overall consensus that homolodromiids are less derived than are members of the Eubrachyura.

In light of the uncertainty concerning classification and relationships of these crabs, in particular the fact that the homolodromiids may be the most primitive extant crab family, it is surprising and unfortunate that so little is known about their basic morphology. For example, the male first and second pleopods have been described for only one other species of *Homolodromia* (*H. paradoxa*; see Milne Edwards and Bouvier, 1902: 13, 14, pl. I, figs. 12, 13) and for a single specimen in the genus *Dicranodromia* (*D. mayheuxi*; Guinot, 1979: 235, fig. 63). The male first and second pleopods of *H. robertsi* are similar to those of the above species (although less so for *D. mayheuxi*)

and to those described for several dromiids and at least one dynomenid (e.g., see Gordon, 1950, 1963; Hartnoll, 1975; Peyrot-Clausade and Serène, 1976) all of which have a heavy, 3-segmented first pleopod and a filamentous second pleopod. The orbital region likewise has not been adequately described elsewhere. The orbital region of *H. robertsi* does not seem to us to differ appreciably from the condition seen in higher (true) brachyurans, i.e., it seems a difference of degree rather than kind. And, although the carapace is weakly calcified and lacks defined anterolateral borders, we are unsure as to the significance of this character in decapod evolution, since carapace morphology varies widely among the reptant decapods (see Martin and Abele, 1988). Clearly, further investigations into the morphology and larval development of the homolodromiids are needed before phylogenetic questions can be adequately addressed.

The range extension of *H. robertsi* more than 2,666 km south is significant in light of the recent find of Feldmann and Wilson (1988) of a fossil homolodromiid (*Homolodromia chaneyi* Feldmann and Wilson) from Antarctica. The fossil, taken from the Eocene La Meseta Formation on Seymour Island, is the only known fossil *Homolodromia* and was preserved in sediments deposited in a cool temperate, nearshore, shallow-water habitat (see Feldmann and Wilson, 1988). Most other occurrences of the genus *Homolodromia* are from southern hemisphere or Gondwana continents (e.g., "*Arachnodromia*" *baffini* from India and the Indo-Pacific, *H. bouvieri* from off Madagascar, *H. robertsi* from South America, and an undescribed species of *Homolodromia* (USNM uncatalogued Anton Bruun material) from the South Atlantic). It is possible that the genus originated in shallow Gondwana seas and radiated northward and into deeper waters. The northern extent of the genus is apparently the Caribbean Sea, where *H. paradoxa* is known (uncatalogued material, USNM, and A. Milne Edwards, 1880).

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