

NEW MORPHOLOGICAL AND DISTRIBUTIONAL INFORMATION ON HOMOLODROMIIDAE AND HOMOLIDAE (DECAPODA: BRACHYURA) FROM THE AMERICAS, WITH DESCRIPTION OF A NEW SPECIES AND COMMENTS ON WESTERN PACIFIC SPECIES

Marcos Tavares¹ and Rafael Lemaitre^{2,*}

¹ Museu de Zoologia, Universidade de São Paulo, Av. Nazareth 481, Ipiranga, 04263-000 São Paulo, SP, Brazil

² Smithsonian Institution, National Museum of Natural History, Department of Invertebrate Zoology,
4210 Silver Hill Road, Suitland, MD 20746, USA

A B S T R A C T

Seventeen crab species of Homolodromiidae and Homolidae, in seven genera, are recognized in the Atlantic and Pacific coasts of the Americas. The genus *Dicranodromia* A. Milne-Edwards, 1880, is recorded for the first time from the eastern Pacific with a new species described from the Galápagos Islands. Nine species, five Homolodromiidae and four Homolidae, are taxonomically evaluated and circumscribed based on morphological information, their geographic and bathymetric distribution clarified and updated, and the similarities and differences of each with other members of the families discussed. Photographs, SEM photomicrographs and line drawings for selected species, including notes on habitat, nomenclature, and distinguishing features, are provided. Biramous uropods and complete pleopod formula in males are discovered to occur in juveniles of *Homola minima* Guinot and Richer de Forges, 1995, providing evidence that homoloidian and eubrachyuran pleonal locking-system (homoloidian and the eubrachyuran sockets) are not homologous. A checklist of all homolodromiid and homolid species known from both ocean sides of the Americas, with their bathymetric ranges, is presented. The diagnostic characters of one western Pacific species, *Lamoha williamsi* (Takeda, 1980), are reevaluated.

KEY WORDS: Decapoda, *Dicranodromia galapagensis* n. sp., eastern Pacific, Homolidae, Homolodromiidae, homoloidian and eubrachyuran locking-system, *Lamoha williamsi*, western Atlantic, western Pacific

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I N T R O D U C T I O N

The primitive crabs of the families Homolodromiidae and Homolidae are known since the Middle and the Late Jurassic, respectively (Krobicki and Zatoń, 2008; Schweitzer and Feldmann, 2010; Klompmaker et al., 2013). Most extant species live in depths from 200 to 1000 m, although at least one species (*Homologenus boucheti* Guinot and Richer de Forges, 1995) ranges to 2195 m. Knowledge of these two morphologically intriguing and evolutionary important families (Guinot et al., 2013) increased exponentially with the detailed revisions by Guinot (1995), and Guinot and Richer de Forges (1995), which were made possible, in large part, by the availability of abundant and remarkable collections obtained in the Indo-Pacific region during French deep-sea expeditions in the 1980s and early 1990s. Subsequent to those revisionary studies, several new species were added to Homolodromiidae (Martin et al., 2001; Ng and McLay, 2005; Ng and Naruse, 2007) and Homolidae (Richer de Forges and Ng, 2007, 2008; Ng and Eldredge, 2012), and as result the homolodromiids now contain two genera and 23 species, and the homolids 14 genera and 65 species.

Except for the taxonomic reviews of Homolodromiidae (Baez and Martin, 1989; Martin, 1990, 1991, 1992, 1994; Martin and Zimmerman, 2001; Martin et al., 2001), most

studies of homolodromiids or homolids have focused on species from the Indo-Pacific. Although major revisions (Guinot, 1995; Guinot and Richer de Forges, 1995) have used type materials and representative specimens from the western Atlantic and eastern Pacific, and several broadly focused decapod inventories have included homolodromiids and homolids (Williams, 1984; Soto, 1985, 1986; Williams et al., 1989; Melo, 1996, 1999; Felder et al., 2009a, b), a significant number of specimens still has remained unstudied in several New World museums. So far, in the eastern Pacific, only one species of homolodromiid, *Homolodromia robertsi* Garth, 1973, and three homolids have been documented; in the western Atlantic, five species of homolodromiids and four homolids are known. The scant materials from the New World included in those studies has made it difficult in some cases to define or provide clear taxonomic boundaries in some species (particularly when specimens of only one sex have been used), or have often obscured the extent of the distributions of species.

While examining a collection of homolodromiids and homolids obtained in deep waters off the coast of Brazil and deposited at Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP), the opportunity arose to study in more detail the taxonomy and distribution of the taxa known to occur

* Corresponding author; e-mail: lemaitr@si.edu

in the western Atlantic, and in particular investigate or confirm which taxa truly ranged to the southwestern Atlantic. Guinot (1995) and Guinot and Richer de Forges (1995) had considered, based on minimal materials, that only two species occurred in South America outside the Caribbean Sea to the southwestern Atlantic: one homolodromiid, *Dicranodromia simplicia* Guinot and Martin, in Guinot, 1995, and questionably one homolid, *Homola minima* Guinot and Richer de Forges, 1995. When the authors began to search for unstudied specimens in National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), numerous specimens were discovered from throughout the western Atlantic that warranted a taxonomic reevaluation and distributional update of several problematic homolodromiid and homolids from this side of the Atlantic. Furthermore, samples found in the USNM that had been obtained using a manned submersible in the Galápagos Islands, were found to contain a new species of *Dicranodromia* A. Milne-Edwards, 1880, a genus previously unrecorded from the eastern Pacific. A full description of this new species, only the second homolodromiid species known from the eastern Pacific, is included in this study. A checklist (Table 1) of all homolodromiids and homolids from both the western Atlantic and eastern Pacific coast of the Americas, with their known bathymetric ranges, is also included.

The study of a large number of specimens deposited in the USNM of *Homola minima*, covering a wide range of size or maturity and degree of pleonal development, has allowed for the discovery in juveniles males of a complete pleopod formula (pleopods 1-5 + biramous uropods). The anatomy of the uropods in juvenile males and females of *H. minima* is described, and a reevaluation of the putative homology between the homoloidian and the eubrachyuran pleonal locking-mechanism (the homoloidian and the eubrachyuran sockets), is discussed.

Finally, the opportunity is taken to reevaluate the diagnostic characters of one western Pacific species, *Lamoha williamsi* (Takeda, 1980), based on type specimens in the USNM.

MATERIALS AND METHODS

Specimens used in this study remain deposited in Museum of Comparative Zoology, Harvard University (MCZ), MZUSP and USNM. Morphological terminology used follows that used by Guinot (1995) and Guinot and Richer de Forges (1995), except that we follow Schram and Koenemann (2004) in the use of "pleon" instead of "abdomen." Measurements (in mm) taken are of carapace length, taken along midline and including the rostrum or pseudorostral spines, and carapace width, taken across the widest portion of the carapace, excluding any lateral spines. Measurements are listed in the sequence carapace length (cl) × carapace width (cw). Measurements are not provided for all materials examined, although the smallest and largest specimens encountered have been measured to provide a size range for each of the species discussed. Morphological or specimen abbreviations used are: G1, G2, first and second male gonopods (pleopods); juv., juvenile(s); ovig., ovigerous; P1, cheliped; P2-P5, second to fifth pereopods; P11-5, first to fifth pleopods; other abbreviations: BALGIM expedition, "Benthos Alboran Golfe Ibéro-Marocain" expedition; BLM, Bureau of Land Management, USA; CIOH-INVEMAR, Centro de Investigaciones Oceanográficas e Hidrográficas del Caribe, Colombia; GEDIP/IOUSP, Executive Group for Industrial Fisheries Development; JSL, Johnson Sea Link submersible; MARMAP, Marine Resources Monitoring, Assessment, and Prediction, South Carolina Department of Natural Resources; MMS, Minerals Management Service, USA; OPISS/IOUSP, Oceanography of the Inner Shelf of São Sebastião/Oceanographic Institute of the University of São Paulo; REVIZEE, Living Resources in the Exclusive Economic Zone; SOFLA, MMS Southwest Florida Shelf Ecosystem Study; sta, station; USCGS, U.S. Coast and Geodetic Survey; USFC, U.S. Fish Commission. Months are abbreviated using the first three letters. In the "Materials examined" the specimens are listed geographically from north to south. Only partial synonymies are presented for each species discussed, and include more recent or relevant references. For full synonymies, the reader should consult Guinot (1995) and Guinot and Richer de Forges (1995).

Table 1. Checklist of Homolodromiidae and Homolidae from the Atlantic and Pacific coasts of the Americas, with depth distributions. WA, western Atlantic; EP, eastern Pacific.

Taxon	Geographical distribution	Depth distribution (m)
HOMOLODROMIIDAE		
<i>Dicranodromia alphonsei</i> Martin and Guinot, 1995	WA	273
<i>Dicranodromia chacei</i> Guinot, 1995	WA	318-467
<i>Dicranodromia felderi</i> Martin, 1990	WA	585-948
<i>Dicranodromia galapagensis</i> n. sp.	EP	559-435
<i>Dicranodromia ovata</i> A. Milne-Edwards, 1880	WA	328
<i>Dicranodromia simplicia</i> Guinot and Martin, 1995	WA	228-320
<i>Dicranodromia spinosa</i> Martin, 1994	WA	156-260
<i>Homolodromia monstrosa</i> Martin et al., 2001	WA	457-750
<i>Homolodromia paradoxa</i> A. Milne-Edwards, 1880	WA	375-914
<i>Homolodromia robertsi</i> Garth, 1973	EP	560-880
HOMOLIDAE		
<i>Homola minima</i> Guinot and Richer de Forges, 1995	WA	55-683
<i>Homola vigil</i> A. Milne-Edwards, 1880	WA	300-800
<i>Homologenus orientalis</i> Zarenkov, 1990	EP	730-800
<i>Homologenus rostratus</i> (A. Milne-Edwards, 1880)	WA	600-1601
<i>Lamoha noar</i> (Williams, 1974)	WA	550
<i>Moloha faxoni</i> (Schmitt, 1921)	EP	80-460
<i>Paromola rathbunae</i> Porter, 1908	EP	280-600

SYSTEMATICS

Homolodromiidae Alcock, 1900

Dicranodromia galapagensis n. sp.

Figs. 1A, 2, 3

Type Material.—*Eastern Pacific*. Galápagos Islands, Marchena Island, R/V Seward Johnson, sta JSL-II-3106, 00°24'N, 90°26'30"W, 559–435 m, 20 Jul 1998, coll. C. Baldwin: female holotype 22.0 × 18.0 mm (USNM 1184606).

Comparative Material.—*Dicranodromia martini* Guinot, 1995. *Philippines*: Cagayanes Islands, Cagayane Island, USFC Albatross, sta 5423, 09°38'30"N, 121°11'E, 930 m, 31 Mar 1909: male holotype (USNM 268803); Mindanao, USFC Albatross, sta 5511, 08°15'20"N, 123°57'00"E, 750 m, 7 Aug 1909: 1 female (damaged) paratype (USNM 268803).

Description of Female Holotype.—Carapace (Fig. 1A), thoracic sternum, pereopods, and pleon covered with moderately long and dense setae interspersed with dense short,

stiff setae. Carapace 1.2 times as long as wide, widest across intestinal region; dorsal surface markedly convex, strongly deflexed anteriorly, smooth dorsally, sparsely spinulated anterolaterally. Cervical groove distinct, smooth, shallower than branchio-cardiac groove. Gastric pits minute, rounded, remarkably deep and close to each other. Branchio-cardiac groove distinct, almost straight, slightly directed anteriorly. Pseudo-rostrum (Figs. 1A, 2A) deeply bifurcated, consisting of narrowly triangular prolongations slightly sloping ventrally, weakly pointed inwards, and each tapering distally to unarmed rounded tip. External orbital tooth strong, straight, outwardly directed, terminating in strong, acute spine. Supraorbital margin separated from external orbital tooth by shallow V-cleft, 3 or 4 spinules mesially to cleft. Infraorbital tooth (Figs. 1A, 2A, B) strong, sharp, basally broad, reaching well beyond external orbital tooth in dorsal view; with scattered small spines basally, and 1 stronger spine close to antennal lateral margin oriented towards orbital cavity. Subhepatic region (Fig. 2B) swollen, produced anteriorly, with scattered small spines. Epistome (Fig. 2B) with scattered, small spines; distal portion subtriangular,

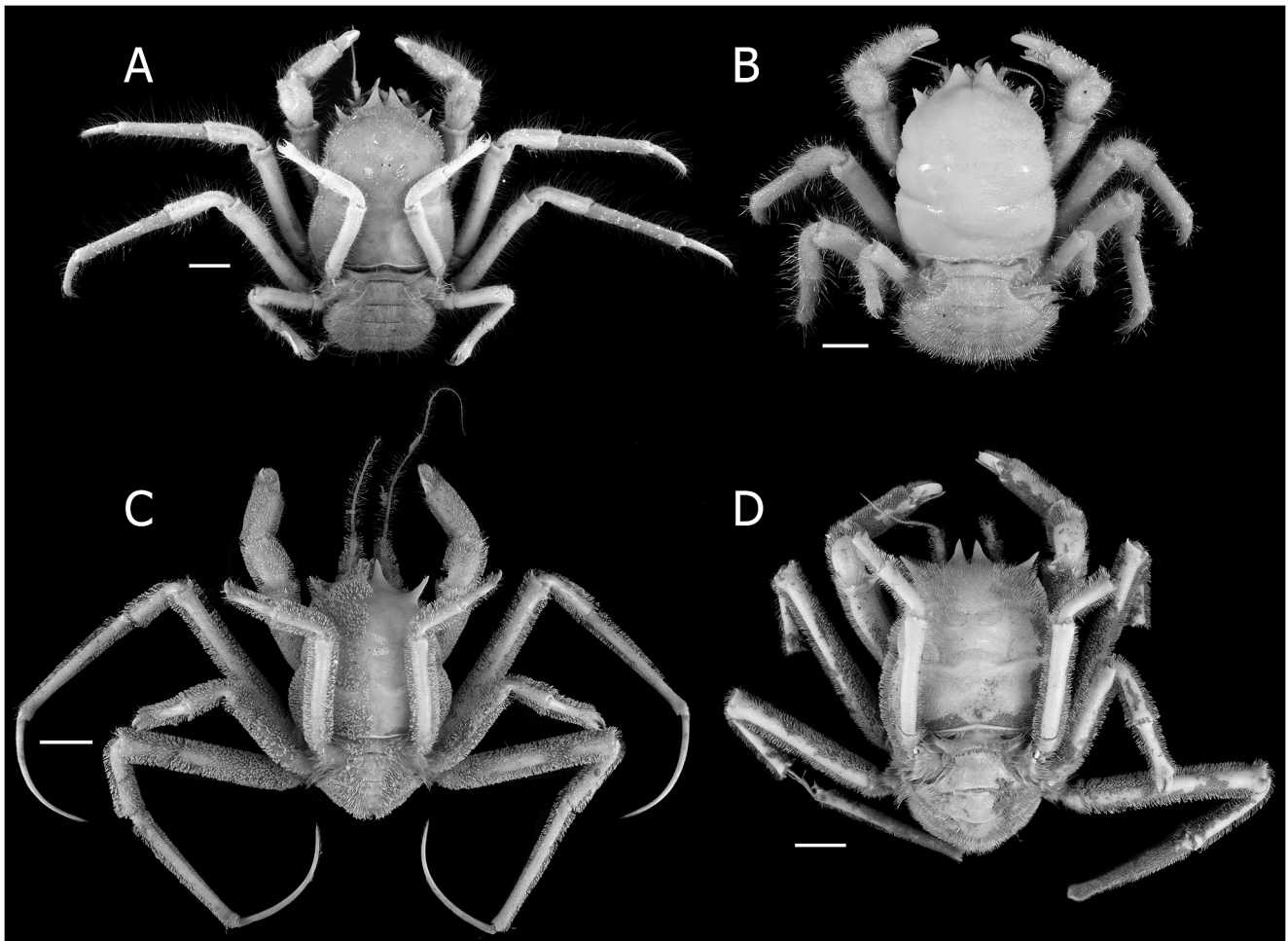


Fig. 1. A, *Dicranodromia galapagensis* n. sp., ovig. female holotype, 22.0 × 18.0 mm, Galápagos Islands, Marchena Island (USNM 1184606): dorsal view; B, *Dicranodromia simplicia* Guinot and Martin, in Guinot, 1995, ovig. female holotype, 21.0 × 16.0 mm, Brazil, Pará (USNM 1005083). C, D, *Homolodromia monstrosa* Martin, Christiansen and Trautwein, 2001: C, long-legged female (P5 meri extend beyond carapace gastric pits), 35.3 × 27.6 mm, Panama (Caribbean) (USNM 1184611); D, paratype, short-legged female (P5 meri end well before carapace gastric pits, possibly representing *H. paradoxo* A. Milne-Edwards, 1880; see Remarks), 37.4 × 48.0 mm, French Guiana (USNM 310890). Scales = 5 mm (A, B), or 10 mm (C, D).

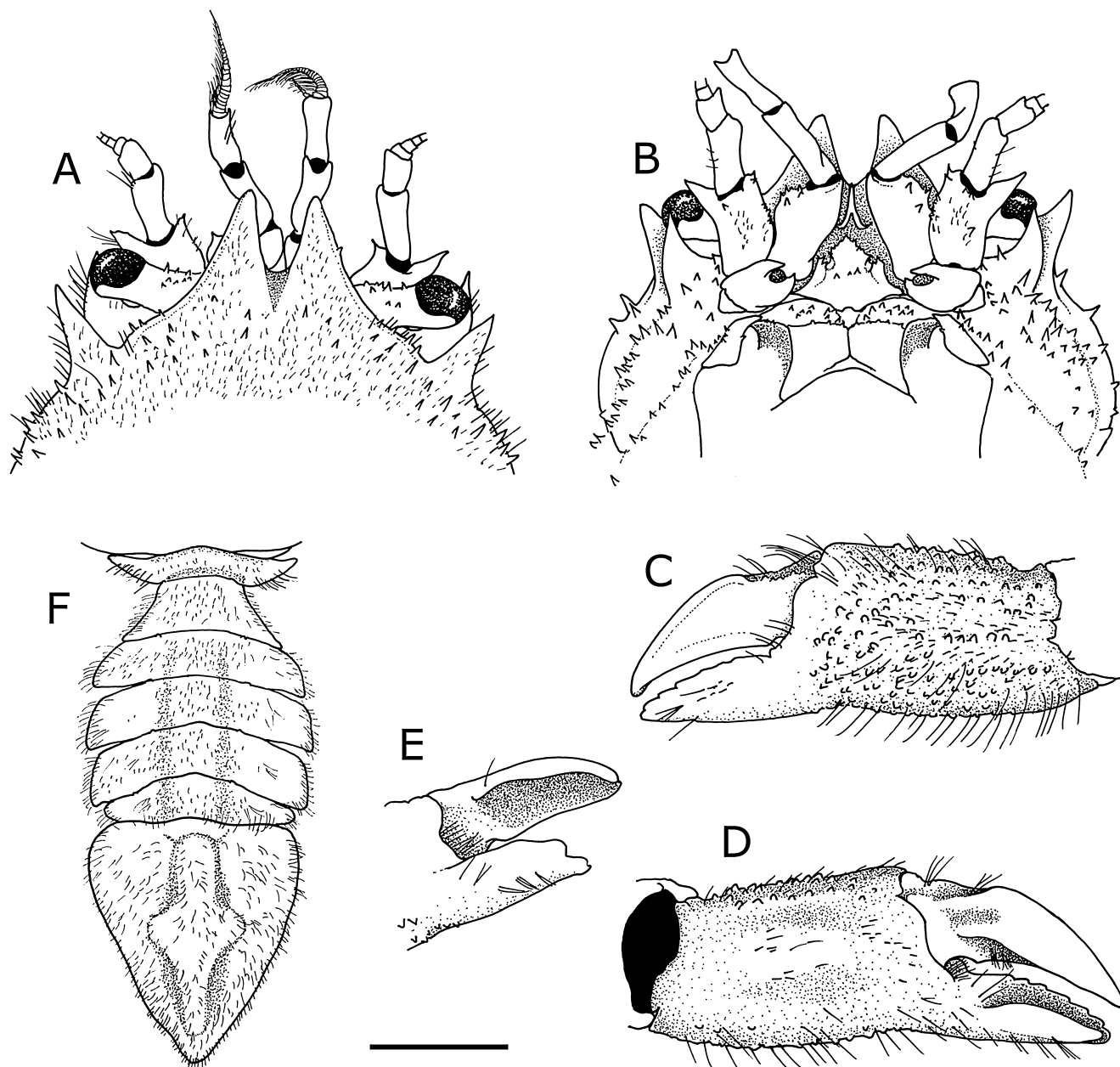


Fig. 2. *Dicranodromia galapagensis* n. sp., ovig. female holotype, 22.0 × 18.0 mm, Galápagos Islands, Marchena Island (USNM 1184606): A, anterior carapace in dorsal view, with ocular, antennular and antennal peduncles; B, same, ventral view, with epistome and anterior portion of endostome; C, chela of left P1, lateral (outer) view; D, same, mesial (inner) view; E, dactyl and fixed finger of left P1, ventromesial view; F, pleon, dorsal view. Scale = 4 mm (A-E), or 2 mm (F).

with spinulose margins and deep subdistal notch on each side of lateral margins; posterior margin upturned, crenulated, gently sloping inward, with median fissure. Endostomial ridge smooth.

Ocular peduncles and cornea (Figs. 1A, 2A, B) each fitting between external orbital and infraorbital tooth (dorsal view); dorsal surface of peduncle with small spines mesially, ventral surface smooth.

Antenna well developed; flagellum long, about 2.2 times as long as length of peduncle; urinary segment with acicle strong, sharp, pointing towards buccal frame. Anterolateral angle of antennal segment 2 + 3 with strong sharp tooth, as long as posterior margin of segment 2 + 3; anteromesial

angle produced, armed with 2 small spines; mesial margin with short row of 3 or 4 small spines medially; ventral surface smooth.

Third maxilliped long, narrow. Ischium slightly wider distally, as long as merus; mesial and lateral margins with small sharp or blunt spines and granules, outer surface smooth. Merus lateral margin with small sharp or blunt spines and granules, outer surface with scattered small spines and granules. Palp long, exceeding (when folded) distal margin of ischium by half length of dactylus. Exopod widest on proximal third, long, reaching well beyond ischio-meral articulation to about half length of merus; distal third of mesial margin with 4 or 5 small, acute tubercles.

Chelipeds symmetrical, more densely setose on dorsal or outer surfaces than on ventral or inner surfaces. Merus triangular in cross section, dorsal and lateral (but not mesial) margins sparsely lined with small spines; ventral surface smooth except for very few scattered granules. Carpus dorsal, lateral and ventral surfaces (but not mesial) with scattered, small, acute tubercles or spines, mesial surface smooth. Palm (Fig. 2C, D) with moderately dense small spines or tubercles on dorsal, lateral (outer) and ventral surfaces; mesial (inner) surface with sparse granules, slightly convex. Fingers (Fig. 2C-E) with occluding surfaces distinctly concave, spoon-like. Fixed finger with distal U-

cleft receiving tip of dactylus when fingers closed; inner cutting edge of occluding surface with 4 low, small rounded teeth, outer cutting edge entire; setae present only proximally to two-thirds of latero and ventromesial surfaces. Dactylus smooth, stout proximally, slender distally, dorsal margin well defined, moderately sharp; cutting edges of occluding surface entire, untoothed, closing against fixed finger on about two-thirds of distal length; with setae on proximal two-thirds of lateral surface.

P2 and P3 of similar size and shape (Figs. 1A, 3A, B). Propodi about 1.4 times as long as dactyli, each with 1 movable, slender ventrodistal spine. Dactyli about as

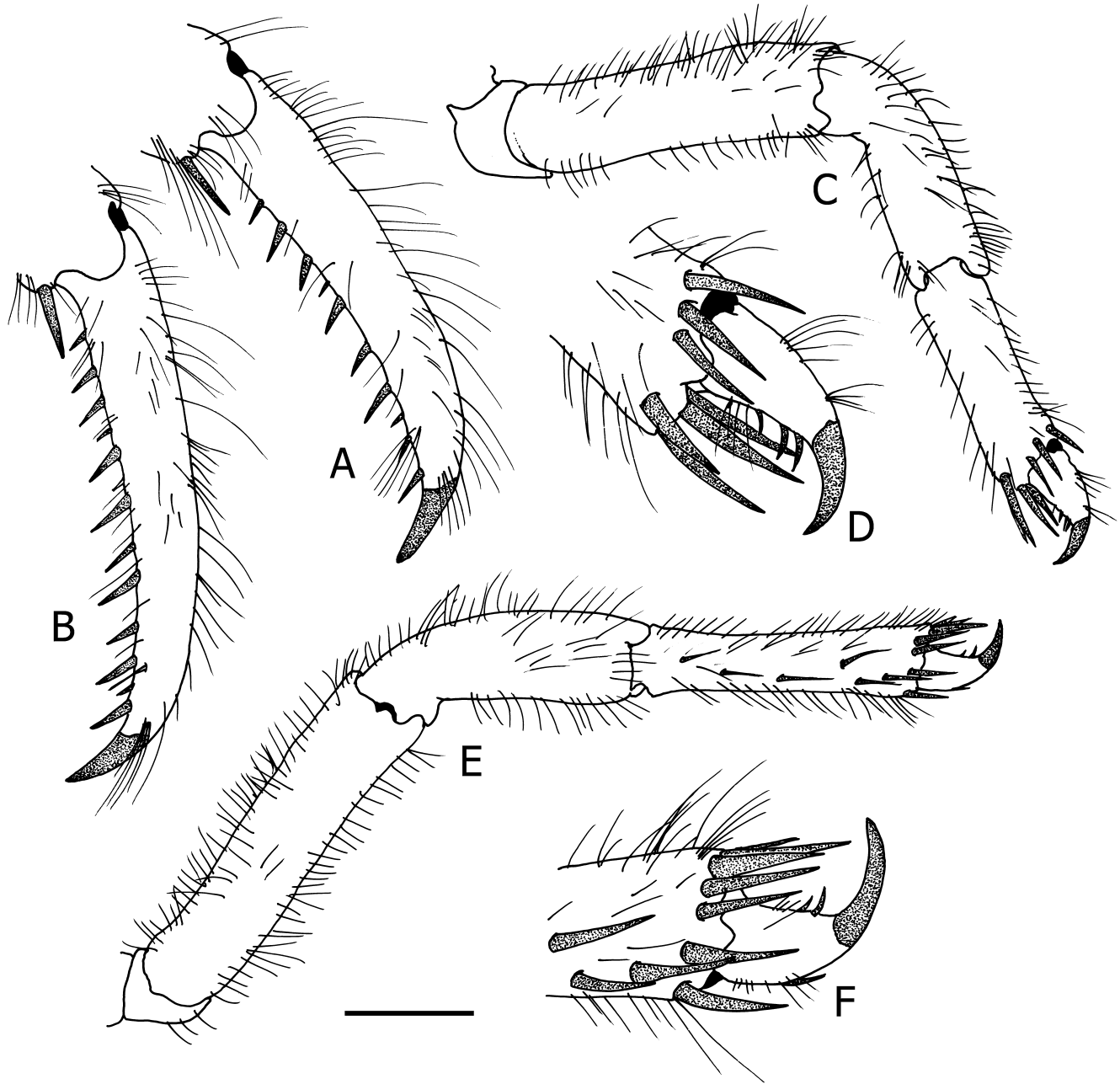


Fig. 3. *Dicranodromia galapagensis* n. sp., ovig. female holotype, 22.0 × 18.0 mm, Galápagos Islands, Marchena Island (USNM 1184606): A, dactyl of P2, lateral view; B, dactyl of P3, lateral view; C, P4, lateral view; D, dactyl and distal portion of propodus of same, lateral view; E, P5, lateral view; F, dactyl and distal portion of propodus of same, lateral view. Scale = 2 mm (A, B), or 3 mm (C-F).

long as carpi, each with strong, inwardly curved unguis, and ventral margin armed with 10-13 strong corneous spines. P4 stouter and slightly shorter than P5. P4 and P5 (Fig. 3C-F) not as setose as P2 and P3; merus of P5, when placed against carapace, reaching to branchio-cardiac groove; carpi unarmed except for setae; propodi each with 7 strong, slender corneous spines subdistally crowning base of dactyl; propodus of P4 unarmed except for setae; propodus of P5 armed with row of 6 slender corneous spines on dorsolateral surface; dactyli closing downward and terminating in strongly, inwardly curved unguis, with 2 or 3 delicate, slender corneous spines on ventral margin; dactyl of P5 with slender movable spine (lacking on P4) on extensor margin.

Thoracic sternite 7 with strong bump immediately anterior to spermathecal aperture, apertures small, rounded, placed at level of female gonopores. Female pleon (Fig. 2F) with 6 free segments and telson; telson long, as long as combined length of second to sixth pleonal segments.

Etymology.—The specific name is given after the Galápagos Islands, where the single known specimen of this new species was found.

Size.—The female holotype measured 22.0 × 18 mm.

Distribution.—Eastern Pacific, so far known only from the type locality, Marchena Island, Galápagos Islands; depth: 559.3 to 434.9 m.

Remarks.—*Dicranodromia galapagensis* is the first representative of the genus *Dicranodromia* A. Milne-Edwards, 1880 known from the entire Eastern Pacific. Among the Indo-Pacific species of *Dicranodromia*, *D. galapagensis* is most similar to *D. martini* Guinot, 1995, known from the Philippines (see Guinot, 1995: figs. 19, 20). In these two species, the carapace is much longer than wide, widest across the intestinal region; the dorsal surface of the carapace is markedly convex, strongly deflexed anteriorly, smooth dorsally and sparsely spinulated anterolaterally; the cervical groove is smooth and shallower than the branchio-cardiac groove; the gastric pits are rounded, minute and remarkably deep and close to each other; the external orbital tooth consists of a strong, straight and basally narrow, outwardly directed spine; and the epistome has scattered, small spines, with a posterior margin upturned and crenulated. However, *D. galapagensis* can be separated from *D. martini* by: 1) the P5 propodus with a row of 6 strong, slender corneous spines dorso-laterally (Fig. 3E), whereas the propodus is unarmed in *D. martini*; 2) the smooth endostomial ridges, (Fig. 2B), whereas the ridges are distinctly granulated in *D. martini*; 3) a shorter endostome (Fig. 2B) in the new species than in *D. martini*; 4) the triangular prolongations of the pseudo-rostrum (Figs. 1A, 2A) which are basally narrower than in *D. martini*, and terminate in unarmed rounded tips instead of having tips with one or two small spines; and 5) the upturned posterior margin of the epistome which is slightly curved mesially, whereas the margin is straight in *D. martini*.

Two other species of *Dicranodromia* are also known from the Philippines: *D. danielae* Ng and McLay, 2005 and *D. chenaie* Ng and Naruse, 2007. *Dicranodromia galapagensis* can be distinguished from *D. chenaie* by the shape and size of the external orbital tooth, which is narrow basally and with

straight margins in this new species (Figs. 1A, 2A), whereas the tooth is broad basally and with a curved posterolateral margin in *D. chenaie* (see Ng and Naruse, 2007: fig. 5a). *Dicranodromia galapagensis* n. sp. can be separated from *D. danielae* by the lateral (outer) surface of the palm of the chelipeds, which is moderately armed with small spines or tubercles in the new species (Fig. 2C), whereas the surface is smooth or without visible granules or spines in *D. danielae* (see Ng and McLay, 2005, fig. 3A, B).

When compared to its Atlantic congeners (Table 1), *D. galapagensis* can be distinguished from *D. felderi* Martin, 1990, by lacking a carina on the ventral surfaces of the meri of P2 and P3 (versus presence of long carina in *D. felderi*). In this new species, the carapace is smooth dorsally, at most sparsely spinulated anterolaterally, whereas the carapace is densely armed with spines dorsally in *D. spinosa* Martin, 1994, *D. mahieuxii* A. Milne-Edwards, 1883, and *D. pequegnati* Guinot, 1995. From *D. simplicia* Guinot and Martin, in Guinot, 1995, this new species differs as follows: the rostrum is more deeply bifurcate, and the rostral prolongations are closer to each other than in *D. simplicia*; the external orbital tooth is stronger and relatively longer than in *D. simplicia*; and the merus of P5, when placed against the carapace, reaches to the branchio-cardiac groove, whereas the merus does not reach the groove in *D. simplicia*. Finally, the new species differs from the three other Atlantic species, *D. chacei* Guinot, 1995, *D. ovata* A. Milne-Edwards, 1880, and *D. alphonsei* Martin and Guinot, in Guinot, 1995, by the sharp and long external orbital tooth, whereas in those three species the external orbital tooth is stout, short and distally blunt.

Dicranodromia felderi Martin, 1990

Dicranodromia felderi Martin, 1990: 709, figs. 1-5 (type locality: E of Dominica, Lesser Antilles, R/V Oregon, sta 5928, 15°38'N, 61°12'W); Guinot, 1995: 250, figs. 3G, H, 32a-e, 33A, B; Felder et al., 2009b: 1072.

Type Material.—*Caribbean Sea*. Lesser Antilles, E of Dominica, R/V Oregon, sta 5928, 15°38'N, 61°12'W, 585 m, 4 Mar 1966: male holotype 23.1 × 17.9 mm (USNM 252204). Paratypes: see Martin (1990: 709).

Additional Material.—*Gulf of Mexico*. Louisiana, Grand Isle, R/V Citation Gulf, sta WC06, 27°42'44"N, 091°32'35"W, 543-783 m, 10 Jun 1985: 1 male 36.3 × 27.3 mm, 1 ovig. female 31.0 × 23.9 mm (USNM 1000826). *Caribbean Sea*. Bahamas, New Providence Island, Nassau, Goulding's Cay, R/V Seward Johnson, sta JSL-3658, 25°01'25"N, 077°35'48"W, 747 m, 14 Feb 1994: 1 male 32.2 × 22.5 mm (USNM 1196479); Lesser Antilles, E of St. Kitts, R/V Oregon II, sta 10844, 17°24'N, 62°28'W, 629 m, 8 Dec 1969: 2 males 15.2 × 11.1, 26.7 × 21.6 mm (USNM 1202393).

Diagnosis.—Carapace long, distinctly constricted near cervical groove; dorsal surface rather smooth, covered with scattered simple setae. External orbital tooth strong, acute. Pseudo-rostrum well developed, triangular, bluntly tipped. Basi-ischium of chelipeds with flattened ventral surface terminating antero-medially in blunt ridge. Merus of pereopods 2 and 3 with strong keel along ventral margin. Spermathecal

apertures located near median longitudinal axis of thoracic sternum at level of P3 coxae.

Size.—Males, 18.7 × 15.7 mm to 36.3 × 27.3 mm; females, 11.0 × 8.0 mm to 25.9 × 22.0 mm; ovig. females, 26.2 × 22.1 mm to 32.0 × 26.8 mm.

Distribution.—Eastern Gulf of Mexico (Grand Isle, Louisiana), and Caribbean Sea (Bahamas, Cuba, St. Kitts, Dominica, Grenada, Panama); depth: 543 to 948 m.

Remarks.—*Dicranodromia felderi* was originally described by Martin (1990) from the Caribbean Sea (Dominica, Grenada, and Panama). Guinot (1995: 250) added records from Cuba (Cardenas and Matanzas Bay) and San Andrés Island, Colombia. Guinot's records of *D. felderi* from off the NW coast of Cuba were considered by Felder et al. (2009b) to fall within their definition of the Gulf of Mexico Basin, and accordingly listed it among the decapod fauna of that Gulf. *Dicranodromia felderi* is herein recorded from three additional localities: the northern Gulf of Mexico from Grand Isle, Louisiana, Bahamas, and in the Caribbean Lesser Antilles, from St. Kitts.

Dicranodromia simplicia Guinot and Martin,
in Guinot, 1995
Figs. 1B, 4A-D

Dicranodromia simplicia Guinot and Martin, in Guinot, 1995: 255, figs. 34a, 35A-B, 37g (type locality: southwestern Atlantic, Amapá, Brazil, R/V Oregon I, sta 2081, 01°52'N, 46°54'W, 01°52'S, 46°54'W).

Type Material.—*Southwestern Atlantic, Brazil*. Amapá, R/V Oregon I, sta 2081, 01°52'N, 46°54'W, 320 m, 17 Nov 1957: ovig. female holotype 21.0 × 16.0 mm (photographed) (USNM 1005083), 1 ovig. female paratype 14.8 × 11.6 mm (USNM 1005084).

Additional Material.—*Southwestern Atlantic, Brazil*. Amapá, R/V Oregon I, sta 2080, 02°04'N, 47°00'W, 229 m, 17 Nov 1957: 1 female 14.8 × 11.6 mm (USNM 1005085); Canopus Seamount, ~120 miles off the coast of Ceará, fishing vessel, 02°14'25"S, 38°22'50"W, depth unknown, 20 Aug 2005, coll. J. Coltro: 1 juv. male 13 × 10 mm, 2 juv. females 7.0 × 5.4 mm and 11.9 × 9.0 mm, 1 ovig. female 21.0 × 17.0 mm (MZUSP 16886).

Diagnosis.—Carapace deeply constricted near cervical groove; dorsal surface strongly convex, sparsely spinulated laterally. External orbital tooth strong, acute. Pseudo-rostrum poorly developed; median rostral tooth minute, triangular. Pereiopods short, stout, mostly unarmed. Spermathecal apertures located near third pereiopod coxae.

Size Range.—Only known male, juv. 13.0 × 10.0 mm; females 7.0 × 5.4 mm to 21.0 × 17.0 mm; ovig. females 14.8 × 11.6 mm to 21.0 × 16.0 mm.

Distribution.—So far known only from the southwestern Atlantic along the coast of Brazil, from Pará to Ceará; depth: 229 to 320 m.

Remarks.—Previous to this study, *D. simplicia* was known from only three females, the holotype (USNM 1005083), a paratype (USNM 1005084), and a non-paratype (USNM

1005085), all collected off Amapá, on the northern coast of Brazil (Guinot, 1995). Herein we report three additional females, two immature and one adult, and one juvenile male, all collected further south, on Canopus Seamount, Ceará. Thus, adult males still remain unknown.

In the specimens from the Canopus seamount (MZUSP 16886), the outer faces of the palm of P1 are distinctly less tuberculated or spinose than in the holotype and paratype females (Fig. 4A-C). It is possible that this difference in armature of P1 in the Canopus Seamount specimens is indicative that they represent a separate, undescribed species. However, given the paucity of specimens from the Ceará region, we provisionally assign these specimens to *D. simplicia*. Additional specimens are needed from the type lo-

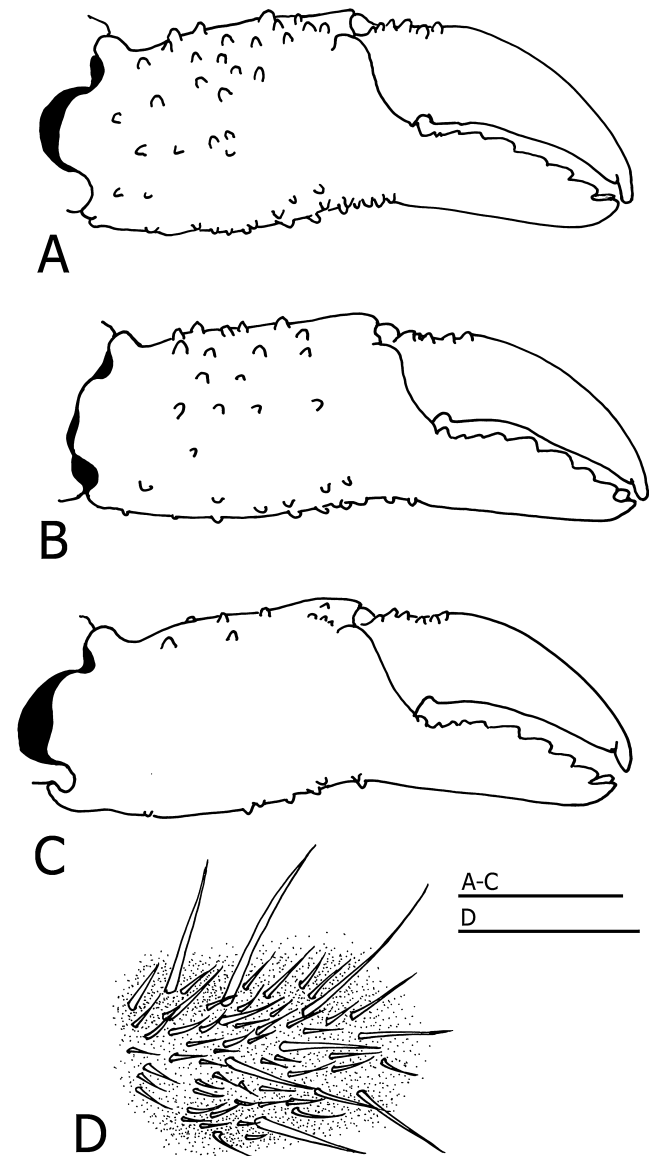


Fig. 4. *Dicranodromia simplicia* Guinot and Martin, in Guinot, 1995. A-C, right chela, lateral (outer) view; D, setation on mid-dorsal surface of carpus of left chela. A, female holotype, 21.0 × 16.0 mm, Brazil, Pará (USNM 1005083); B, female paratype, 14.8 × 11.6 mm, Brazil, Pará (USNM 1005084); C, D, ovig. female, 21.0 × 17.0 mm (MZUSP 16886). Scales = 2 mm (A-C), or 1 mm (D).

cality or vicinities, or from the Canopus Seamount area, to evaluate whether more than one species of *Dicranodromia* exists within the current distribution range of *D. simplicia*.

Given the lack of information on males of *D. simplicia*, it is of interest to document the following morphological features of the juvenile male measuring 13.0×10.0 mm (MZUSP 16886). The pleon has six free segments and telson, the segments being relatively short; the telson is as long as the combined length of pleomeres 3 to 6; pleonal segments 3 to 5 each have a pair of unequal pleopodal buds, with the right P15 distinctly larger than the left P15; and the uropods, as in the generic diagnosis, are vestigial and on the ventral side, consisting of small lobes.

In the western Atlantic, adult *D. simplicia* resemble *D. felderi*. Guinot (1995: 258) summarized the similarities of these two species, including the presence in both of setation that consists of simple setae (Fig. 4D), as well as the differences. The former species can be easily separated by the absence of a carina on the ventral surface of the meri of P2 and P3, whereas a distinct carina is present on the meri in *D. felderi*.

Homolodromia paradoxa A. Milne-Edwards, 1880

Fig. 5

Homolodromia paradoxa A. Milne-Edwards, 1880: 33 (type locality: Lesser Antilles, Nevis, USCGS Blake, sta 151, $23^{\circ}11'22''$ N, $62^{\circ}42'00''$ W, 651 m).

Homolodromia paradoxa. Takeda, 1983: 112 (*pro parte*), unnumbered photographs (= *Homolodromia monstrosa* Martin et al., 2001); Martin et al., 2001: 314.

? *Homolodromia paradoxa*. Feldmann and Gazdzicki, 1998: 3, fig. 2B; Guinot, 1995: 191, figs. 2A, B, 3A, B, 5C; Martin and Zimmerman, 2001: 411; Felder et al., 2009b: 1072.

Type Material.—*Caribbean* Sea. Lesser Antilles, Nevis, USCGS Blake, sta 151, $23^{\circ}11'22''$ N, $62^{\circ}42'00''$ W, 651 m: male holotype, 15.7×12.4 mm (excluding rostral horns) (MCZ 6512).

Additional Material (Tentatively Assigned to *H. paradoxa*; See Remarks).—*Gulf of Mexico*. Off Florida, R/V Oregon II, sta 11486, $28^{\circ}15'N$, $86^{\circ}06'W$, 589 m, 26 Jun 1971: 1 female 41.3×33.4 mm (USNM 1201721); off Florida, R/V Citation, cruise IV, sta E2D, $28^{\circ}07'38''N$, $85^{\circ}51'36''W$, 624–631 m, 16 May 1985: 2 males (USNM 1000590); 145 SE of Galveston, R/V Oregon II, sta 4661, 549 m, 30 Jan 1964: 1 ovig. female 47.5×33.0 mm (USNM 1201724);

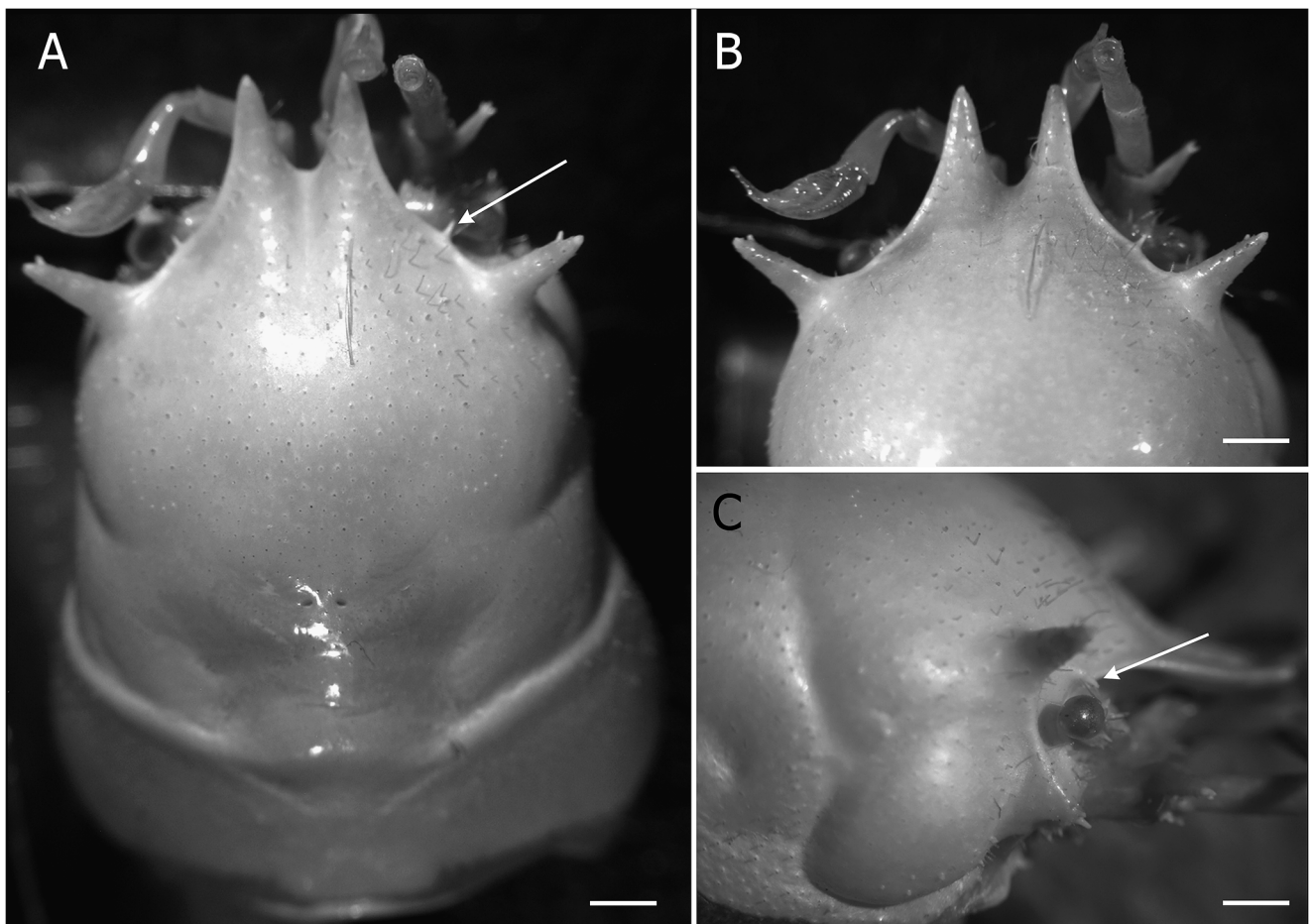


Fig. 5. *Homolodromia paradoxa* A. Milne-Edwards, 1880, male holotype, 15.7×12.4 mm, Lesser Antilles, Nevis (MCZ 6512): A, carapace, dorsal view; B, same, frontal region, dorsal view; C, same, lateral view. Scales = 2 mm. Arrows indicate supraorbital spine.

R/V Oregon, sta 4572, 23°23'N, 86°56'W, 549 m, 8 Dec 1963: 1 male, 1 female (USNM 181442); off Campeche Bank, R/V Oregon, sta 4571, 23°04'N, 86°3'W, 732 m, 7 Dec 1963: 1 male, 23.6 × 18.0 mm, 1 ovig. female 45.8 × 35.8 mm (USNM 1196470); off Mosquito Bank, R/V Oregon, sta 1910, 12°40'N, 82°18'W, 640 m, 11 Sep 1957: 1 ovig. female 41.5 × 33.5 mm (USNM 1196476). *Caribbean Sea*. *Virgin Islands*: 150 miles ESE of St. Thomas, R/V Oregon, sta 10846, 17°38'N, 62°59'W, 649 m, 9 Dec 1969: 1 male 31.6 × 24.5 mm (USNM 1202380). *Guadeloupe*: Marie Galante Island, Drake Passage, R/V Oregon II, sta 10827, 15°40'N, 61°09'W, 622 m, 1 Dec 1969: 1 ovig. female 38.0 × 28.7 mm (1201722). *Colombia*: off Isla de San Andres, R/V Oregon, sta 1909, 12°35'N, 82°19'W, 640 m, 11 Sep 1957: 1 female, 41.5 × 31.8 mm (USNM 1196475); *Nicaragua*: off E central coast, R/V Oregon, sta 1908, 12°33'N, 82°20'W, 640 m, 11 Sep 1957: 1 male 20.7 × 15.0 mm (USNM 1202389). *Northeastern South America*. *Suriname*: R/V Oregon II, sta 10603, 07°48'N, 54°25'W, 644 m, 10 May 1969: 1 ovig. female (USNM 310689); R/V Oregon II, sta 2011, 07°46'N, 54°36'W, 732 m, 7 Nov 1957: 1 female, 1 ovig. female (USNM 310687); R/V Oregon II, sta 10817, 07°46'N, 54°06'W, 585 m, 25 Nov 1969: 2 females (USNM 310688). *French Guiana*: R/V Oregon II, sta 10808, 07°40'N, 53°42'W, 640 m, 21 Nov 1969: 1 ovig. female (USNM 310686).

Size Range.—Males, 23.6 × 18.0 mm to 27.1 × 21.0 mm; females, 21.7 × 16.2 mm to 41.5 × 31.8 mm; ovig. females, 34.2 × 28.0 mm to 45.8 × 35.8 mm.

Distribution.—Western Atlantic, from the Gulf of Mexico, Caribbean Sea, and Suriname to Brazil; depth: 549 to 933 m.

Remarks.—*Homolodromia paradoxa* was briefly described by A. Milne-Edwards (1880) based on a single holotype male specimen, and only subsequently described and illustrated in detail (A. Milne-Edwards, 1883; A. Milne-Edwards and Bouvier, 1902; Martin et al., 2001: 314). The only other congener in the western Atlantic is *H. monstrosa* Martin, Christiansen and Trautwein, 2001, a species described based on two females, one of which is the holotype, and two males. According to Martin et al. (2001: 324), males of *H. monstrosa* and *H. paradoxa* can be separated mostly by the small eyestalks and corneae, and weakly pigmented corneae of the former, whereas the eyestalks and corneae are large, and the corneae well pigmented in *H. paradoxa* (see also Remarks under *H. monstrosa*). Previous to this study, no reliable characters were known so far to distinguish between females of *H. paradoxa* and *H. monstrosa*, and thus, all records and distributions for these two taxa based on females alone needed to be validated.

While reviewing the species of *Homolodromia* from the western Atlantic, we recognized two different female morphotypes, short- and long-legged, which differ in the length of P5 meri (when the meri are placed longitudinally on the carapace) relative to the position of the carapace gastric pits. In mature, short-legged females (Fig. 1D) the P5 meri end well before the carapace gastric pits, whereas in mature, long-legged females (Fig. 1C) the P5 meri attain the gastric pits or, more commonly, extend beyond the gastric pits. The differences in P5 meri length in short- and long-

legged specimens may well reflect the existence of two different species. However, relating short- or long-legged specimens to the type specimens of *H. paradoxa* or *H. monstrosa* is currently difficult because in the holotype male of *H. paradoxa* the legs are detached from the body and there are no females in the type series of *H. paradoxa*.

In the female holotype of *H. monstrosa*, the P5 meri overreach the gastric pits and is thus long-legged, whereas in the female paratype the P5 meri end well before the gastric pits and is thus short-legged (Fig. 1D). If our interpretation is correct, then the type series of *H. monstrosa* actually would contain two species, *H. monstrosa* s.s. and *H. paradoxa*. However, in the absence of other current available criteria to relate the short- and the long-legged morphological conditions to either *H. paradoxa* or *H. monstrosa*, and because the holotype female of *H. monstrosa* is long-legged, we only tentatively assign the long-legged condition to *H. monstrosa*. Also, this assignment best serves the stability of nomenclature. Thus, the material examined and listed under “Additional material” is herein tentatively attributed to *H. paradoxa* on the account of being either short-legged females or males having supraorbital spines and having bifurcated antennal spines (the variations discussed next under *H. monstrosa* not withstanding). DNA analyses of the type series of *H. monstrosa* and additional USNM preserved specimens of *H. paradoxa* and *H. monstrosa* were attempted to determine whether the relative length of the P5 meri is indeed a defining character reflecting two species. Regrettably, the samples were contaminated and the molecular analysis failed.

Homolodromia monstrosa Martin, Christiansen and Trautwein, 2001
Fig. 1C, D

Homolodromia monstrosa Martin, Christiansen and Trautwein, 2001: 319, figs. 4-7 (type locality: ~250 km NW of Paramaribo, Suriname, and 500 km ENE of Georgetown, Guyana, R/V Oregon, sta 10824, 07°42'N, 53°49'W).

Type Material.—French Guiana, R/V Oregon II: sta 10824, 07°42'N, 53°49'W, 631 m, 27 Nov 1969: female holotype 40.0 × 32.3 mm (USNM 310889); paratypes: same station as holotype: 2 males 32.6 × 26.7 mm, 44.3 × 33.0 mm, 1 female 37.4 × 48.0 mm (photographed) (USNM 310890).

Additional Material (Tentatively Assigned to *H. monstrosa*; See Remarks).—*Florida east coast*: E of St. Augustine, R/V Columbus Iselin, sta 8007-062, 29°47'N, 77°09'W, 918 m, 21 Sep 1980: 1 male 24.8 × 18.0 mm (USNM 1202387); R/V Oregon II, sta 11481, 28°02'N, 85°37'W, 585 m, 24 Jun 1971: 1 female (USNM 1184608). *Gulf of Mexico*: Florida, R/V Oregon II, sta 11481, 28°02'N, 85°37'W, 585 m, 24 Jun 1971: 1 female (USNM 1184608); R/V Oregon, sta 4634, 27°30'N, 94°40'W, 914 m, 22 Jan 1964: 1 female, 22.0 × 17.6 mm (USNM 1196472); Texas, off Aransas Bay, R/V Western Gulf, sta 19, 27°38'N, 95°00'W, 658-695 m, 27 Jul 1968: 1 ovig. female (USNM 128426); off Campeche Bank, R/V Oregon II, sta 11139, 24°33'N, 87°47'W, 594 m, 10 Aug 1970: 1 male (moulting) (USNM 1184607); off Campeche Bank, R/V Oregon II, sta 11139, 24°33'N, 87°47'W, 594 m, 10 Aug 1970: 1 male (moulting) (USNM 1184607); R/V Oregon, sta 4371, 24°28'N, 83°27'W, 375 m, 6 Aug 1963:

2 females (USNM 1153761); Mexico, [off Campeche], R/V Oregon II, sta 10984, 19°28'N, 92°55'W, 613 m, 9 Jun 1970: 1 male 40.0 × 30.0 mm (USNM 1201719). *Caribbean Sea. Virgin Islands*: east of St. Croix, 17°38'N, 63°48'W, 651 m, R/V Oregon II, sta 10831, 651 m, 3 Dec 1969: 1 male (USNM 310891); east of St. Croix, 17°38'N, 63°48'W, 651 m, R/V Oregon II, sta 10831, 651 m, 3 Dec 1969: 1 male (USNM 310891); N of St. Kitts, R/V Oregon, sta 6721, 17°37'N, 30°62'48"W, 622-695 m, 5 Jun 1967: 1 juv. female 23.1 × 18.0 mm (USNM 1201720); St. Kitts and Nevis, R/V Oregon, sta 6705, 17°14'N, 63°01'W, 704-777 m, 22 May 1967: 1 ovig. female 29.9 × 22.5 mm (USNM 1202385). *Netherlands Antilles*: N of Saba Island, R/V Oregon, sta 6697, 17°47'N, 63°09'W, 805-841 m, 18 May 1967: 2 ovig. females (USNM 155741); off NE coast of St. Eustatius, R/V Oregon, sta 6696, 17°46'N, 62°59'W, 649-668 m, 18 May 1967: 2 females 9.8 × 7.2 mm, 17.6 × 13.0 mm (USNM 1201712); Saba, R/V Oregon, cruise 62, sta 2637, 17°40'N, 63°40'W, 658-695 m, 30 Sep 1959: 2 females (USNM 285379). *Antigua and Barbuda*: R/V Oregon, sta 6703, 16°53'N, 61°53'W, 750-841 m, 21 May 1967: 3 males, 1 female, 1 ovig. female (USNM 285378). *Dominica*: R/V Oregon II, sta 10825, 15°42'N, 61°08'W, 640 m, 1 Dec 1969: 1 male 26.1 × 20.6 mm, 2 females 23.3 × 18.1 mm, 32.3 × 24.9 mm (USNM 1202382). *Honduras*: R/V Oregon, sta 3635, 16°58'N, 87°53'W, 457-732 m, 10 Jun 1962: 1 male (USNM 310892); R/V Oregon II, sta 11218, 16°32'N, 83°24'W, 914 m, 24 Oct 1970: 3 females 16.8 × 12.3 mm to 32.3 × 25.2 mm (USNM 1202381) R/V Oregon II, cruise 22, sta 11217, 16°26'N, 83°31'W, 933 m, 24 Oct 1970: 2 juv. female (USNM 1184610). *Nicaragua*: NE of Puerto Cabezas, R/V Oregon, sta 3561, 16°35'N, 80°04'W, 732 m, 18 May 1962: 2 females 21.7 × 16.2 mm, 32.3 × 24.6 mm (USNM 1196477); R/V Oregon, sta 3571, 14°10'N, 81°50'W, 549-604 m, 21 May 1962: 1 female (USNM 310685); E of Rio Grande, R/V Oregon, sta 1915, 13°13'N, 82°13'W, 640 m, 12 Sep 1957: 1 female 35.7 × 27.3 mm (USNM 1196469). *Dominica*: NE of Crompton Point, R/V Oregon, sta 5929, 15°39'N, 61°10'W, 649 m, 5 Mar 1966: 2 males 27.1 × 21.0 mm, 27.1 × 20.5 mm (USNM 1196478); Dominica Passage, R/V Oregon II, sta 10828, 15°42'N, 61°18'W, 677 m, 2 Dec 1969: 1 male, 23.1 × 11.4 mm (USNM 1196487); off Marigot, R/V Oregon II, sta 10826, 15°36'N, 61°09'W, 666 m, 1 Dec 1969: 1 female 22.7 × 16.7 mm (USNM 1196473). *Panama*: R/V Oregon, sta 3586, 9°20'N, 81°24'W, 914 m, 25 May 1962: 1 male 26.5 × 21.0 mm (USNM 1202383); E. of Escudo de Veraguas, Gulf of Mosquitos, R/V Oregon, sta 3601, 09°07'N, 81°10'W, 732 m, 31 May 1962: 1 ovig. female, 34.2 × 28.0 mm (USNM 1196474). *Colombia*: Guajira peninsula, N of Riohacha, R/V Oregon II, sta 11285, 11°41'N, 73°24'W, 0-640 m, 19 Nov 1970: 1 male 27.4 × 20.2 mm (USNM 1196486); R/V Oregon II, sta 11250, 11°13'N, 74°26'W, 631 m, 9 Nov 1970: 1 male 25.1 × 19.0 mm, 1 juv. female 18.0 × 14.5 mm (USNM 1201716); SW of Cartagena, R/V Oregon II, sta 11243, 10°09'00"N, 76°14'00"W, [no depth], 5 Nov 1970: 1 female (USNM 1184609). *Venezuela*: off Punta Zamoro, R/V Oregon, sta 4428, 11°41'N, 68°57'W, 732 m, 6 Oct 1963: 1 female 34.0 × 27.7 mm, 1 ovig.

female 38.1 × 29.6 mm (USNM 1201727); R/V Oregon, sta 4442, 10°50'N, 67°48'W, 732 m, 9 Oct 1963: 1 female 32.0 × 27.5 mm (USNM 1201718). *Northeastern South America. Suriname*: off Paramaribo, R/V Oregon II, sta 10602, 07°46'N, 54°35'W, 547 m, 10 May 1969: 1 female 46.0 × 34.4 mm (USNM 1196471); N of Suriname, R/V Oregon, sta 10807, 07°44'N, 53°59'W, 594 m, 21 Nov 1969: 2 males, 34.0 × 26.0 mm to 36.1 × 25.0 mm, 3 males (1 damaged) (USNM 1196488). *French Guiana*: N of Cayenne, R/V Oregon II, sta 10816, 07°36'N, 53°32'W, 686 m, 24 Nov 1969: 1 male 29.0 × 22.0 mm (USNM 1202386). *Brazil*: 50 miles W of Belém, R/V Oregon II, sta 11230, 09°06'N, 81°15'W, 777 m, 29 Oct 1970: 2 females 35.3 × 27.6 mm (photographed), 28.3 × 23.7 mm (USNM 1184611); Rio Grande do Norte, 04°18'10"S, 36°23'52"W, 987 m, 12 May 2011: 1 juv. female 24 × 19.5 mm (MZUSP 25790).

Size Range.—Males, 23.1 × 11.4 mm to 36.1 × 25.0 mm; females 21.7 × 16.2 mm to 46.0 × 34.4 mm; ovig. female 34.2 × 28.0 mm.

Distribution.—Eastern United States (Florida); Gulf of Mexico (Florida; Texas, off Aransas Bay; off Campeche Bank); Caribbean Sea (Dominica, St. Croix, Saba, Antigua, Barbuda); Honduras; Nicaragua; Panama; Colombia (Guajira peninsula, Cartagena); Suriname (off Paramaribo); French Guiana; Brazil (Belém; Rio Grande do Norte); depth: 375 to 918 m.

Remarks.—According to Martin et al. (2001: 324), and as previously mentioned under *Homolodromia paradoxa*, both males and females of *H. monstrosa* and *H. paradoxa* can be separated by differences in the eyestalks and cornea (i.e., eyestalks and cornea small, and cornea weakly pigmented in *H. monstrosa* vs. eyestalks and cornea large and well pigmented in *H. paradoxa*). Martin et al. (2001) also indicated that in males of *H. monstrosa*, the distal armature on G1 is slightly more complex than in *H. paradoxa*; there is a blunt lateral antennal spine that is not bifurcated distally; the cheliped has a smaller outer carpal spine (relative to the size of the carpus); and lack a supraorbital spine, whereas there is a sharp supraorbital spine in *H. paradoxa*. Martin et al. defined the differences in males of the two species by comparing the small holotype male (15.7 × 12.4 mm) of *H. paradoxa* with distinctly larger paratype males (38.6 × 32.9 mm to 28.7 × 26.2 mm) of *H. monstrosa*. This raised the question as to whether the morphological differences observed by Martin et al. in males of these two species represent growth variations in the same species. The examination of 11 males, including two males similar in size to the holotype of *H. paradoxa* (USNM 1202389, USNM 1201716), revealed that indeed Martin et al.'s putative characters or their combinations, to identify these two species actually vary between and within specimens. Some individuals can have both single and bifurcated (or semi-bifurcated) antennal spines, one on each side of the body. Also, the supraorbital and the outer carpal spines can be present on only one side of the body. Specimens identified in collections as *H. paradoxa* (e.g., USNM 120238, USNM 1202389), based on having supraorbital spines, have single, instead of bifurcated antennal spines, or have a single and a bifurcated antennal spine in the same specimen.

Conversely, specimens identified as *H. monstrosa* (USNM 310892) based on the lack of supraorbital spines, have bifurcated antennal spines. In addition, small individuals with supraorbital and single antennal spines (instead of bifurcated distally) can have darkly brown pigmented cornea that are wider than the distal width of the eyestalk. In view of the morphological variations observed herein in characters previously considered of diagnostic importance in *H. paradoxa* and *H. monstrosa*, it would appear that the validity of the latter, junior taxon is questionable. However, it is still possible that the two morphological conditions observed in females and discussed under the Remarks of *H. paradoxa* as short- and long-legged, are indicative of the existence of two different species. Thus, until further, more compelling evidence is available, both species names are considered valid. The material examined herein and listed under "Additional Material" is tentatively attributed to *H. monstrosa* on the account of being long-legged females or males lacking supraorbital spines and having single-pointed antennal spines.

Guinot (1995: 192) examined a male from R/V Oregon stn 4371 deposited in the USNM (no catalogue number provided) and stated that it probably represented *H. paradoxa*. We were not able to locate any male in the USNM collections from that station, but we did find instead two females not seen by Guinot from that same station that we herein assign to *H. paradoxa* (USNM 1153761).

Homolidae

Homola minima Guinot and Richer de Forges, 1995

Figs 6A, 7-9

Thelxiope barbata. Rathbun, 1937: 63, fig. 16, tbl. 17, pl. 15, figs. 1, 2; Chace, 1940: 8.

Homola barbata. Williams, 1984: 261, fig. 193; Melo, 1985: 32; 1996: 75, unnumbered fig; 1999: 440, fig. 2; Melo et al., 1998: 440; Nizinski, 2003: 123. (See Remarks)

Homola minima Guinot and Richer de Forges, 1995: 326, figs. 8c, d, f, 9b (type locality: northwestern Atlantic, USFC Fish Hawk, 38°33'N, 73°18'W); Martin and Zimmerman, 2001: 412; Nizinski, 2003: 123; Felder et al., 2009b: 1072.

Type Material.—*Northwestern Atlantic*. Off the cape south of Delaware, USFC Fish Hawk, sta 1046, 38°33'N, 73°18'W, 190.2 m, 10 Oct 1881: male holotype 22.0 × 17.0 mm (USNM 4988). Paratypes: same station as holotype, 1 male, 2 females (USNM 1150214); Massachusetts, Martha's Vineyard: USFC Fish Hawk, 40°03'00"N, 70°31'00"W, 949 m, 23 Aug 1881: 1 ovig. female, 1 juv. (USNM 7301); off North Carolina, R/V Dan Moore, sta OS05, 33°48'18"N, 76°34'06"W, 100 m, 14 May 1981: 1 male, 5 female, 1 ovig. female (USNM 202818); Florida (east coast), R/V Dolphin, MARMAP, sta 574223, 29°37'30"N, 80°14'30"W, 72 m, 23 Aug 1974: 1 female, 1 ovig. female, 1 juv. (USNM 188635).

Additional Material.—*Northwestern Atlantic*. *Massachusetts*: Nantucket Shoals, USFC Albatross, sta 2088, 39°59'15"N, 70°36'30"W, 262 m, 20 Sep 1883: 1 male (USNM 5371); S of Nantucket Shoals: USFC Albatross, sta 2197, 39°56'30"N, 69°43'20"W, 154 m, 6 Aug 1884: 1 male (USNM 8045). *Virginia*: R/V Gilliss, sta GI-76-01-37, trawl 106, 37°07'N, 74°39'W, 25 Jan 1976: 1 male (USNM 1185758); R/V Gilliss, sta GI-74-04-80, 36°44'30"N,

74°39'06"W, 186 m, 18 Nov 1974: 1 male (USNM 1185763); R/V Gilliss, sta GI-76-01-42, 36°43'24"N, 74°43'36"W, 87 m, 26 Jan 1976: 1 male (USNM 1185755); R/V Gilliss, sta GI-75-08-95, 36°41'12"N, 74°41'30"W, 118 m, 20 Sep 1975: 1 ovig. female [with abnormal rostrum] (USNM 1196489); R/V Gilliss, sta GI-75-08-95, 36°41'12"N, 74°41'30"W, 118 m, 20 Sep 1975: 1 female (USNM 1185760); R/V Columbus Iselin, sta CI-73-10-37, 36°40'48"N, 74°44'00"W, 87 m, 7 Jun 1973: 1 male (USNM 1185756); R/V Gilliss, sta GI-74-04-81, 36°38'54"N, 74°38'36"W, 18 Nov 1974, 578 m: 1 male (USNM 1185764); R/V Gilliss, sta GI-76-01-45, 36°37'30"N, 74°45'W, 109 m, 26 Jan 1976: 1 female (USNM 1185759); SE of Virginia Beach, R/V Gilliss, cruise 75-08, sta 96, 36°35'54"N, 74°42'06"W, 110-150 m, 20 Sep 1975: 3 males 23.8 × 17.2 mm to 30.8 × 22.2 mm, 1 female 23.0 × 17.7 mm, 1 ovig. female 24.0 × 18.0 mm (USNM 1184623); R/V Gilliss, sta GI-75-08-96, 36°35'54"N, 74°42'06"W, 128 m, 20 Sep 1975: 1 female (USNM 1185757); E of Norfolk, R/V Columbus Iselin, sta 73-10-54, 36°35'42"N, 74°40'42"W, 136 m, 10 Jun 1973: 1 male 27.6 × 20.3 mm (USNM 1185766); R/V Gilliss, sta GI-75-08-97, 36°34'12"N, 74°42'36"W, 144 m, 20 Sep 1975: 1 male 34.3 × 25.3 mm (photographed) (USNM 1185767); R/V Albatross IV, cruise 74-4, sta 33, 36°35'N, 74°43'W, 331 m, 17 Mar 1974: 1 female, 29 × 21 mm (USNM 1184604); Norfolk Canyon, R/V Eastward, cruise V-72, sta JAM-72V8, [no coordinates or depth], 1972: 1 male, 1 ovig. female (USNM 1185762), 3 males 15.2 × 10.2 mm to 27.8 × 20.5 mm (USNM 1185788). *North Carolina*: R/V Gilliss, sta GI-76-01-68, 37°01'30"N, 74°39'W, 150 m, 31 Jan 1976: 1 male, 1 ovig. female (USNM 1185765); off North Carolina, R/V Delaware, sta 60-7, 36°08'N, 74°49'W, 117 m, 16 May 1960: 1 female 17.7 × 12.5 mm (USNM 1185778); 36°07'N, 74°47'W, R/V Silver Bay, sta 4109, 146 m, 1 Jun 1962: 2 males, 1 female (USNM 1185783); R/V Oregon II, sta 10694, 35°19'N, 74°59'W, 124 m, 26 Jul 1969: 1 male, 3 female (USNM 1185770); off Cape Lookout, R/V Combat, sta 405, 34°18'N, 75°58'W, 137 m, 21 Jun 1957: 1 ovig. female (USNM 101668). *South Carolina*: R/V Dolphin, MARMAP sta 574149, 33°47'N, 76°37'30"W, 64 m, 3 May 1974: 1 ovig. female (USNM 186367); R/V Dan Moore, BLM/MMS Expedition LMRS, sta OS05, 33°48'12"N, 76°34'24"W, 116 m, 14 May 1981: 2 males and 1 female (USNM 221007); R/V Dolphin, sta OS01, 31°32'06"N, 79°44'06"W, 59 m, 12 Sep 1980: 1 male (USNM 221006). *Georgia*: Cumberland Island, USFC Albatross, sta 2666, 30°47'30"N, 79°49'00"W, 494 m, 5 May 1886: 1 male 9.7 × 7.7 mm (USNM 11410). *Florida (east coast)*: 40 miles E of Daytona Beach, R/V Silver Bay, sta 3438, 29°34'N, 80°15'W, 73-74.1 m, 24 Sep 1961: 1 female (USNM 1185779); 75 miles SE of Daytona Beach, R/V Silver Bay, sta 2010, 28°17'N, 80°01'W, 62-75 m, 25 Apr 1960: 1 ovig. female (USNM 1185771); R/V Silver Bay, sta 2664, 28°04'N, 80°04'W, 43.9 m, 24 Jan 1961: 1 juv. female 8.6 × 6.6 mm (USNM 1235147); SE of Melbourne Beach, R/V Silver Bay, sta 5107, 27°59'N, 80°01'W, 73 m, 28 Sep 1963: 1 female (USNM 1235149); Palm Beach, rocky reef off Palm Beach, R/V Triton, 55-73 m, 28 Jul 1950, coll. Thompson and McGinty: 1 ovig. female (USNM

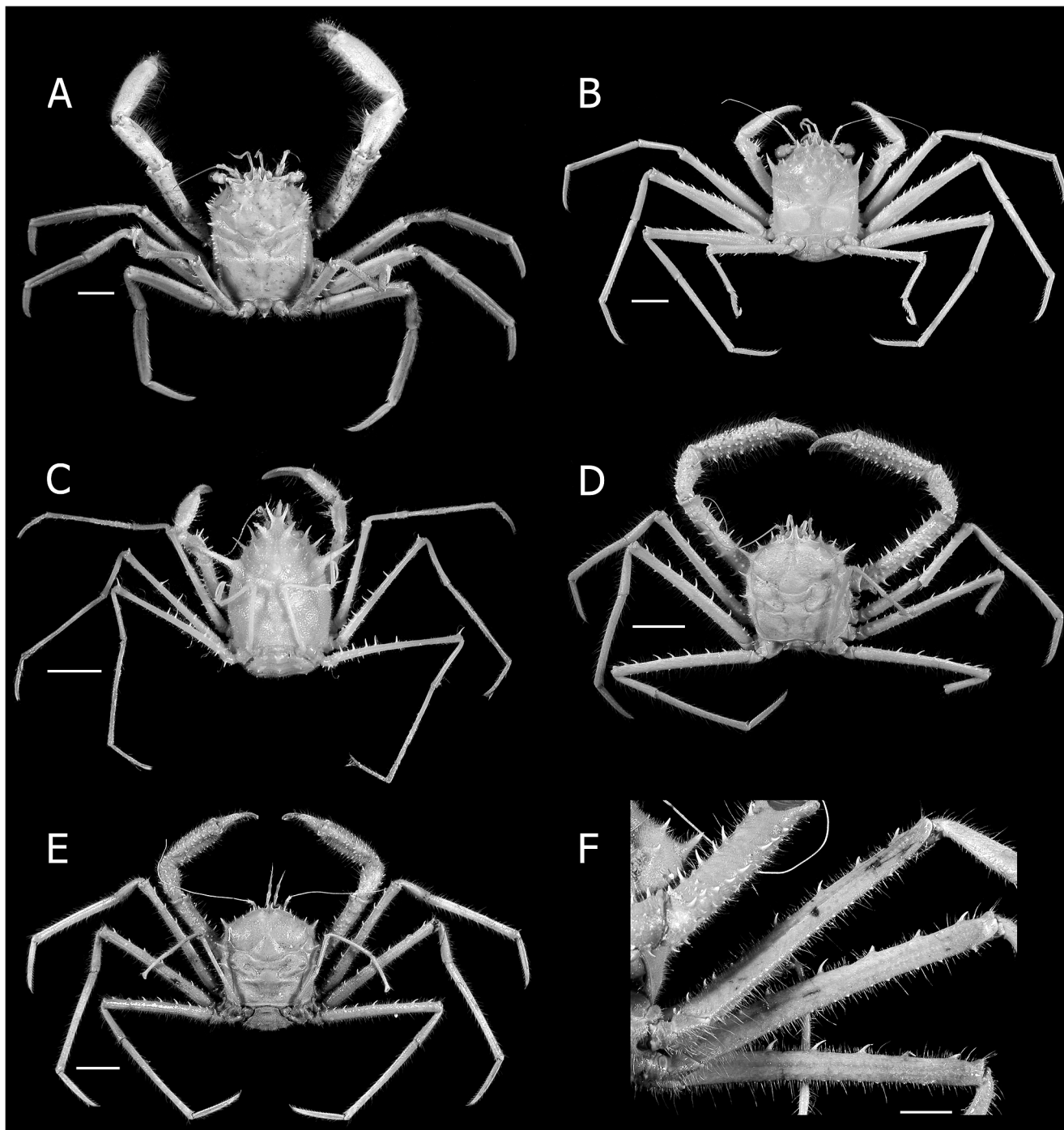


Fig. 6. A, *Homola minima* Guinot and Richer de Forges, 1995, male, 34.3 × 25.3 mm, off Virginia (USNM 1185767); B, *Homola vigil* A. Milne-Edwards, 1880, ovig. female, 27.7 × 23.0 mm, Caribbean Sea, St. Kitts and Nevis (USNM 1184613); C, *Homologenus rostratus* (A. Milne-Edwards, 1880), ovig. female, 14.1 × 9.5 mm, eastern coast of United States, Florida (USNM 1196484); D, *Lamoha williamsi* (Takeda, 1980), male paratype, 41.0 × 38.0 mm, northwestern Pacific Ocean, Northern Mariana Islands (USNM 222531); E, F, *Lamoha noar* (Williams, 1974), ovig. female, 48.0 × 45.0 mm, U.S. Virgin Islands, St. Croix (USNM 205275); E, dorsal view; F, meri of left P1-4, mesioventral view. Scales = 10 mm (A, B, F), 5 mm (C), or 20 mm (D, E).

1196466); Palm Beach County, off Palm Beach, edge of Rocky Reef, R/V Triton, sta 27, 91-10 m, 28 Jan 1950: 1 ovig. female (USNM 1196467); Palm Beach County, off Palm Beach, rocky reef, R/V Triton, 55-73 m, 20 Apr 1950: 2 females (USNM 1196468); Florida Straits, R/V Combat, sta 457, 25°16'N, 80°07'W, 119 m, 26 Jul 1957: 1 ovig. fe-

male (USNM 101391); R/V Coral Reef II, E of Port Everglades Inlet, Broward County, Florida, 140 m, 5 June 1999, coll. C. G. Messing: 1 male, 9.4 × 6.7 mm, 1 female, 8.9 × 6.6 mm (USNM 1201725); R/V Clearview III, cruise CV-74-01, sta 209, [no coordinates or depth], 8 May 1974, coll. Cawell: 1 female 16.7 × 12.4 mm (USNM

1185761). *Gulf of Mexico*: textitFlorida (west coast): R/V Oregon, sta 326, 29°57'N, 86°57'30"W, 150 m, 30 Apr 1951: 1 female (USNM 92339). MMS-SOFLA: 1/IV-10-OTH, sta 10, 26°16'44"N, 83°42'49"W, 71.3 m, 30 Apr 1981: 1 male (USNM 241231); 1/III-11-OTS, sta 11, 26°16'43"N, 83°46'49"W, 77 m, 4 Nov 1980: 1 female (USNM 241239); 2/III-11-TDS-A, sta 11, 26°16'43"N, 83°46'49"W, 77 m, 6 Feb 1982: 1 male (USNM 241240); 2/III-32-OTH-A, sta 32, 26°16'40"N, 84°04'05"W, 137 m, 6 Feb 1982: 1 female, 1 juv. female (USNM 241238); 2/II-32-TDS-C, sta 32, 26°16'40"N, 84°04'05"W, 137 m, 25 Jul 1981: 1 male (USNM 241237); 2/III-32-TDS-A, sta 32, 26°16'40"N, 84°04'05"W, 137 m, 6 Feb 1982: 1 male, female juv. (USNM 241236); 2/II-35-TDS-A, sta 35, 25°44'50"N, 84°21'02"W, 159 m, 26 Jul 1981: 1 damaged juv. male ~7.5 × 6.0 mm (USNM 241235); 2/III-35-OTH-A, sta 35, 25°44'50"N, 84°21'02"W, 159 m, 7 Feb 1982: 1 juv. female (USNM 241233); 2/II-35-OTH-A, sta 35, 25°44'50"N, 84°21'02"W, 159 m, 26 Jul 1981: 1 male (USNM 241234); 2/II-36-TDS-C, sta 36, 25°16'50"N, 83°57'21"W, 127 m, 2 Aug 1981: 1 male (USNM 241229); 2/III-36-TDS-A, sta 36, 25°16'50"N, 83°57'21"W, 127 m, 9 Feb 1982: 1 ovig. female (USNM 241225); 2/II-36-TDS-B, SOFLA, sta 36, 25°16'50"N, 83°57'21"W, 127 m, 2 Aug 1981: 1 ovig. female (USNM 241230); 2/II-38-OTH-A, sta 38, 25°16'30"N, 84°14'46"W, 159 m, 2 Aug 1981: 1 ovig. female (USNM 273440); 2/III-38-TDS-C, sta 38, 25°16'30"N, 84°14'46"W, 159 m, 10 Feb 1982: 1 juv. male (USNM 241227); 2/II-38-OTH-A, sta 38, 25°16'30"N, 84°14'46"W, 159 m, 2 Aug 1981: 1 male, 3 juv. females (USNM 241228); 2/II-38-OTH-A, sta 38, 25°16'30"N, 84°14'46"W, 159 m, 2 Aug 1981: 1 juv. female (USNM 241226); 1/III-30-OTH-A, sta 30, 24°47'25"N, 83°51'09"W, 76.1 m, 1 Nov 1980: 1 juv. male, 1 female (USNM 241232); 1/III-30-TDS, sta 30, 24°47'25"N, 83°51'09"W, 76.1 m, 21 Nov 1980: 1 female (USNM 242740). USFC Albatross, sta 2316, Florida Keys, off Key West, 24°25'30"N, 81°47'45"W, 91 m, 15 Jan 1885: 1 juv. female (USNM 21713); R/V Oregon, sta 218, 23°02'N, 89°34'W, 227 m, 10 Jan 1951: 1 female (USNM 92156); Florida Keys, Dry Tortugas, south of Loggerhead Key, no. 2 Red Buoy, 73 m, 4 Aug 1931, coll. Loughley and Manter: 1 male (USNM 71363). *Caribbean Sea*. *Bahamas*: Great Bahama Bank, R/V Oregon, sta 10861, 23°12'N, 78°49'W, 274 m, 15 Dec 1969: 1 male, 24.0 × 17.5 mm, 1 female 19.9 × 13.6 mm, 1 ovig. female 19.1 × 14.3 mm (USNM 1184622); Bahamas, Great Inagua Island, 20 miles SE of Matthew Town, R/V Oregon, sta 5421, 20°54'N, 73°36'W, 229 m, 25 May 1965: 2 juv. females 7.5 × 5.2 mm, 7.6 × 5.2 mm (USNM 1196465). *Yucatan Channel*: Havana, Cuba to Yucatan, USFC Albatross, sta 2354, 20°59'30"N, 86°23'45"W, 142.6 m, 22 Jan 1885: 2 males (USNM 21714). *Great Inagua Island*: off Mathew Town, R/V Silver Bay, sta 3496, 20°53'N, 73°42'W, 183 m, 4 Nov 1961: 1 male (USNM 1235146). *Mexico*: Quintana Roo, east of Isla de Cozumel, R/V Oregon, sta 4938, 20°31'00"N, 86°12'00"W, 274-300 m, 11 Jun 1964: 1 male 15.3 × 10.5 mm (USNM 1185772); Quintana Roo, Yucatan Channel, E of Cozumel Island, R/V Oregon, sta 4939, 20°25'N, 86°13'W, 274 m, 11 Jun 1964: 1 juv. female 8.3 × 6.0 mm (USNM 1196464). *Puerto Rico*: 60 miles WNW of San Juan, R/V Oregon, sta 2655, 18°24'N, 67°15'W, 183 m, 6 Oct 1959: 1 male (USNM 1185768); Mona Passage, R/V Silver Bay, sta 5193, 18°16'N, 67°22'W, 274 m, 18 Oct 1963: 1 female (USNM 1185777). *Jamaica*: R/V Oregon, sta 3548, 20 miles S of Black River, 17°53'N, 77°56'W, 274 m, 16 May 1962: 1 male 10.6 × 9.4 mm (USNM 1185773). *Belize*: 100 miles E of Belize, R/V Oregon, sta 3636, 17°17'N, 87°59'W, 229 m, 10 Jun 1962: 2 males 22.1 × 15.2 mm, 22.5 × 15.7 mm (USNM 1196463). *Nicaragua*: 100 miles E of Huani, R/V Oregon, sta 10190, 14°42'N, 81°38'W, 141 m, 19 Nov 1968: 2 males 15.8 × 11.7 mm, 23.2 × 16.8 mm, 1 female, 16.0 × 11.0 mm, 1 ovig. female 19.7 × 14.3 mm (USNM 1185769); R/V Oregon, sta 4832, 14°15'30"N, 80°27'06"W, 219-238 m, 12 May 1964: 1 female (USNM 1235148); 100 miles E of Puerto Cabezas, R/V Oregon, sta 4928, 14°05'N, 81°21'W, 183 m, 8 Jun 1964: 1 male 16.6 × 12.5 mm, 1 female 12.4 × 9.0 mm (USNM 1185780); W of Old Providence Island, R/V Oregon, sta 6424, 13°12'30"N, 82°15'36"W, 201-219 m, 4 Feb 1967: 2 males 21.4 × 16.1 mm, 25.5 × 18.3 mm, 1 ovig. female 24.6 × 18.2 mm (USNM 1185787); W of Isla de San Andres, R/V Oregon, sta 6443, 12°25'N, 82°28'30"W, 190-199 m, 6 Feb 1967: 2 males 15.8 × 11.7 mm, 23.2 × 16.8 mm, 1 female 16.0 × 11.0 mm, 1 ovig. female 19.7 × 14.3 mm (USNM 1185785). *Barbados*: off W coast, 146-183 m, coll. J. Lewis: 2 males 26.0 × 19.5 mm, 29.2 × 21.1 mm (USNM 152623). *Panama*: R/V Oregon, sta 5739, 09°43'N, 79°20'W, 95 m, 19 Oct 1965: 3 males 11.0 × 8.0 mm to 18.6 × 13.1 mm, 1 female 11.6 × 8.4 mm (USNM 1185776). *Colombia*: 50 miles W of Riohacha, R/V Oregon, sta 4908, 11°23'N, 73°33'30"W, 46-51 m, 31 May 1964: 1 male 15.5 × 12.0 mm (USNM 1185781); SW of Cartagena, R/V Oregon II, sta 10212, 9°55'N, 76°03'W, 128 m, 24 Nov 1968: 1 male (USNM 1185774); NW of Tinajones, mouth of Sinú River, 9°28'34"N, 75°55'15"W, CIOH-INVEMAR-Smithsonian 1995 Expedition, sta T8, 5 Aug 1995, 8 m, coll. R. Lemaitre and N. H. Campos: 1 male, 1 juv. female (USNM 1071587). *Venezuela*: off La Guaira, R/V Oregon, sta 4465, 10°45'N, 66°37'W, 229 m, 17 Oct 1963: 1 female 26.9 × 19.8 mm (USNM 1185784); 25 miles NE of Caracas, R/V Oregon, sta 4461, 10°50'N, 66°55'W, 97 m, 13 Oct 1963: 1 female 20.7 × 15.0 mm (USNM 1185775). *Northeastern South America*. *Suriname*: NE of Paramaribo, R/V Oregon, sta 2289, 07°25'N, 54°35'W, 137-146 m, 8 Sep 1958: 4 males, 3 females, 1 ovig. female (USNM 1185786). *Southwestern Atlantic*. *Brazil*: Para, R/V Oregon, sta 2080, 02°04'S, 47°00'W, 229 m, 17 Nov 1957: 1 female 16.0 × 11.0 mm (USNM 1185782); Rio Grande do Norte, sta MT 53, 04°41'S, 50°48'S to 36°34', 49°98'W, 22 May 2011, 150 m: 2 females (MZUSP 25786); REVIZEE-Comissão Central, sta D3, 22°52'S, 41°09'W, 80 m, 23 Mar 1996, coll. M. Tavares: 1 male (MZUSP 25792); OPISS/IOUSP, São Sebastião, São Paulo, inner side of continental shelf: 1 male, 1 female (MZUSP 17556); Santos, São Paulo, 150-200 m, [no day] Apr 2002, coll. C. Magenta: 1 male (MZUSP 155557); Rio Grande do Sul, GEDIP/IOUSP, sta 1873, 13 Jul 1972: 2 males (MZUSP 3932). *Uruguay*: 34°04'S, 51°32'W, 130 m, 17 Jun 1980, coll. L. Chao: 1 male, 2 juv. females (USNM 256500). R/V Lerez, sta 8203, trawl 25, 34°58'S, 52°13'W, 200 m, 25 Feb 1982, Nov 2013,

coll. F. Scarabino: 2 males (MZUSP 29970). R/V Lerez, sta 8205, trawl 4, 35°25'S, 52°29'W, 700 m, 22 Mar 1982, Nov 2013, coll. F. Scarabino: 1 male (MZUSP 29969). Sta L18, 35°34'S, 52°52'W to 35°35'S, 52°53'W, 140-147 m, 2 Oct 2007, coll. F. Scarabino. Nov 2013: 1 male (MZUSP 29968). R/V Lerez, sta 8202, trawl 48, 35°41'S, 53°40'W, 53 m, 19 Feb 1982, Nov 2013, coll. F. Scarabino: 1 male, 1 ovig. female (MZUSP 29967).

Comparative Material.—*Homola barbata* (Fabricius, 1793): *Mediterranean Sea*: Naples, Italy, coll. Zoological Station Naples: 1 male, 1 female 33.0 × 25.3 mm (USNM 23182); Nice, France, sta MP-8, [no coordinates or other sta data]: 1 male, 1 ovig. female (USNM 184578). *Southeastern Atlantic*: Congo, near Pointe Noire, 04°56'S, 11°31'E, 95-97 m, 21 Sep 1965: 2 males (USNM 125576).

Size Range.—Males, 7.6 × 5.0 mm to 34.3 × 25.3 mm; females, 7.5 × 5.2 mm to 29.0 × 21.0 mm; ovig. females, 9.7 × 7.5 mm to 28.7 × 22.2 mm.

Distribution.—Northeastern coast of the United States, from Massachusetts to Florida, Bahamas, Gulf of Mexico, Caribbean Sea, and eastern coast of South America, from Suriname to Uruguay; depth: 55 to 700 m.

Remarks.—This western Atlantic species has traditionally been confused with *Homola barbata*, a species originally described from the Mediterranean (Bay of Naples), and also reported from the eastern Atlantic (Açores, Congo and Gulf of Guinea) and western Indian Ocean (south of Madagascar) by Guinot and Richer de Forges (1995). Guinot and Richer de Forges' (1995) description of *H. minima* was based on several males, females, and unsexed juveniles, from six localities on the US east coast and Gulf of Mexico, collected from 40°N to 25°N. They also assigned as paratypes of *H. minima*, with some reservation, two unsexed juveniles and one small male from the southwestern Atlantic, collected from 23°S to 32°S. Since then, the identity of the southwestern Atlantic paratype specimens have remained doubtful, and thus the southernmost range of *H. minima* uncertain. In a recent inventory of decapods from the Gulf of Mexico by Felder et al. (2009a, b), the occurrence of *H. minima* in the southern Caribbean and Brazil was still questioned.

Guinot and Richer de Forges (1995) observed that one of the primary distinctions between *Homola minima* and *H. barbata* was the difference in size, with the former rarely exceeding cl 25-26 mm, whereas specimens of the latter could reach cl 40 mm or more. Furthermore, Guinot and Richer de Forges indicated that the carapace in *H. minima* was narrower than in *H. barbata*, implying a significant difference between the two species in cl/cw ratio. Based on the study of much larger samples than those studied by Guinot and Richer de Forges' (1995), particularly from the southwestern Atlantic, we found that *H. minima* grows to a larger size than previously thought, with some specimens reaching cl 34.3 mm, and specimens of cl 28 mm or more in size are not uncommon (see Size Range). In the specimens studied herein, the ratio cl/cw, and therefore narrowness, is similar in the two species, varying from about 1.4 to 1.5. For example, the ratio in a male *H. minima* is

29.5 mm/20 mm = 1.47 (MZUSP 1557), and in a male *H. barbata* it is 30 mm/22 mm = 1.37 (USNM 23182).

Other diagnostic characters used by Guinot and Richer de Forges (1995) to distinguish between *Homola minima* and *H. barbata*, such as the armature of P4 merus, and the indentation at the anterolateral angle of the sixth pleonal segment, were found to be variable or so similar, that they are not useful in distinguishing the two species. The spinulation on the upper margin of the P4 merus vary in the same individual and between individuals (a male, MZUSP 1557, *H. minima* has four spines on the left P4, the right P4 is missing; a male, USNM 23182, *H. barbata* has four spines on the left P4, and three on the right P4). Guinot and Richer de Forges (1995: 328), however, were unsure whether the armature of P4 is a useful character to separate between the two species until more material became available for evaluation. The indentation at the anterolateral angle of the sixth pleonal segment is only slightly less protruded in *H. minima* than in *H. barbata*. The G1 and G2 of *H. minima* (Fig. 7) are very similar to that of *H. barbata*. The only reliable adult diagnostic character that we have found for separating *H. minima* from *H. barbata* is indeed the length of P5. The distal end of P5 meri reaches at most to the cervical groove in *H. minima*, whereas the P5 meri distinctly overreach the cervical groove in *H. barbata*.

Biramous Uropod and Pleopod Formula.—With few exceptions, adult Brachyura retain uropods as dorsal plates, ventral lobes, or sockets (see Guinot and Tavares, 2001; Guinot et al., 2013). Uropods showing as ventral lobes or dorsal plates are found in Homolodromioidea and Dromioidea, whereas in Homoloidea and Eubrachyura the uropods are modified into sockets that act along with a pair of tubercles present on thoracic sternite 4 or 5, respectively, to form an pleonal locking-system. The uropods are completely lost in the Cyclodorippoidea and Raninoidea (Lyreidinae excepted). The existence of uropods modified into sockets in two distinct and not closely related brachyuran clades (Homoloidea and Eubrachyura) is a matter of great interest to hypotheses on the evolution of the brachyuran urosome and, therefore, to brachyuran phylogeny.

Surmising that the uropods evolved differently in Homoloidea and Eubrachyura, Guinot and Tavares (2001) used the anatomical terms homoloidian socket [“fossettes homoloïdiennes”] as opposed to eubrachyuran socket. Based on our study of juvenile males and females of *Homola minima*, we provide anatomical evidence that the homoloidian socket and the eubrachyuran socket are indeed not homologous. While the eubrachyuran socket is appendicular in origin, resulting from the striking modification of the uropod (Pérez, 1928a, b, 1929), in Homoloidea, at least as revealed by the condition in juvenile males and females of *Homola minima* (Figs. 8, 9) the socket is hollowed directly on the sixth pleonal sternite and therefore is scleritical in origin rather than appendicular. In juvenile males and females of *H. minima* scleritical sockets and uropods co-exist. Clearly, two structures are not homologous if they co-exist in the same organism (see also Rieppel, 1988). Indeed, in juvenile males and females of *H. minima*, the bud-like endopod and exopod arise from the vestigial one-segmented uropod protopod. Separated from the uropods, large and deep scleritical

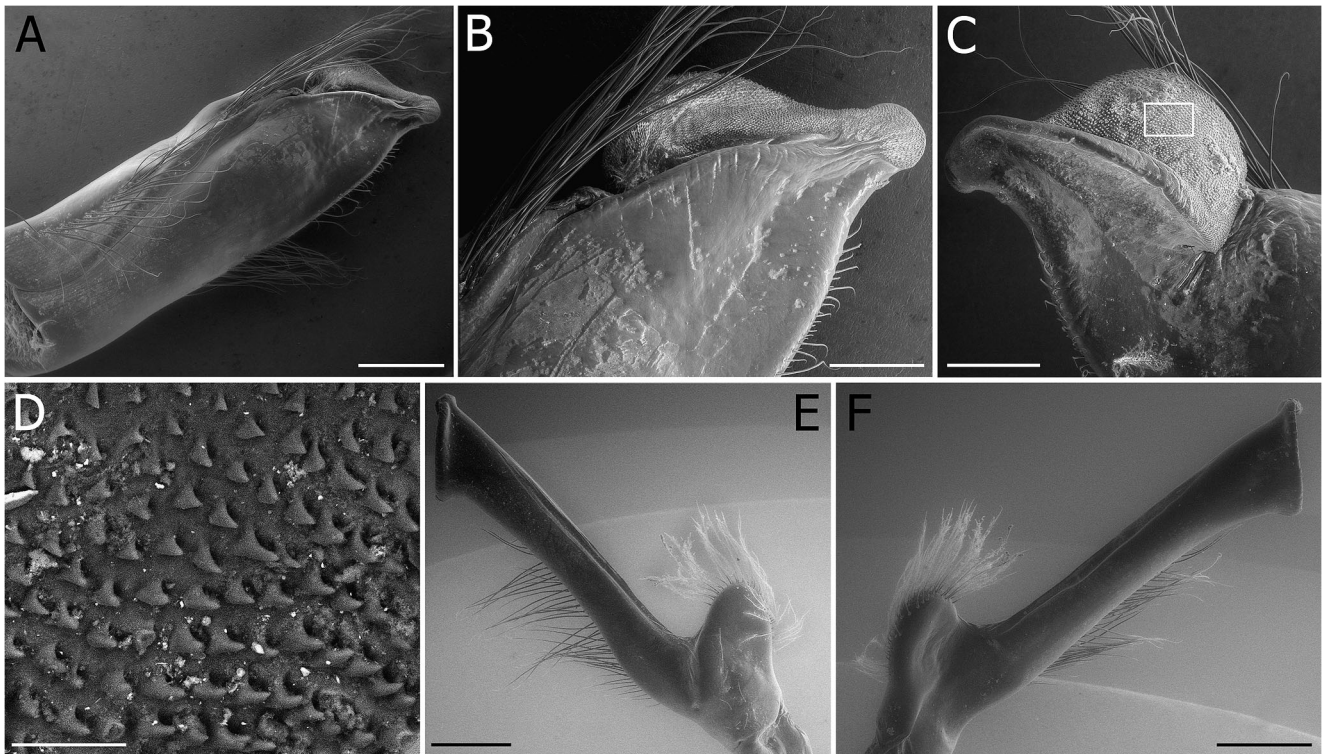


Fig. 7. *Homola minima* Guinot and Richer de Forges, 1995, SEM photomicrographs of G1 and G2 of male, 29.2 × 21.1 mm mm (USNM 152623). A, G1, mesial view; B, distal portion of same, mesial view; C, same, lateral view; D, view of area demarcated by square in C; E, F, G2 in lateral (E) and mesial (F) views. Scales = 1 mm (A, E, F), 500 μm (B, C), or 50 μm (D).

sockets are well visible ventrally at the anterolateral angles of the sixth pleonal somite. In juvenile males and females of *H. minima* a pair of tubercles positioned on the fourth thoracic sternum match the scleritical socket, thus forming the complementary part of the pleonal locking-system, which is functional without the uropods. The uropods are completely lost in the adult male and female of *H. minima*, where there is also a functional pleonal locking-system. The scleritical homoloidian socket and the appendicular eubranchyuran socket are therefore homoplastic, and hence each is useful only as indicators of relationships in members of their own evolutionary branch. As a consequence of the homoplasmy between the scleritical homoloidian socket and the appendicular eubranchyuran socket, their pleonal locking-system is also homoplastic.

Retention of P13-5, in juvenile and adult males is not known in podotreme crabs other than Homolodromioidea and some Dromioidea. Here we report juvenile males of *Homola minima* (e.g., USNM 241235; 241237) with a complete pleopod formula (P11-5 + vestigial, biramous uropods). In juveniles, G1 is stout and uniramous and already different from P12-5 (Fig. 8). P12-5 are similar in shape and size to one another, biramous, slender, and the mesial rami are much shorter than the lateral ones. In juveniles, the penis is transparent and shows as an unfolded bud. The P12-5 are lost in adults. Juvenile females of *H. minima* (e.g., USNM 241226; 1071587) also have a complete pleopod formula (P11-5 + vestigial, biramous uropods). The P11 is uniramous, whereas P12-5 are biramous with endopods and exopods of about the same size. In

juveniles, the gonopore on P3 is well recognizable. The adult female retains the uniramous P11 (not ovigerous) and P12-5 (Fig. 9).

Homola vigil A. Milne-Edwards, 1880

Fig. 6B

Homola vigil A. Milne-Edwards, 1880: 33 (type locality: Caribbean Sea, Martinique, USCGS Blake, sta 193, 14°43'48"N, 61°11'25"W); Guinot and Richer de Forges, 1995: 330, figs. 9i, 13b, 14c, d; Felder et al., 2009b: 1072.

Thelxiope vigil. Rathbun, 1937: 66, pl. 16, figs. 1-3; Chace, 1940: 9.

Type Material.—Not examined.

Material Examined.—*Northwestern Atlantic. Straits of Florida*: W end of Grand Bahama Island, R/V Seward Johnson, sta JSL-II-3685, 27°04'29"N, 79°19'11"W, 616 m, 23 Jul 2009, coll. T. Frank: 1 male 19.2 × 16.0 mm (USNM 1184612). *Gulf of Mexico*: Florida, R/V Oregon, sta 4572, 23°23'N, 86°56'W, 549 m, 8 Dec 1963: 1 male 16.6 × 14.5 mm (USNM 1184617). *Caribbean Sea*: Cuba, Havana, off Playa Baracoa, Harvard-Havana Expedition, R/V Atlantis, sta 3303, 23°05'N, 82°33'W, 23 Mar 1939, 475.5 m: 1 male (USNM 81930); Dominican Republic, E of Puerto Plata, R/V Silver Bay, sta 5168, 19°47'N, 70°21'30"W, 640-732 m, 15 Oct 1963: 1 male 24.2 × 20.5 mm (USNM 1184618); Cayman Islands, Grand Cayman, R/V Eastward, cruise E-II-77, sta 31465, 19°20'45"N, 81°27'36"W, 630-990 m, [no day/month] 1977: 1 male 28.6 × 23.3 mm (USNM 1184619); Anguilla, Anegada Passage, NW of Dog Island, R/V Oregon II, sta 10835, 18°28'N, 63°23'W, 658 m,

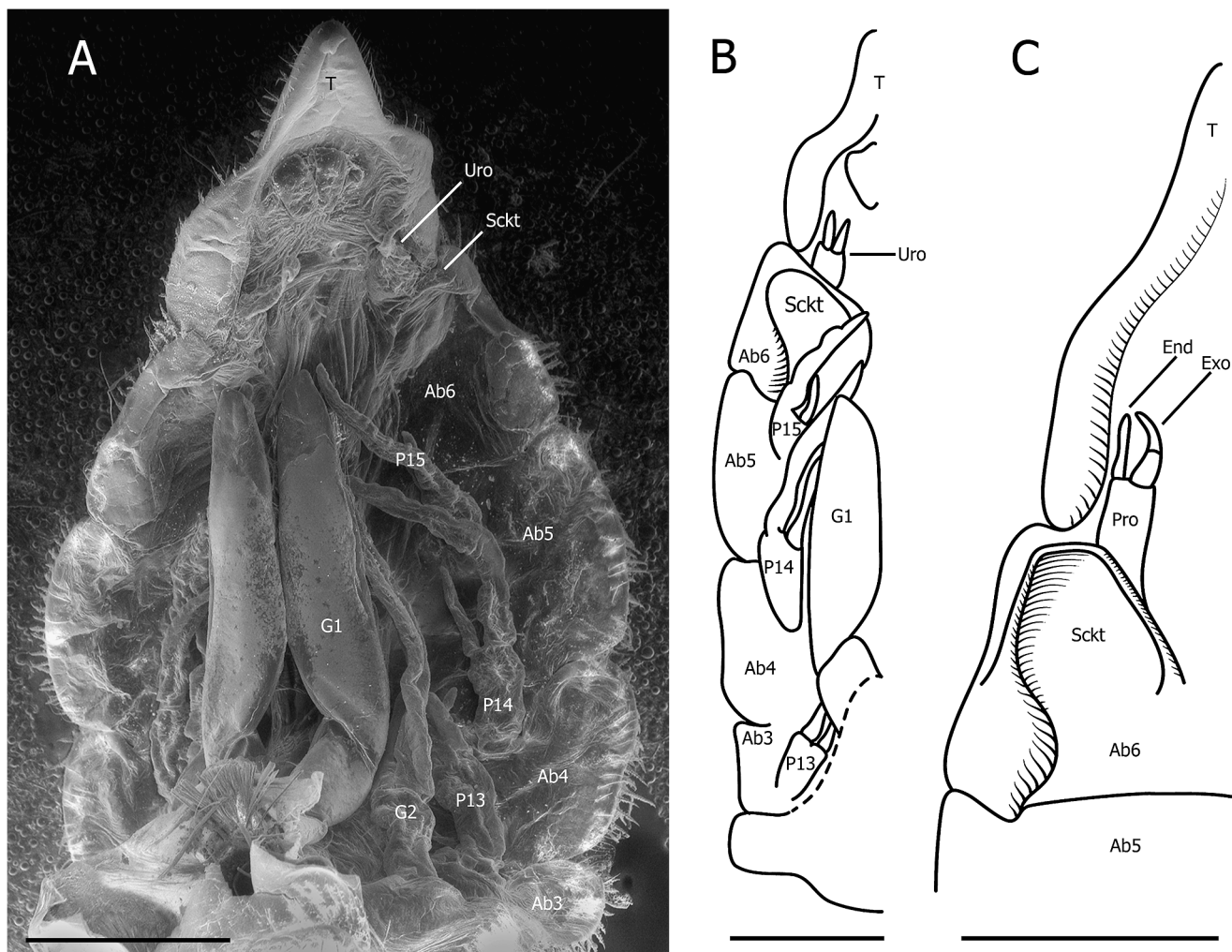


Fig. 8. *Homola minima* Guinot and Richer de Forges, 1995, juvenile male pleon. A, SEM photomicrograph, ventral view (8.8 × 6.8 mm, USNM 241237); B, schematic drawing of left side of pleon, ventral view (7.5 × 6.0 mm, USNM 241235); C, distal portion of same. Abbreviations: Ab3-6, pleomeres 3 to 6; G1, G2, gonopods 1 and 2; End, uropod endopod; Exo, uropod exopod; P13-5, pleopods 3 to 5; Pro, uropod protopod; Sckt, homoloidian socket; T, telson; Uro, uropod. Scales = 1 mm.

6 Dec 1969: 1 male (damaged) (USNM 1196481); R/V Oregon, sta 6695, 17°41'N, 62°50'50"W, 549-585 m, 18 May 1967: 1 male 25.3 × 20.7 mm (USNM 1184614); St. Kitts and Nevis, off St. Christopher, R/V Oregon, sta 6721, 17°37'30"N, 62°48'W, 622-695 m, 5 Jun 1967: 3 males 13.6 × 10.5 mm to 19.3 × 17.2 mm, 3 females 20.0 × 17.0 mm to 26.0 × 22.0 mm (USNM 1184621); St. Kitts and Nevis, N of Black Rocks, R/V Oregon II, sta 10845, 17°33'N, 62°46'W, 668 m, 9 Dec 1969: 1 ovig. female 27.7 × 23.0 mm (photographed) (USNM 1184613); St. Kitts and Nevis, NE of St. Kitts, R/V Oregon, sta 10844, 17°24'N, 62°28'W, 629 m, 8 Dec 1969: 2 males 16.0 × 14.0 mm, and 18.0 × 14.2 mm, and 1 female 20.7 × 16.7 mm (USNM 1184615); St. Kitts and Nevis, E of St. Kitts, R/V Oregon II, sta 10842, 17°15'N, 62°22'W, 578 m, 8 Dec 1969: 1 female 16.6 × 13.6 mm (USNM 1184616); St. Kitts and Nevis, SE of Nevis, R/V Oregon, sta 10843, 17°06'N, 62°17'W, 589 m, 8 Dec 1969: 1 male 23.6 × 20.0 mm, 1 ovig. female 23.0 × 19.5 mm (USNM 1184605), 1 female 16.0 × 13.8 mm (USNM 1196480); Martinique, F/V Polka, sta

MART 28, 900 m, 23 Apr 1992, coll. J. Poupin: 1 male (MZUSP 25793); off Nicaragua, W of Isla de San Andres, R/V Oregon, sta 3609, 12°26'N, 82°24'W, 503 m, 2 Jun 1962: 1 male 25.7 × 21.7 mm (USNM 1184620).

Size.—Males, 13.6 × 10.5 mm to 28.6 × 23.3 mm; females, 16.0 × 13.8 mm to 27.7 × 23.0 mm; ovig. females, 17.0 × 19.0 mm to 23.0 × 19.5 mm to 28.7 × 22.2 mm.

Distribution.—Southeastern coast of the United States, from Georgia to Florida, Gulf of Mexico, Bahamas, and Caribbean Sea; depth: 300 to 990 m.

Remarks.—*Homola vigil* and *H. minima* co-occur in the Western Atlantic, the former ranging from the southeastern coast of the United States to the Caribbean Sea, and the latter broadly ranging from the northeastern coast of the United States to Uruguay. In addition to the characters mentioned by Guinot and Richer de Forges (1995: 331) to distinguish between *H. vigil* and *H. minima*, the following are useful if chelipeds and/or P5 are missing (compare Figs. 6A and 6B): a sinuous row of seven strong spines extend

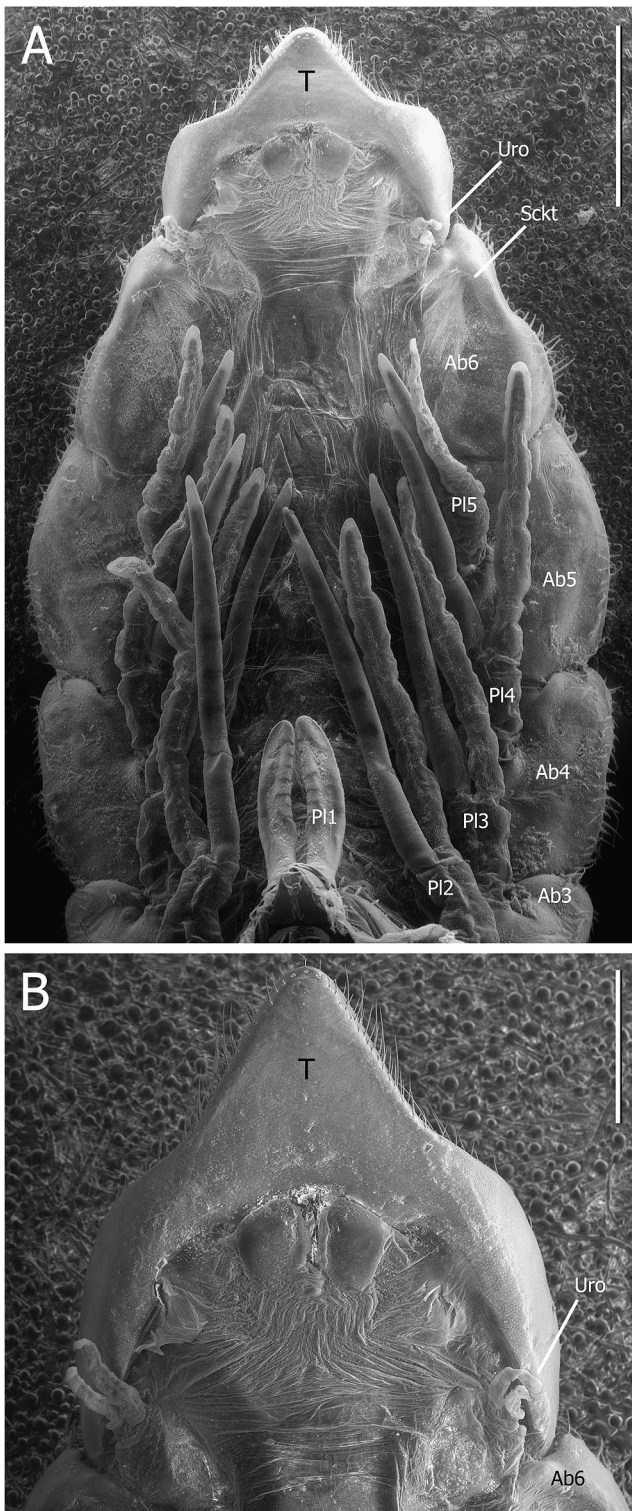


Fig. 9. *Homola minima* Guinot and Richer de Forges, 1995, SEM photomicrographs of juvenile female pleon, ventral view, 9.0 × 8.0 mm (USNM 1071587). A, entire pleon; B, same, distal portion showing uropods. Abbreviations: End, uropod endopod; Exo, uropod exopod; P11-P15, pleopods 1 to 5; Sckt, homoloidian socket. (Compare panel A, where juvenile female P11 is uniramous, and endopods and exopods of P1 2-5 are similar in size, with Fig. 8A of juvenile male where G1 is already formed, and endopods of P1 2-5 are much shorter than exopods). Scales = 1 mm (A), or 500 μm (B).

transversally across the carapace between the anterolateral teeth, excluding anterolateral teeth, versus only six strong spines extending transversally across the carapace in *H. minima*; P3 and P4 meri each twice as long as the P3 and P4 carpi, versus P3 and P4 meri distinctly less than twice the length of the P3 and P4 carpi in *H. minima*; and mesogastric region of carapace at most with a weak tubercle, versus mesogastric region with distinct, strong tubercle in *H. minima*. A male of *H. minima* (USNM 11410) has a rostrum and P2-P5 as in *H. vigil*, but only five spines across the carapace between the anterolateral spines instead of seven.

Homologenus rostratus (A. Milne-Edwards, 1880)
Fig. 6C

Homolopsis rostratus A. Milne-Edwards, 1880: 34 (type locality: Antilles, between St. Thomas and Santa Cruz, USCGS Blake, sta 124, 17°47'30"N, 64°53'45"W); Manning and Holthuis, 1981: 25.

Homologenus rostratus. Rathbun, 1937: 70; Chace, 1940: 9; Powers, 1977: 22; Soto, 1991: 627; Guinot and Richer de Forges, 1995: 471; Lalana et al., 2004: 7; Cleva et al., 2007: 250; Serejo et al., 2007: 141; Felder et al., 2009b: 1072; Almeida et al., 2010: 360.

nec *Homologenus rostratus*. A. Milne-Edwards and Bouvier, 1900: 11 [= *Homologenus boucheti* Guinot and Richer de Forges, 1995].

Type Material.—USCGS Blake, sta 124, Virgin Island off St. Croix, 17°47'30"N, 64°53'45"W, 1061 m, 3 Jan 1879, coll. A. Agassiz: male holotype 10.1 × 7.0 mm (MCZ 6513).

Material Examined.—*Northwestern Atlantic*. Delaware, S of Lydonia Canyon, R/V Delaware II, cruise 11, sta 16, 39°52'34"N, 67°26'26"W, 1439-1460 m, 5 Dec 2000: 1 ovig. female 12.7 mm × 10.4 mm (USNM 1196483); Florida, E of Melbourne, R/V Columbus Iselin, sta CI-8007-064, 28°56'N, 77°17'W, 1086 m, 21 Sep 1980: 3 males 10.0 × 5.5 mm to 9.8 × 6.6 mm, 2 females 12.8 × 9.2 mm, 14.9 × 9.7 mm, 1 ovig. female 15.3 × 10.2 mm (USNM 1196485); Florida, Palm Beach, R/V Columbus Iselin, sta CI-8007-063, 28°06'N, 77°08'W, 1093 m, 21 Sep 1980: 1 male 11.5 × 6.6 mm, 3 ovig. females 14.1 × 9.5 mm (photographed) to 13.7 × 10.4 mm (USNM 1196484); Straits of Florida, R/V Gerda, sta 403, 27°48'30"N, 78°45'00"W, 824 m, 20 Sep 1964: 1 male and 1 ovig. female (USNM 136825); Straits of Florida, R/V Gerda, sta 296, 25°39'00"N, 79°23'00"W, 715 m, 5 Apr 1964: 1 female 15.6 × 10.0 mm (USNM 136824); Straits of Florida, R/V Gerda, sta 148, 25°05'30"N, 79°29'30"W, 805 m, 23 Jun 1963: 1 female (USNM 136823); Florida, Straits of Florida, S of Key West, R/V Gerda sta 448, 23°54'N, 88°21'W, 1134-1183 m, 1 Dec 1964: 1 damaged male (USNM 136826). Cuba, off Bahia de Cardenas, R/V Atlantis, Harvard-Havana Expedition, sta 2995, 23°24'N, 81°00'30"W, 676-1106 m, 16 Mar 1938: 1 ovig. female, F. A. Chace det. (USNM81932). *Gulf of Mexico*. Mexico, Tamaulipas, E of La Pesca, R/V Oregon, sta 4811, 24°01'N, 96°33'W, 1829 m, 11 Apr 1964: 1 ovig. female 15.7 × 11.9 mm (USNM 1196482). *North-eastern South America*. Venezuela, Aves Islands, A. Milne-Edwards det.: 1 male (USNM 7802). Brazil, Rio Grande do Norte, 04°33.9768'S, 36°43.8026'W, 987 m, 15 May 2011: 1 ovig. female (MZUSP 25788).

Comparative Material.—Paratypes of *Homologenus bouche-ti* Guinot and Richer de Forges, 1995: *Northeastern Atlantic*: Spain, Gulf of Cadiz, BALGIM Expedition, R/V Cryos, sta CP 99, 34°28'N, 07°43'W, 1848–1892 m, 9 Jun 1984: 1 male, 1 female (USNM 268914).

Size Range.—Males, 9.8 × 6.6 mm to 11.5 × 6.6 mm; females, 15.6 × 10.0 mm to 9.2 × 12.8 mm; ovig. females, 12.7 × 10.4 mm to 15.7 × 11.9 mm.

Distribution.—Eastern United States (Delaware to Florida), Straits of Florida, Gulf of Mexico, Cuba, Venezuela, and Brazil (Rio Grande do Norte, Bahia); depth: 600 to 1829 m.

Remarks.—*Homologenus rostratus*, historically regarded as an ampho-Atlantic species, was separated into two species by Guinot and Richer de Forges (1995) who restricted *H. rostratus* to the western Atlantic, and named its eastern Atlantic counterpart as *H. bouche-ti* Guinot and Richer de Forges, 1995. The availability of material from the southern end of the distribution (northeastern Brazil) of *H. rostratus* prompted us to compare it with northern specimens and also reassess the morphological criteria used to separate *H. rostratus* from *H. bouche-ti*. We found that the morphological characters used by Guinot and Richer de Forges' (1995) to diagnose these two species, based on differences in thickness of cheliped propodus, and evenness and strength of its margins and spines, and cheliped coxa protrusion, and strength of its terminal spines, are actually variable among specimens and thus not diagnostically useful. The most reliable character to distinguish between *H. rostratus* and *H. bouche-ti* is the relative length of the P5 meri. The distal end of P5 meri overreach (in males) or reach (in females) the cervical groove in *H. rostratus*, whereas the P5 meri of males and females do not reach to the cervical groove in *H. bouche-ti*. Additionally, in *H. rostratus* the dorsal margin of the cheliped propodus is as long as the fixed finger, whereas in *H. bouche-ti* the cheliped propodus is distinctly shorter than the fixed finger. Otherwise the movable and fixed fingers are similar between the two species.

Lamoha noar (Williams, 1974)

Fig. 6E, F

Hypsophrys noar Williams, 1974: 485, figs. 1–7, 10–12 (type locality: Straits of Florida, SW of Dry Tortugas, R/V Silver Bay, sta 1196, 24°11'00"N, 83°21'30"W); 1976: 889, pl. 1, pl. 2, figs. 8, 9, pl. 3; Takeda, 1980: 285; Guinot and Richer de Forges, 1995: 447, fig. 60a–c.

Lamoha noar. Felder et al., 2009b: 1072.

Type Material.—Holotype of *Hypsophrys noar* Williams, 1974, Straits of Florida, SW of Dry Tortugas, R/V Silver Bay, sta 1196, 24°11'00"N, 83°21'30"W, 732 m, 8 Jun 1959: male 41 × 36 mm (USNM 150816).

Additional Material.—*Caribbean Sea. U.S. Virgin Islands*: St. Croix Island, N of Salt River Canyon, sta #011, [no coordinates], 512 m, 31 Aug 1982, coll. W. Tobias: 1 male 59 × 51 mm and 2 ovig. females 55 × 49 mm, 48 × 45 mm (photographed) (USNM 205275).

Size Range.—Males, 41.0 × 36.0 mm to 59.0 × 51.0 mm; ovig. females, 48.0 × 45.0 mm to 55.0 × 49.0 mm.

Distribution.—Eastern United States (Straits of Florida) and Caribbean Sea (St. Croix Island and Guadeloupe); depth: 512 to 732 m.

Remarks.—Williams (1974) described *Hypsophrys noar*, the single representative of the genus in the Atlantic. The genus *Hypsophrys* Wood-Mason, in Wood-Mason and Alcock, 1891, was later found by Ng (1998) to be a junior homonym of *Hypsophrys* Agassiz, 1859, and the replacement name *Lamoha* Ng, 1998 was proposed for all brachyuran species previously under *Hypsophrys*. Williams compared his species with *L. longipes* (Alcock and Anderson, 1899) and *L. superciliosa* (Wood-Mason in Wood-Mason and Alcock, 1891), both from the Indo-Pacific and at the time only other known species of *Lamoha* (= *Hypsophrys*). According to Williams, *L. noar* could be distinguished from *L. superciliosa* by the bifid rostrum in the former versus a simple rostrum in the latter; and from *L. longipes* by the relative length of the P5 propodus, i.e., the P5 propodus as long as the P5 carpus in the *L. noar*, whereas the P5 propodus is much shorter than the P5 carpus in *L. longipes*. In addition, the unarmed Mxp3 also serves to differentiate *L. noar* from *L. longipes*, the Mxp3 being unarmed in the former, whereas the Mxp3 is armed with spines on the ischium and merus in the latter. Subsequently, six additional species were added to *Lamoha* (see Guinot and Richer de Forges, 1995; Ng, 1998), and discriminating between some became more difficult.

In a key to the world species of *Lamoha*, Guinot and Richer de Forges (1995: 443, as *Hypsophrys*) differentiated *L. noar* from *L. williamsi* and *L. personata*, primarily by the armature of the ventral surface of the P2–P4 meri, being unarmed in *L. noar*, and armed with spinules or tubercles in *L. williamsi* (Takeda, 1980) and *L. personata* (Guinot and Richer de Forges, 1981). Regrettably, the armature of the P2–P4 meri ventral surface was not described by Williams (1974: 487, fig. 1) for *L. noar*, and the ventral surface of the P2–P4 meri are shadowed in his photograph, thus rendering unrecognizable in his species the armature on that surface. Guinot and Richer de Forges (1995: 449) examined two males and three females of *L. noar* from Guadeloupe and characterized the ventral surface of the P2–P4 meri in that species as granulose (“seulement granuleux”). We examined three adult specimens of *L. noar* from St. Croix (USNM 205275) and found that the ventral surface of the P2–P3 meri is actually distinctly spinulated and granulated, although less densely so that in *L. williamsi*. In *L. noar*, the P4 merus is indeed sparsely granulated only. This prompted us to reassess Guinot and Richer de Forges's (1995) observations of the holotype of *L. noar*, and we found that the ventral surface of P2–P4 match those in the specimens from St. Croix, i.e., the ventral surface of the P2–P3 meri are distinctly spinulated and granulated (Figs. 6E, F), whereas the P4 merus is only sparsely granulated. Therefore, only the armature of the P4 merus is reliable in separating *L. noar* from *L. williamsi* and *L. personata*, and the armature of the P2–P3 meri is not a reliable character.

The three specimens from St. Croix (USNM 205275) are much larger than the holotype of *L. noar*, with which they agree well in the shape and ornamentation of the carapace, chelipeds, pereopods and gonopods. In males and females of *L. noar*, the chelipeds are homochelous and homodonts,

but the P1 propodus is much stronger in males than in females, and the dark spot at the base of the lateral and mesial surfaces of the fixed fingers are also distinctly larger in male than in females. In male and females the dark spot at the lateral and mesial bases of the fixed fingers and the dark coloration of the fixed fingers are separated from each other (Figs. 6E, F). Both ovigerous females carry numerous, minute eggs (~0.4 mm maximum width).

Lamoha williamsi (Takeda, 1980)

Fig. 6D

Hypsophrys williamsi Takeda, 1980: 282, figs. 2, 3 (type locality: Komahashi Seamount, Kyushu-Palaos Ridge, 28°04'N, 134°20'E).

Type Material.—Paratype of *Hypsophrys williamsi* Takeda, 1980: North Pacific Ocean, Northern Mariana Islands, Saipan Island, W of Saipan Harbor, Sango Expedition, R/V Townsend Cromwell, sta TC78-02, 15°12'06"N, 145°37'36"E, 27-31 m, 23 Jun 1978, coll. R. K. Kropp: 1 male 41 × 38 mm (photographed) (USNM 222531).

Additional Material.—*Northwestern Pacific Ocean. Northern Mariana Islands*: Farallon de Medinilla, R/V Townsend Cromwell, cruise TC-82-03, sta 110, 16°10'N, 146°05'E, 677 m, 21 Jun 1982: 2 male, 1 female, 1 ovig. female (USNM 1150824); Farallón de Medinilla, R/V Townsend Cromwell, cruise TC-84-04, sta 71, [no coordinates], 649 m, 23 Apr 1984: 1 male, 2 females (USNM 1150823); Rota Bank, R/V Townsend Cromwell, cruise TC-84-04, [no coordinates or depth], 25 Apr 1984: 1 male (USNM 1150827); A Bank, R/V Townsend Cromwell, cruise TC-84-04, sta 14, 14°15'N, 142°51'E, 1 May 1984: 2 male, 1 female, 1 ovig. female (USNM 1150822).

Distribution.—Northwestern Pacific, so far known only from the Komahashi Seamount, on the Kyushu-Palaos Ridge, and off Saipan, northern Mariana Islands; depth: 520 to 677 m.

Remarks.—*Lamoha williamsi* is known from four male type specimens, the holotype from the Kyushu-Palau Ridge and three paratypes from Saipan (Mariana Islands), one of which is housed at the Smithsonian Institution (USNM 222531). Takeda (1980) designated the paratypes in an addendum published along with the original description of the holotype (Takeda, 1980, Addendum: 287). The left cheliped is missing in the holotype and, as stated by Guinot and Richer de Forges (1995: 451, fig. 61d), the right cheliped is atrophied compared to that of other species of *Lamoha*, and incompletely regenerated. Unaware of Takeda's (1980) description of *L. williamsi*, Guinot and Richer de Forges (1981) described a new species from Vanuatu as *Lamoha personata*. Subsequently, Guinot and Richer de Forges (1995) examined the holotype of *L. williamsi* and compared it with a number of specimens of *L. personata*. According to Guinot and Richer de Forges (1995: 451, fig. 61d), in *L. williamsi* the right cheliped is unarmed or nearly so, the cutting edges of the fingers are toothless proximally, and the spot on the base of the fixed finger and the dark portion of the fixed finger are not separated from each other. In contrast, still according to Guinot and Richer

de Forges, *L. personata* has stronger, densely spinulated and granulated chelipeds and the spot at the base of the fixed finger is separated from the dark portion of the fixed finger. The cheliped of the holotype of *L. williamsi* does appear different from the chelipeds in specimens of *L. personata*, although due to the atrophied right cheliped of the holotype of *L. williamsi*, it is unclear whether these differences are meaningful. In a key to the species of *Lamoha* (as *Hypsophrys*), Guinot and Richer de Forges (1995: 443, 453) provisionally proposed separation of *L. williamsi* and *L. personata* based on differences in cheliped characteristics alone, but warning that additional material is needed to better define *L. williamsi* and assure the validity of *L. personata*. From our observations, the male paratype of *L. williamsi* as well the six males and six females examined (see "Additional Material"), are similar to the male of *L. personata* (cf. Guinot and Richer de Forges, 1995: fig. 61a-b) in having densely spinulated and granulated strong chelipeds (Fig. 6D), and at the base of the fixed finger, a slit-shaped spot that is not separated from the dark portion of the fixed finger. Thus, both species cannot clearly be distinguished by differences in their chelipeds alone.

Additionally, it has been suggested that *L. williamsi* has the segments of P2-P4 longer, slender and less armed ("moins armés") than those of *L. personata* (Guinot and Richer de Forges, 1995: 453). Nevertheless, in the male paratype of *L. williamsi* the length of the dactylus of P3, for example, is 2.63 as long as that of the P3 merus, and 1.81 as long as that of the P3 propodus, whereas in *L. personata* the proportions of the segments are similar, 2.72 and 1.81, respectively (measurements taken from Guinot and Richer de Forges, 1995: fig. 59a). In summary, although our observations suggest that *L. williamsi* and *L. personata* could be synonymous, we refrain from any action until sufficient material becomes available for a more complete character evaluation.

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