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BIOLOGICAL RESULTS OF THE UNIVERSITY OF MIAMI DEEP-SEA EXPEDITIONS. 94.

A REEXAMINATION OF *DARDANUS VENOSUS* (H. MILNE EDWARDS) AND *D. IMPERATOR* (MIERS), WITH A DESCRIPTION OF A NEW SPECIES OF *DARDANUS* FROM THE WESTERN ATLANTIC (CRUSTACEA, DECAPODA, DIOGENIDAE)[1]

THOMAS A. BIFFAR[2] AND ANTHONY J. PROVENZANO, JR.
University of Miami, Rosenstiel School of Marine and Atmospheric Science

ABSTRACT

A new species of the hermit crab genus *Dardanus* is described. It is very closely related to *Dardanus venosus*, with which it has been confused in previous publications. Evidence for the separation of the two species is based on larval as well as adult morphology. Previous citations of "*D. venosus*" have been researched to determine the species to which the authors referred, and numerous new records for both species are presented. Other species of *Dardanus* described from the Atlantic Ocean are considered, especially *D. imperator*, which is partially redescribed and illustrated.

INTRODUCTION

Dardanus venosus was originally described by H. Milne Edwards (1848). The species has since been collected and identified from numerous sites in the western Atlantic, and the number of authors describing, or at least citing, this species is quite large. One of us (AJP) suspected that more than one species was included under the name *D. venosus* after observing live specimens being maintained in the laboratory. Marked differences in eye coloration led to further investigation and discovery of additional characters that could be used to separate the specimens into two groups, recognized now as two distinct species. Supporting evidence was obtained from rearing of larvae hatched from known females and from planktonic material kept alive through metamorphosis.

Based on information provided by one of us (AJP), Forest and St. Laurent (1967:165) have already noted the presence, in the western Atlantic, of the new species of *Dardanus*. Dr. Forest examined the type-series of *D. venosus* and provided the information which allowed us to affix that name to one of the two forms.

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[1] Contribution No. 1549 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science. This paper is one of a series resulting from the National Geographic Society–University of Miami Deep-Sea Biology Program. The work was supported by grant GB-7075X from the National Science Foundation, by Public Health Service Grant GM-11244-05 from the Institute of General Medical Services, and the National Geographic Society–University of Miami Deep-Sea Biology Program.

[2] Present address: Department of Biology, Old Dominion University, Norfolk, Virginia 23508.

In the present study we distinguish these species using morphological characters of adults and larvae, and we have attempted to determine the identity of material to which previous authors have attributed the name *D. venosus*. Only characters that have been found useful in making the separation are described, since the two species are very similar and separable only by certain of their morphological features. Characters left undescribed generally fall within the limits noted in previous descriptions of "*Dardanus venosus*" (see Verrill, 1908a; Provenzano, 1959).

Because *Dardanus imperator* (Miers, 1881) is closely related to both *D. venosus* and the new species, the type of *D. imperator* has been re-examined and partially redescribed.

Measurements given in the Material Examined sections refer to dorsal shield (anterior carapace) length. Specimens with UMML catalog numbers are in the collection of the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

Acknowledgments

We are indebted to Dr. Jacques Forest, Muséum National d'Histoire Naturelle (MNHN), Paris, and to Dr. Lemos de Castro, Museu Nacional, Brasil, for examining material at our request. Material was also examined, or supplied, by Dr. C. G. Bookhout, Duke University Marine Laboratory (DML); Mr. C. E. Cutress, University of Puerto Rico, Department of Marine Sciences (UPR-DMS); Dr. W. K. Emerson, American Museum of Natural History (AMNH); Dr. W. Hartman, Peabody Museum of Natural History, Yale University (YPM); Dr. H. Levi, Museum of Comparative Zoology, Harvard University (MCZ); Dr. R. B. Manning, National Museum of Natural History, Smithsonian Institution (USNM); Dr. A. L. Rice, British Museum of Natural History (BMNH); and Dr. A. B. Williams, University of North Carolina Institute of Marine Sciences (UNC-IFR). We wish to thank Dr. L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden (LM), for his efforts to establish the validity of several species of *Dardanus*. The glaucothoes of *Dardanus venosus* and the new species were reared and maintained in the laboratory by the late Mrs. C. Edith Marks. The illustrations were prepared by Mrs. Kathy Wilson.

Dardanus venosus (H. Milne Edwards, 1848)

Figs. 1,B; 2,B; 3,B; 4,B; 5,A; 6,A

Pagurus venosus H. Milne Edwards, 1848: 61.

Petrochirus insignis, Rathbun, 1900: 144 (not *Dardanus insignis* [Saussure, 1858]).

Petrocheirus insignis, Verrill, 1900: 578 (not *Dardanus insignis* [Saussure, 1858]).

Pagurias insignis, Benedict, 1901: 141 (part, not *Dardanus insignis* [Saussure, 1858]).

Pagurus arrosor, Moreira, 1901: 24 (not *Dardanus arrosor* [Herbst, 1796]).
Pagurus arrosor var. *divergens* Moreira, 1906: 13, pl. 4, fig. 1.
Dardanus venosus, Verrill, 1908a: 441, figs. 58 & 59, pl. 26, figs. 4 & 5 (part); 1908b: 290.—Schmitt, 1924: 95; 1935: 201, fig. 62 (part); 1936: 376; 1939: 28.—Provenzano, 1959: 374, fig. 6 (part); 1960: 119; 1961: 153; 1963a: 11, figs. 1-5.—Forest & St. Laurent, 1967: 94.—Ross & Sutton, 1968: 380.—Shoup, 1968: cover photograph.—Cutress & Ross, 1969: 225, pl. 1, figs. a & b.—Cutress, Ross, & Sutton, 1970: 371.
Pagurus insignis, Bouvier, 1918: 6 (not *Dardanus insignis* [Saussure, 1858]).

Material Examined.—BERMUDA: 1 ♀, 7.5 mm; Ferry Reach; ANA; 4 m; F. G. W. Knowles; USNM 90385.—1 ♀, 6.2 mm; Ferry Reach; ANB; 4 m; F. G. W. Knowles; November 1949; USNM 90386.—1 ♀, 7.1 mm; A. E. Verrill Expedition; F. V. Hamlin; "fig'd & described"; 1898; YPM 3236. BAHAMAS: 1 ♂, 6.7 mm; Bimini; L. M. Passano; 1950; YPM 3641. —1 ♂, 20.6 mm; Bimini; Coll. by Lerner Lab for Bill Thompson; YPM. —1 ♂, 20.6 mm; 1 ♀, 20.2 mm; Bimini, NW corner South Bimini, in fish trap; in *Tonna*; YPM.—1 ♂, 19.5 mm; Bimini; Sta. 11; 5 September 1947; AMNH 10157.—1 ♂, 8.3 mm; off Ambergris Cay; 4 m; Bahama Expedition Sta. 8; grassy bottom; 19 July 1904; MCZ 13100. FLORIDA: 1 ♀, 7.5 mm; Miami, Bear Cut; zoology class; 21 December 1934; UMML 32.139.—1 ♀, 14.0 mm; Miami, Virginia Key; marine biology class; 12 July 1958; UMML 32.2314.—1 ♂, 8.5 mm; Miami, Virginia Key, southeast shore; Clyde Roper; 4 April 1960; UMML 32.2535.—1 ♀ (ovig.), 14.5 mm; Long Reef, Dade County; Gene Shinn; 1958; YPM 4410.—1 ♂, 13.9 mm; 2½ mi SSW of Alligator Reef; 46 m; WAS II; 22 May 1960; UMML 32.2312.—1 ♀, 11.1 mm; Margot Shoal; 1.5 m; R. Work; 15 August 1967; UMML 32.4182.—1 ♂, 11.0 mm; Key Largo; 24 February 1968; UMML 32.4181.—1 ♂, 9.1 mm; south end of Bahia Honda Bridge; in young *Strombus gigas* shell; A. J. Provenzano, Jr.; 9 March 1958; UMML 32.322. —1 ♀, 14.5 mm; Straits of Florida; SILVER BAY Sta. 2399; 24°37'N, 81°0'W; 91 m; 27 October 1960; UMML 32.2301.—1 ♀, 12 mm; Tortugas; Sta. 15; C. R. Shoemaker; USNM 102691.—1 specimen; Tortugas; W. L. Schmitt; 11 August 1930; USNM 102693.—1 ♀, 11.6 mm; Tortugas, Fort Jefferson dock; from rocks; Dexter Collection; 15 June 1925; USNM 102694. CUBA: 1 ♂, 16.9 mm; Bahia Honda; No. 153; Mario S. Roig; 1924; USNM 58664.—1 ♂, 4.8 mm; Bahia Honda; Tomas Barrera Expedition; coll. 471; Henderson & Bartsch; 7 June 1914; USNM 48750.—1 ♀, 8.3 mm; Punta Colorado; Tomas Barrera Expedition; Sta. 10; coll. 252; 2-3 fms; USNM 48651. JAMAICA: 1 ♂, 7.8 mm; Drunken Man's Cay, off Kingston; 450 H. G.; Humes & Gooding; 3 September 1959; USNM 104257. HAITI: 1 ♂, 12.0 mm; Muentos Island, off north coast; Poole & Perrigo; February 1929; USNM 102690.—1 ♂, 16.2 mm; Fort Liberte; Poole & Perrigo; USNM 102688. PUERTO RICO: 1 ♂, 15.0 mm; Arroyo; FISH HAWK; 4 February 1889; USNM 42553.—1 ♀,

11 m; entrance to Guayanilla Harbor; AMNH 2245.—18 ♂, 10.0-19.7 mm; 2 ♀, 10.5-22.2 mm; 1 ♀ (ovig.), 15.3 mm; off La Parguera; from fish traps; 18-24 m; C. E. Cutress; UPR-DMS. VIRGIN ISLANDS: 1 ♀ (ovig.), 17.5 mm; St. John, 2 mi south of Lameshur Bay; in fish trap; 43 m; J. Chess; 23 March 1960; UMML 32.2307.—1 ♂, 9.6 mm; St. John, Concordia Bay; Voss; 23 January 1959; UMML 32.2308.—1 ♂, 7.0 mm; 1 ♀ (ovig.), 10.0 mm; St. John, point between Salt Pond Bay and Petit Head Bay; coral rubble and sand; 9 m; J. Randall; 29 May 1960; UMML 32.2309.—2 ♂, 14.5-15.8 mm; St. John, Greater Lameshur Bay; Rumph & Randall; 30 January 1959; UMML 32.2310.—2 ♀, 10.2-15.5 mm; St. John, Salt Pond Bay; 9 m; J. Randall; 21 April 1960; UMML 32.2313.—1 ♂, 12.5 mm; Cabritte Horn Point, in trap; Chess & Matthias; 22 March 1960; UMML 32.2315. SOMBRERO: 1 ♀, 21.9 mm; B. Brook; September 1859; MCZ 12673. GUADELOUPE: 1 ♂, 18.6 mm; (LECTOTYPE); Beauperthuis; MNHN. DOMINICA: 3 ♂, 15.2-16.1 mm; in large *Murex*; A. H. Verrill; 1906; YPM. BARBADOS: 1 ♂, 13.5 mm; U. of Iowa; 1918; USNM 68963. OLD PROVIDENCE ISLAND: 2 ♂, 4.8-5.7 mm; 2 juveniles; F. D. R. Presidential Cruise; No. 3; shore, reef & tide pool collection; W. L. Schmitt; 6 August 1938; USNM 78220. PANAMA: 1 ♂, 10.0 mm; PILLSBURY Sta. 438; 8°54.3'N, 80°54.8'W; 20-22 m; 20 July 1966; UMML 32.4178. BONAIRE: 1 ♀ (ovig.), 12.6 mm; Lac (entrance); in young *Strombus*; No. 75; 4-7 m; P. Hummelinck (don.); 5 October 1930; USNM 67424. VENEZUELA: 2 ♂, 19.0-20.1 mm; Cumana; Capt. Couthouy; 1859; MCZ 543. BRAZIL: 1 ♂, 20.0 mm; OREGON Sta. 4229; 1°50'S, 43°6'W; 66 m; 10 March 1963; USNM 128784.—2 ♀, 6.5-7.8 mm; OREGON Sta. 4231; 1°50' S, 42°43' W; 66 m; 10 March 1963; USNM 128785.—1 ♂, 12.2 mm; OREGON Sta. 4238; 2°10'S, 42°24'W; 48 m; 11 March 1963; USNM 128786.—1 ♂, 5.2 mm; OREGON Sta. 4252; 2°10'S, 39°52'W; 137 m; 12 March 1963; UMML 32.4179.—2 ♂, 7.0-18.8 mm; OREGON Sta. 4251; 2°20'S, 40°24'W; 40 m; 12 March 1963; USNM 128787.—1 ♀ (ovig.), 16.1 mm; OREGON Sta. 4246; 2°37'S, 41°3'W; 29 m; 12 March 1963; UMML 32.4180.—1 ♂, 4.6 mm; Rio Goyanna stone reef; Branner-Agassiz Expedition; A. W. Greeley; 8 June 1899; USNM 25767.—1 ♀, 8.4 mm; Alagoas, Maceio coral reef; Branner-Agassiz Expedition; A. W. Greeley; 22 July 1899; USNM 25768.

Description.—Ventral margin of dactylus of third pereiopod on left side a rounded ridge with series of rounded tubercles proximally, series of tufts of setae immediately adjacent on both sides. Lateral surface of segment with vertical tuberculate ridges interrupted dorsomedially by shallow groove, continuation of ridges below groove raised forming rounded longitudinal ridge with 2-4 tubercles at location of each vertical ridge along apex, ridges below longitudinal ridge with 1-3 strong tubercles, largest

FIGURE 1. Eyestalks of: A, *Dardanus fucosus*, holotype; B, *D. venosus*, lectotype; C, *D. imperator*, holotype. (Scales represent 5.0 mm.)

ventrally and proximally. Tuberculation well developed, base of each tubercle arising on surface of ridge rather than on edge.

Propodus of third pereiopod similarly sculptured. Lateral surface with shallower groove medially, more tubercles on vertical ridges particularly in ventral half, ventral ridges usually slightly concave with stronger ventral tubercles.

Carpus of large cheliped with continuous fringe of setae along distal margin on lateral surface, overlapping articulation with propodus.

Lateral surface of palm with numerous scales, each with one or more tubercles (75 per cent of all specimens have from one to a maximum of three per scale, the remaining specimens have scales with up to six tubercles). Tubercles well developed, set back from anterior edge of scales, directed laterally and distally.

Width of cornea slightly greater than width of eyestalks, length of eyestalks usually more than 2.0 times greatest width of cornea.

Color.—Cornea, in life, greenish blue with central black spot and narrow radiating bands forming a star or asterisk when viewed from front.

Palm of large cheliped basically red, ocassionally deep crimson, tubercles red or pink, occasionally purple.

Second and third pereiopods with broad bands of orange-red on merus, carpus, and propodus, width of band on carpus and propodus equalling about 0.5 length of segment.

Lectotype.—Muséum National d'Histoire Naturelle, Paris.

Type-Locality.—Guadeloupe.

Range.—Bermuda; South Florida to Maceio, Brazil.

Dardanus fucosus, n. sp.

Figs. 1,A; 2,A; 3,A; 4,A; 5,B; 6,B

Pagurias insignis, Benedict, 1901: 141 (part, not *Dardanus insignis* [Saussure, 1858]).

Dardanus venosus, Verrill, 1908a: 441, figs. 58 & 59, pl. 26, figs. 4 & 5 (part).—Schmitt, 1935: 201, fig. 62 (part).—Provenzano, 1959: 374, fig. 6 (part).—Holthuis, 1959: 153.—Cerame-Vivas, Williams & Gray, 1963: 157.—Williams, 1965: 123, fig. 99 (not *Dardanus venosus* [H. Milne Edwards, 1848]).

Petrochirus diogenes, Provenzano, 1963b: 242, figs. 1-8 (not *Petrochirus diogenes* [L.]).

Material Examined.—HOLOTYPE: 1 ♂, 18.8 mm; Brazil; OREGON Sta. 4202; 5°29′N, 51°37′W; 64 m; 23 February 1963; USNM 141460. PARATYPES: 1 ♀ (ovig.), 11.7 mm; Florida, off St. Augustine; COMBAT Sta. 353; 30°24′N, 80°20′W; 44 m; 3 June 1957; USNM 103413.—1 ♂, 13.1 mm; 1 ♀, 9.5 mm; Florida, Miami, Cape Florida flats; H. Doochin; 13 July

1948; UMML 32.449.—1 ♂, 11.0 mm; Florida, Tortugas, north end of Loggerhead Key, fish trap in eel grass, Fort Jefferson moat; W. L. Schmitt; 11 August 1924; USNM 102687.—1 ♂, 7.8 mm; Panama; PILLSBURY Sta. 434; 9°14.6'N, 80°21.8'W; 48-49 m; 20 July 1966; LM.—2 ♂, 7.3-9.0 mm; Venezuela; PILLSBURY Sta. 763; 11°25.1'N, 70°52.1'W; 18 m; 27 July 1968; UMML 32.4158.—1 ♂, 9.1 mm; 1 ♀, 6.6 mm; Guyana; OREGON Sta. 2236; 8°9'N, 58°23'W; 42 m; 29 August 1958; USNM 102406.—1 ♂, 12.9 mm; Brazil; OREGON Sta. 4201; 5°24'N, 51°34'W; 64 m; 23 February 1963; USNM 128780. ADDITIONAL MATERIAL.—NORTH CAROLINA: 1 ♀, 4.2 mm; SILVER BAY Sta. 1634; 35°02'N, 75°26'W; 55-59 m; 23 February 1960; USNM 128769.—1 ♂, 3.6 mm; south of Cape Hatteras; 34°58'N, 75°31'W; 51 m; M. Cerame-Vivas; 19 December 1962; DML 633.—1 ♂, 3.1 mm; 2 ♀, 3.7-3.9 mm; SILVER BAY Sta. 2926; 34°54'N, 75°32'W; 51 m; 13 March 1961; UMML 32.4139.—1 ♂, 6.5 mm; EASTWARD Sta. 3645; 34°38.8'N, 76°19.6'W; 30 m; E-6-66; Gray; 13 January 1966; DML 244.—1 ♀, 6.8 mm; off Cape Lookout, 1-5 mi ESE Knuckle Buoy; E. Bayer; 7 January 1963; UNC-IFR 1599.—4 ♂, 5.7-9.7 mm; 1 ♀, 6.6 mm; ESE Cape Lookout; 31-37 m; E. Bayer from "Josephine"; 23-24 March 1964; UNC-IFR 1963.—2 ♀, 6.9-8.7 mm; ESE Cape Lookout; 31-37 m; trawl fishery; 23-25 March 1964; UNC-IFR 2133.—1 ♀, 8.9 mm; ESE Lookout Point; E. Bayer & C. Noe; 18 January 1963; UNC-IFR 1615.—2 ♂, 4.2-8.3 mm; 4 ♀, 4.2-5.1 mm; SE of Cape Lookout; 46 m; E. Bayer from "Edith M"; 25 February 1964; UNC-IFR 1864.—11 ♂, 6.0-9.1 mm; 7 ♀, 7.3-10.7 mm; SE of Cape Lookout; 46 m; E. Bayer from "Edith M"; 25 February 1964; UNC-IFR 1860.—1 ♀, 5.15 mm; off Beaufort Inlet, Carteret County; M. Cerame-Vivas; autumn 1961; UNC-IFR 1899.—1 ♀ (ovig.), 10.2 mm; SE of Cape Lookout; 34°15'N, 76°15'W; 37 m; M. Cerame-Vivas; 14 September 1962; UNC-IFR 1808.—1 ♂, 8.1 mm; SILVER BAY Sta. 1700; 34°9.5'N, 76°31'W; 31 m; 29 February 1960; USNM 128770.—1 ♂, 8.5 mm; EASTWARD Sta. 1410; 34°5.5'N, 76°36'W; 30 m; E-28-65; Gray; 20 May 1965; DML 242.—1 ♀, 5.6 mm; EASTWARD Sta. 1410; 33°55.5'N, 76°28.4'W; 63 m; E-28-65; Gray; 21 May 1965; DML 243. SOUTH CAROLINA: 1 specimen; PELICAN Sta. 182-23; 32°51.5'N, 78°59'W; 27 m; 12 February 1940; USNM 102800. GEORGIA: 1 ♀, 10.5 mm; PELICAN Sta. 179-4; 31°28.5'N, 79°46'W; 46 m; 1 February 1940; USNM 102802. FLORIDA: 1 ♂, 11.3 mm; COMBAT Sta. 347; 29°31'N, 80°31'W; 33 m; 2 June 1957; USNM 128768.—1 ♂, 10.2 mm; SILVER BAY Sta. 1911; 29°11.5'N, 80°36'W; 22-27 m; 18 April 1960; USNM 128771.—1 ♂, 9.5 mm; 1 ♀, 3.7 mm; SILVER BAY Sta. 3147; 28°47'N, 80°09'W; 55 m; 9 May 1961; UMML 32.4140.—1 ♀, 5.2 mm; 1 juvenile; SILVER BAY Sta. 3704; 28°30'N, 80°02'W; 68-73 m; 25 January 1962; USNM.—1 ♂, 15.2 mm; SILVER BAY Sta. 5096; 27°55'N, 80°07'W; 35-38 m; 26 September 1963; USNM 128773.—1 ♀,

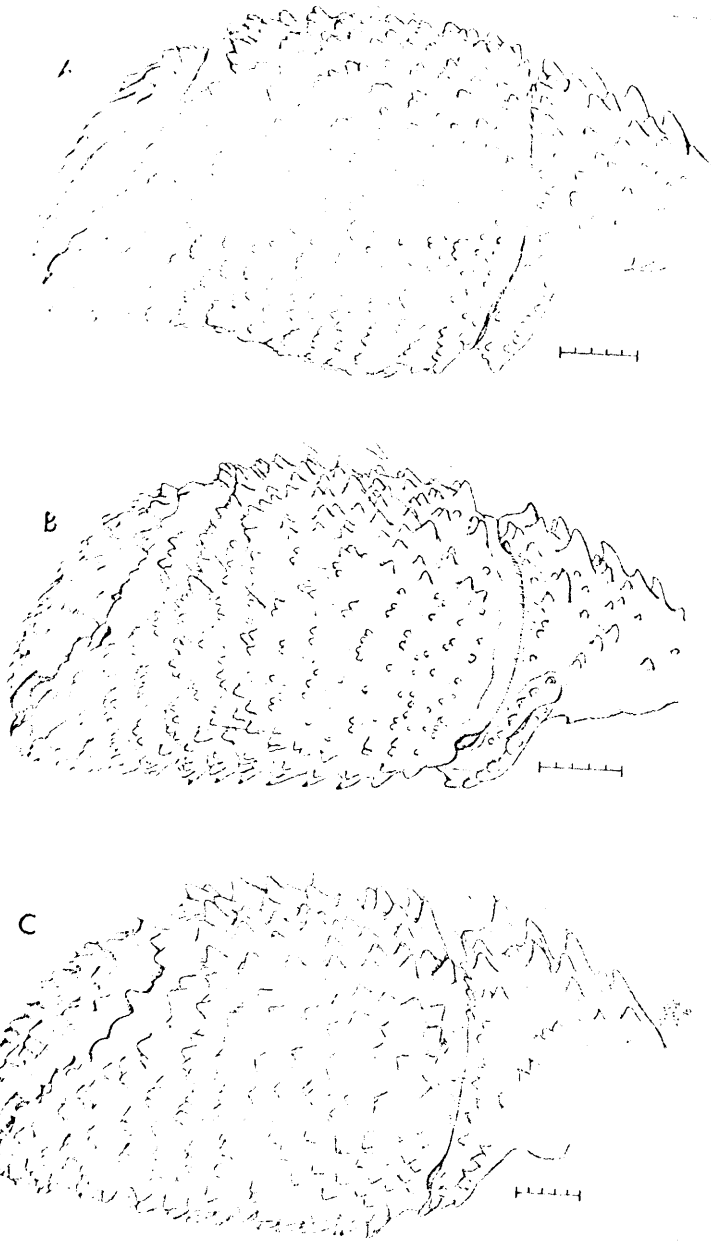

FIGURE 2. Lateral view of major chela of: A, *Dardanus fucosus*, holotype; B, *D. venosus*, lectotype; C, *D. imperator*, holotype. (Scales represent 5.0 mm.)

13 mm; Biscayne Bay; H. L. Clark; March-April 1937; MCZ 9696.—2 ♂, 5.2-5.7 mm; 2 ♀, 4.1-4.2 mm; Miami, Key Biscayne, Cape Florida; J. W. Miller; January 1925; USNM 102692.—1 ♀, 17.0 mm; Miami, Fowey Rocks; May 1947; UMML 32.266.—1 ♂, 7.0 mm; Dade County, Soldier Key; J. J. McEwan; 22 February 1948; UMML 32.458.—1 ♀, 9.7 mm; off Ragged Key; G. Cope; 3 May 1957; UMML 32.2303.—1 ♀, 11.6 mm; Ragged Key; A. J. Provenzano; 30 March 1957; UMML 32.2304.—1 ♂, 15.1 mm; Long Reef; G. Voss; 5 September 1953; UMML 32.938.—2 ♂, 13.4-15.7 mm; 1 ♀, 5.0 mm; Monroe County, 2 mi S of Alligator Reef Light; 40 m; H. A. Feddern & W. A. Stark; 18 November 1961; UMML 32.4141.—1 ♀, 4.5 mm; Conch Reef, ¼ mi. NW of red can buoy; 35 m; W. Stark; 5 September 1959; UMML 32.2302.—1 ♂, 2.7 mm; GERDA Sta. 755; 24°50′N, 80°38′W; 42-46 m; 15 September 1965; USNM 128762.—2 ♂, 8.1-12.1 mm; GERDA Sta. 756; 24°50′N, 80°38′W; 40-48 m; 15 September 1965; UMML 32.4142.—1 ♂, 3.0 mm; 1 ♀, 5.7 mm; GERDA Sta. 1037; 24°50′N, 80°37.5′W; 42 m; 26 February 1969; LM.—1 ♂, 13.7 mm; GERDA Sta. 594; 24°50′N, 80°37′W; 37 m; 14 April 1965; UMML 32.4143.—1 ♂, 2.8 mm; 1 ♀, 3.5 mm; GERDA Sta. 753; 24°49′N, 80°39′W; 37-48 m; 15 September 1965; USNM 128761.—3 ♀, 3.1-3.9 mm; GERDA Sta. 1033; 24°36.2′N, 81°6.5′W; 42 m; 26 February 1969; UMML 32.4144.—1 ♀, 3.9 mm; Key West, SE ship channel; 52 m; Bill Hess; 30 December 1953; UMML 32.2306.—1 ♂, 8.7 mm; Tortugas shrimp grounds; 24°45′50″N, 82°10′30″W; 18-33 m; R. B. Manning; 10-12 March 1958; USNM 101263.—1 ♀, 10.6 mm; Fort Jefferson; 25 June 1925; USNM 102689.—1 ♂, 3.3 mm; GERDA Sta. 565; 24°26′N, 82°58′W; 62-70 m; 12 April 1965; UMML 32.4145. BAHAMAS: 1 ♀, 5.5 mm; off Matthew Town, Greater Inagua Island; R. A. McLean & B. Shreve; 1 August 1931; MCZ 10350. MEXICO: 1 ♀, 5.7 mm; OREGON Sta. 3638; 21°10′N, 86°26′W; 33 m; 11 June 1962; UMML 32.2306. JAMAICA: 1 ♂, 9.7 mm; R. P. Bigelow; USNM 42497.—1 ♂, 6.2 mm; OREGON Sta. 5395; 17°52′N, 77°46.5′W; 20-22 m; 18 May 1965; USNM 128756. PUERTO RICO: 2 ♂, 8.5-13.4 mm; Arroyo; FISH HAWK; 4 February 1889; USNM 42553.—1 ♀, 10.9 mm; Cayo Caribeto, Cayo Parguera; 25 June 1915; AMNH 2171.—1 ♀ (ovig.), 4.0 mm; 25 June 1915; AMNH 2153.—1 ♂, 4.5 mm; OREGON Sta. 5455; 18°5.5′N, 67°21.5′W; 22 m; 3 June 1965; USNM 128782. SOMBRERO: 1 ♂, 3.0 mm; PILLSBURY Sta. 986 18°29.7′N, 63°17′W; 57 m; 22 July 1969; LM. DOMINICA: 1 ♀, 12.2 mm; in large *Murex*; A. H. Verrill; 1906; YPM. MARTINIQUE: 8 ♂, 2.2-9.8 mm; 8 ♀, 2.8-5.0 mm; PILLSBURY Sta. 913; 14°53.8′N, 61°4.9′W; 84-89 m; 10 July 1969; UMML 32.4147. GRENADINES: 1 ♂, 6.0 mm; 1 ♀, 2.5 mm; PILLSBURY Sta. 868; 13°1.2′N, 61°16.4′W; 93-101 m; 5 July 1969; LM. GRENADA: 1 ♂, 2.1 mm; PILLSBURY Sta. 852; 11°52.8′N, 61°53.3′W; 24 m; 3 July 1969; UMML 32.4148. TOBAGO: 1 ♂, 3.4 mm;

1 ♀, 4.0 mm; PILLSBURY Sta. 842; 11°10.6'N, 60°31.2'W; 124-134 m; 1 July 1969; UMML 32.4149. HONDURAS: 1 ♀, 6.4 mm; PILLSBURY Sta. 574; 16°16'N, 82°26.5'W; 37 m; 20 May 1967; UMML 32.4146. PANAMA: 2 ♂, 2.5-3.0 mm; 1 ♀, 4.0 mm; PILLSBURY Sta. 437; 9°0.1'N, 80°45.8'W; 55 m; 20 July 1966; UMML 32.4150.—2 ♂, 10.3-11.1 mm; 1 ♀, 5.6 mm; 4 ♀ (ovig.), 7.8-9.4 mm; entrance to Limón Bay; PILLSBURY Sta. 451; 12 m; 23 July 1966; USNM 128766.– 1 ♀, 3.0 mm; PILLSBURY Sta. 430; 9°31'N, 79°51'W; 60-64 m; 20 July 1966; LM.—1 ♀, 4.0 mm; PILLSBURY Sta. 330; 9°37.5'N, 78°54'W; 64-128 m; 8 July 1966; USNM 128757.—1 ♂, 4.2 mm; PILLSBURY Sta. 334; 9°33'N, 78°50'W; 51 m; 8 July 1966; UMML 32.4151.—1 ♂, 2.6 mm; PILLSBURY Sta. 423; 9°37.2'N, 78°44.3'W; 62 m; 19 July 1966; UMML 32.4152.—1 ♂, 3.0 mm; PILLSBURY Sta. 422; 9°33.8'N, 78°36.2'W; 70-73 m; 19 July 1966; UMML 32.4153. COLOMBIA: 1 ♂, 1.8 mm; 1 ♀, 3.2 mm; 1 ♀ (ovig.), 3.2 mm; PILLSBURY Sta. 411; 8°40.7'N, 77°21.8'W; 29-42 m; 18 July 1966; USNM 128764.—2 ♂, 2.3-4.3 mm; PILLSBURY Sta. 412; 8°38.9'N, 77°13.2'W; 55-60 m; 18 July 1966; USNM 128759.—1 ♂, 5.0 mm; PILLSBURY Sta. 392; 9°45.1'N, 76°9.1'W; 75-79 m; 16 July 1966; LM.—1 ♂, 4.5 mm; 1 ♀ (ovig.), 7.0 mm; PILLSBURY Sta. 371; 9°40'N, 76°1.5'W; 46-55 m; 13 July 1966; USNM 128758 & 128765.—3 ♂, 2.2-6.5 mm; 3 ♀, 3.3-5.1 mm; PILLSBURY Sta. 793; 10°40'N, 75°31'W; 26-29 m; 1 August 1968; LM.—2 ♂, 2.4-5.4 mm; 1 ♀, 3.2 mm; 1 ♀ (ovig.), 4.6 mm; PILLSBURY Sta. 787; 11°4'N, 74°30'W; 18 m; 31 July 1968; UMML 32.4155.—3 ♀, 5.6-6.9 mm; OREGON Sta. 4861; 11°03'N, 74°26'W; 18 m; 20 May 1964; USNM 128755.—3 ♂, 2.9-4.0 mm; 4 ♀, 2.7-4.6 mm; 3 intersex, 2.7-5.4 mm (parasitized); PILLSBURY Sta. 772; 12°20.2'N, 71°55.1'W; 11 m; 29 July 1968; UMML 32.4156.—6 ♂, 3.1-13.24 mm; 2 ♀, 3.6-4.0 mm; PILLSBURY Sta. 767; 12°16.1'N, 71°3.3'W; 24-26 m; 28 July 1968; UMML 32.4157. VENEZUELA: 1 ♂, 2.1 mm; PILLSBURY Sta. 761; 11°52'N, 70°22'W; 35 m; 27 July 1968; UMML 32.4159.—2 ♂, 2.2-2.6 mm; 2 ♀, 2.7-4.9 mm; 1 intersex, 3.6 mm (parasitized); PILLSBURY Sta. 758; 11°42.2'N, 69°40'W; 15-18 m; 27 July 1968; UMML 32.4160.—2 ♂, 2.0-2.5 mm; 3 ♀, 3.6-5.6 mm; PILLSBURY Sta. 750; 10°36.1'N, 68°12.2'W; 22-26 m; 25 July 1968; LM.—2 ♂, 2.2-4.0 mm; PILLSBURY Sta. 749; 10°37'N, 67°57.9'W; 59 m; 25 July 1968; UMML 32.4161.—2 ♂, 3.0-3.6 mm; 1 ♀ (ovig.), 5.2 mm; PILLSBURY Sta. 746; 11°54.5'N, 66°54.5'W; 23-27 m; 24 July 1968; LM.—1 ♂, 4.2 mm; Los Roques Islands; N. LaSalle & F. H. Weibegahn; USNM 95708.—2 ♂, 2.5-4.7 mm; 2 ♀, 2.4-4.9 mm; PILLSBURY Sta. 737; 10°44'N, 66°7'W; 60-73 m; 22 July 1968; USNM 128760.—1 ♂, 2.2 mm; PILLSBURY Sta. 734; 11°1.8'N, 65°34.2'W; 60-68 m; 22 July 1968; UMML 32.4162.—1 ♀, 7.2 mm; OREGON Sta. 4472; 10°13'N, 65°23'W; 33 m; 19 October 1963; USNM 128754.—1 ♂, 2.0 mm; PILLSBURY Sta. 727;

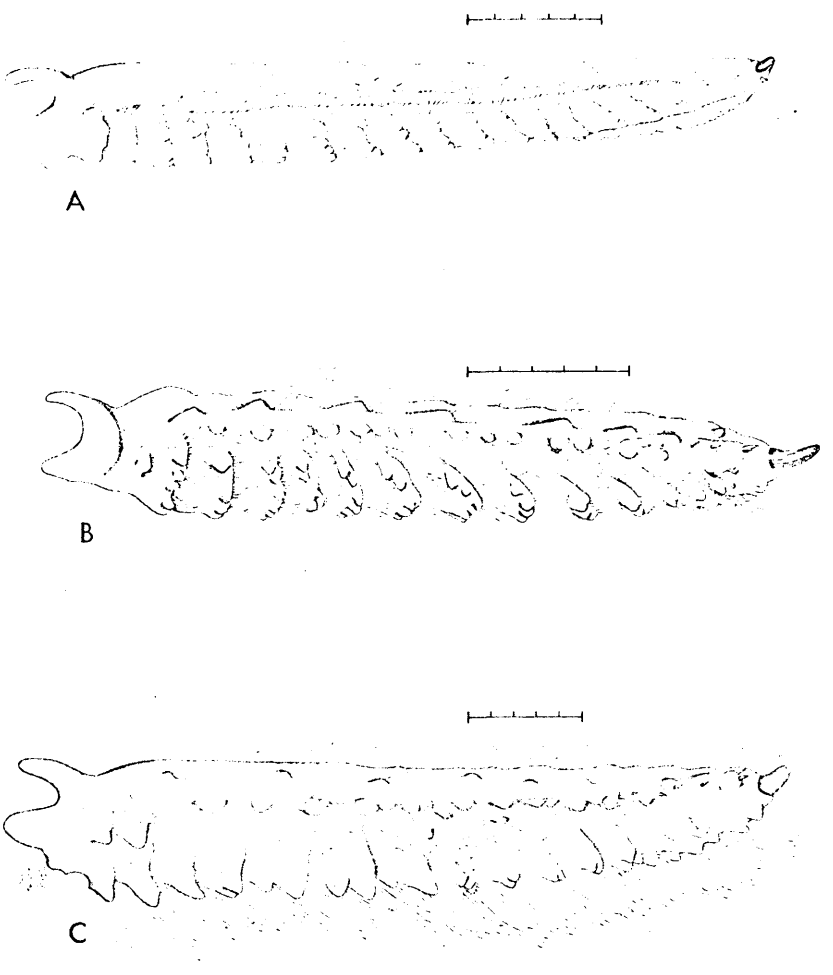

FIGURE 3. Ventral view of dactyl of third pereiopod of: A, *Dardanus fucosus*, holotype; B, *D. venosus*, lectotype; C, *D. imperator*, holotype. (Scales represent 5.0 mm.)

10°20'N, 65°2'W; 64 m; 21 July 1968; UMML 32.4163.—5 ♂, 2.2-15.2 mm; 9 ♀, 2.5-6.2 mm; PILLSBURY Sta. 721; 11°6.5'N, 64°22.5'W; 26-27 m; 21 July 1968; UMML 32.4164.—1 ♂, 3.0 mm; PILLSBURY Sta. 718; 11°22.5'N, 64°8.6'W; 64 m; 20 July 1968; LM.—1 ♂, 4.1 mm; 1 ♀ (ovig.), 6.2 mm; Margarita Island; Arrastre 5; 27 m; 6 October 1963; UMML 32.4165.—1 ♀, 4.6 mm; Margarita Island; Arrastre 7; 37 m; 6

October 1963; USNM 128763.—9 ♂, 1.6-9.1 mm; 7 ♀, 2.2-5.9 mm; PILLSBURY Sta. 712; 11°8'N, 63°18'W; 24-27 m; 19 July 1968; UMML 32.4166.—1 ♀ (ovig.), 7.4 mm; PILLSBURY Sta. 708; 11°24.7'N, 62°40.5'W; 70-73 m; 19 July 1968; LM. GUYANA: 5 ♂, 3.5-13.8 mm; 3 ♀, 2.5-4.4 mm; 1 ♀ (ovig.), 4.3 mm; PILLSBURY Sta. 695; 8°12'N, 58°33'W; 37 m; 15 July 1968; UMML 32.4167.—1 ♂, 7.4 mm; OREGON Sta. 2244; 8°12'N, 58°21'W; 57-71 m; 31 August 1958; USNM 103412. – 1 ♂, 8.2 mm; 1 ♀, 4.8 mm; 1 ♀ (ovig.), 5.4 mm; OREGON Sta. 4164; 8°0'N, 58°5'W; 55 m; 18 February 1963; USNM 128774.—1 ♂, 9.1 mm; 3 ♀, 4.2-7.4 mm; OREGON Sta. 2342; 7°28'N, 57°38'W; 27-31 m; 18-19 September 1958; USNM 103410.—1 ♀, 8.4 mm; OREGON Sta. 2248; 7°45'N, 57°34'W; 55-64 m; 31 August 1958; USNM 103409.—1 ♂, 16.0 mm; OREGON Sta. 2249; 7°40'N, 57°34'W; 49-55 m; 31 August 1958; USNM 103341.—1 ♀, 5.0 mm; OREGON Sta. 2000; 7°55'N, 57°30'W; 82 m; 5 November 1957; USNM 103408.—1 ♂, 5.6 mm; 1 ♀, 3.9 mm; PILLSBURY Sta. 686; 7°0'N, 57°8'W; 26-27 m; 15 July 1968; LM. SURINAM: 2 ♂, 3.2-3.5 mm; 2 ♀, 3.5-3.8 mm; PILLSBURY Sta. 684; 7°19'N, 56°51'W; 55-59 m; 14 July 1968; UMML 32.4168.—2 ♂, 12.0-12.7 mm; 6°12'N, 56°32'W; 18 m; Fernando Cervignon; 25 July 1967; UMML 32.4169.—1 ♂, 5.7 mm; 1 ♀, 4.8 mm; OREGON Sta. 4171; 6°16'N, 55°56'W; 27 m; 19 February 1963; USNM 128775.—1 ♂, 5.1 mm; 1 ♀, 4.1 mm; mouth of the Suriname River; COQUETTE 29; 6°49'N, 55°54'W; 48 m; 12 May 1957; USNM 103297.—1 ♀ (ovig.), 5.2 mm; NE of mouth of Suriname River; COQUETTE 36; 6°22'N, 55°54'W; 55 m; 12 May 1957; USNM 103236.—2 juveniles, 2.5-3.0 mm; NE of mouth of Coppename River; COQUETTE 287; 6°52'N, 55°50'W; 48 m; 26 June 1957; USNM 103298.—3 ♂, 11.3-17.3 mm; 6°19'N, 55°49'W; 27 m; Fernando Cervignon; 29 July 1967; UMML 32.4170.—1 ♂, 12.4 mm; 6°18'N, 55°46'W; 27 m; Fernando Cervignon; 29 July 1967; UMML 32.4171.—1 ♀ (ovig.), 5.5 mm; between mouth of the Coppename and Suriname Rivers; COQUETTE 306; 6°42'N, 55°38'W; 44 m; 20 July 1957; USNM 103237.—1 ♀, 4.8 mm; between mouth of the Coppename and Suriname Rivers; COQUETTE 318; 6°42'N, 55°38'W; 44 m; 20 July 1957; USNM 103299.—9 ♂, 3.0-10.1 mm; 2 ♀, 3.7-5.3 mm; 2 ♀ (ovig.), 4.1-5.8 mm; OREGON Sta. 2334-5; 6°50'N, 55°34'W; 51-57 m; 17 September 1958; USNM 103407.—10 ♂, 2.1-15.0 mm; 5 ♀, 3.0-4.1 mm; PILLSBURY Sta. 669; 6°39'N, 55°15'W; 33 m; 10 July 1968; UMML 32.4172.—10 ♂, 4.5-13.7 mm; 2 ♀, 4.5-5.7 mm; 2 ♀ (ovig.), 3.9-4.9 mm; OREGON Sta. 2284; 6°48'N, 55°12'W; 46 m; 8 September 1958; USNM 103404.—1 ♂, 7.3 mm; COQUETTE 1; 6°22'N, 55°6'W; 26 m; 11 May 1957; USNM 103294.—1 ♂, 7.1 mm; COQUETTE 2; 6°23'N, 55°5.5'W; 27 m; 11 May 1957; USNM 103241.—1 juvenile, 2.5 mm; COQUETTE 3; 6°24'N, 55°5'W; 27 m; 11 May 1957; USNM 103295.—1 juvenile, 2.4 mm;

COQUETTE 159; 6°22'N, 55°2.5'W; 26 m; 4 June 1957; USNM 103300. —1 ♀, 6.5 mm; COQUETTE 23; 6°24'N, 54°59.5'W; 27 m; 12 May 1957; USNM 103238.—1 ♀, 2.9 mm; COQUETTE 26; 6°40'N, 54°58'W; 37 m; 12 May 1957; USNM 103296.—1 ♂, 3.1 mm; COQUETTE 28; 6°48'N, 54°54'W; 46 m; 12 May 1957; USNM 103240.—2 ♂, 5.3-10.4 mm; COQUETTE 32; 6°51'N, 54°53.5'W; 51 m; 12 May 1957; USNM 103239. —2 ♂, 2.9-4.7 mm; 1 ♀, 2.6 mm; 1 ♀ (ovig.), 6.2 mm; PILLSBURY Sta. 663; 6°29'N, 54°41'W; 24 m; 10 July 1968; LM.—1 ♂, 10.5 mm; 6°47'N, 54°36'W; 46 m; Fernando Cervignon; 28 July 1967; UMML 32.4173. FRENCH GUIANA: 7 ♂, 1.8-9.5 mm; 3 ♀, 3.2-3.8 mm; 1 ♀ (ovig.), 6.1 mm; PILLSBURY Sta. 655; 6°7'N, 53°39'W; 26 m; 9 July 1968; UMML 32.4174.—1 ♂, 7.0 mm; OREGON Sta. 4185; 6°35'N, 53°35'W; 48 m; 21 February 1963; USNM 128776.—2 ♂, 7.1-7.9 mm; OREGON Sta. 2322; 6°50'N, 53°29'W; 62 m; 14 September 1958; USNM 103411.—1 ♂, 3.2 mm; PILLSBURY Sta. 654; 6°7'N, 53°19'W; 31 m; 9 July 1968; UMML 32.4175.—2 ♂, 2.5-2.6 mm; 4 ♀, 3.4-4.1 mm; 1 ♀ (ovig.), 3.8 mm; OREGON Sta. 2320; 7°5'N, 52°47'W; 366 m; 14 September 1951; USNM 103414.—1 ♀ (ovig.), 4.6 mm; PILLSBURY Sta. 652; 6°20'N, 52°34'W; 60 m; 8 July 1968; UMML 32.4176.—4 ♂, 4.4-10.0 mm; 1 ♀ (ovig.), 4.3 mm; OREGON Sta. 4192; 6°0'N, 52°27'W; 64 m; 22 February 1963; USNM 128753 & 128779.—1 ♂, 11.0 mm; 1 ♀ (ovig.), 11.0 mm; OREGON Sta. 2308; 5°56'N, 52°20'W; 57 m; 12 September 1958; USNM. —36 ♂, 2.1-7.9 mm; 19 ♀, 2.1-6.8 mm; 1 ♀ (ovig.), 3.6 mm; PILLSBURY Sta. 650; 6°7'N, 52°19'W; 84-91 m; 8 July 1968; UMML 32.4177. —2 ♂, 5.6-9.0 mm; 2 ♀ (ovig.), 4.3-5.5 mm; PILLSBURY Sta. 648; 5°26'N, 52°12'W; 42 m; 8 July 1968; LM.—3 ♂, 3.6-8.1 mm; 2 ♀, 6.4-8.2 mm; OREGON Sta. 4204; 5°29'N, 52°7'W; 55 m; 24 February 1963; UMML 32.2680. BRAZIL: 2 ♂, 6.3-13.2 mm; 2 ♀, 4.3-7.0 mm; 1 ♀ (ovig.), 5.7 mm; OREGON Sta. 4207; 4°46'N, 51°21'W; 59 m; 26 February 1963; USNM 128781.—1 ♂, 11.5 mm; OREGON Sta. 4208; 4°38'N, 51°5'W; 59 m; 26 September 1963; UMML 32.2674.—2 ♂, 7.7-10.6 mm; OREGON Sta. 2051; 4°5'N, 50°27'W; 91 m; 13 November 1957; USNM 103415.—1 ♀, 5.5 mm; OREGON Sta. 2050; 4°4'N, 50°23'W; 73 m; 13 November 1957; UMML 32.2332.—5 ♂, 6.2-10.6 mm; 2 ♀, 6.4-9.1 mm; 1 ♀ (ovig.), 7.5 mm; OREGON Sta. 2049; 4°2'N, 50°33'W; 70 m; 13 November 1957; USNM.

Description.—Ventral margin of dactylus of third pereiopod on left side a shallow groove with series of tufts of setae immediately adjacent on both sides. Lateral surface of segment with vertical tuberculate ridges interrupted medially by broad longitudinal groove, continuation of vertical ridges ventrally, each ridge with series of small tubercles along distal margin, ventral-most tubercles largest. Ridges dorsally and ventrally low, flattened; tuberculation indistinct, situated on distal margin of ridge.

Propodus of third pereiopod similarly sculptured, tuberculation slightly stronger. Ventral ridges on lateral surface raised medially forming broad longitudinal ridge, concave ventrally, ventral tubercles strongest.

Carpus of large cheliped lacking distal fringe of setae on lateral surface, only scattered tufts or fans of setae at base of tubercles.

Lateral surface of palm with numerous scales, each with series of low rounded tubercles (over 90 per cent of specimens examined with maximum of 6 tubercles per scale). Tubercles situated on anterior margin of scale, sometimes (13 per cent) acute and directed laterally.

Corneal width often much greater than width of eyestalks, length of eyestalks less than 2.0 times greatest width of cornea.

Color.—Cornea, in life, bluish or greenish with broad black bar running horizontally when viewed from front.

Palm of large cheliped basically purple or reddish purple, tubercles dark purple or blue.

Second and third pereiopods with narrow bands of brown-orange on merus, carpus, and propodus, width of band on carpus or propodus about 0.2-0.3 length of segment.

Holotype.—National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Type-Locality. OREGON Sta. 4202, NE Brazil near border of French Guiana.

Range.—Cape Hatteras, North Carolina, to Amazon River.

Etymology.—In addition to meaning "colored," the specific name *fucosus* can also be translated as "under false colors" or "counterfeited," which is certainly an apt description of a species that has remained hidden under another name for over 100 years.

Dardanus imperator (Miers, 1881)

Figs. 1,C; 2,C; 3,C; 4,C

?*Pagurus bernhardus*, Melliss, 1875: 203 (not *Pagurus bernhardus* [L., 1758]).

Pagurus imperator Miers, 1881: 275.—Ortmann, 1892: 285.—Alcock, 1905: 170. Cunningham, 1910: 120, fig. 6.

Dardanus imperator, Forest, 1955: 90.—Gordan, 1956: 314.—Chace, 1966: 634.

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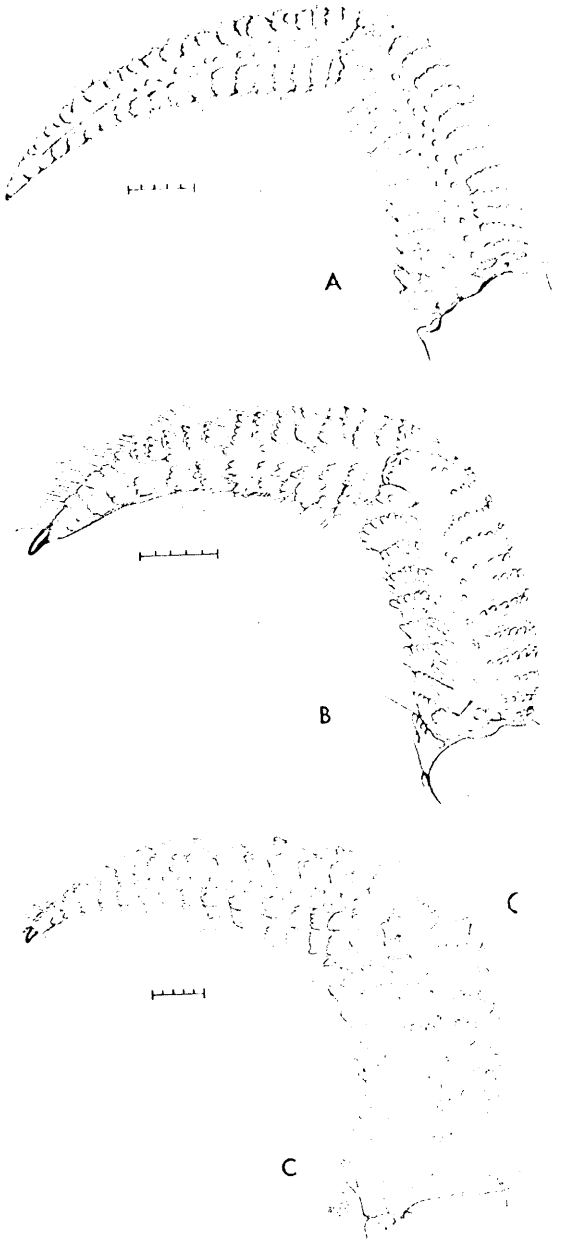
FIGURE 4. Lateral view of third left pereiopod of: A, *Dardanus fucosus*, holotype; B, *D. venosus*, lectotype; C, *D. imperator*, holotype. (Scales represent 5.0 mm.)


A
B
C
C

Material Examined.—ST. HELENA: 1 ♂, 23.6 mm; H. Dessin; BMNH 1873.5 (holotype).—1 ♀, 8.0 mm; James Bay; A. Loveridge; 17 November 1964; USNM 125507.

Description.—Ventral margin of dactyl of third pereiopod on left side a rounded ridge with rounded tubercles distally, proximal tubercles large and curved, large tufts of setae immediately adjacent to ridge on lateral surface. Lateral surface of segment with weak tuberculate ridges interrupted medially by strong, deep, longitudinal groove, longitudinal tuberculate ridge below groove with 1-3 well-developed tubercles arranged vertically along apex of ridge corresponding to location of vertical ridges. Area below longitudinal ridge strongly concave, each ridge ending ventrally in one strong tubercle. Ridges flattened, dorsal series with one or two subacute tubercles on distal margin of ridge, ventral series of ridges lacking tubercles except at ventral extremity.

Propodus of third pereiopod similarly sculptured, vertical ridges more evident, ridges tuberculate dorsally, tubercles centered on ridge, ventral series of ridges smooth except for 2-3 rows of tubercles ventrally, median longitudinal ridge well defined by dorsal and ventral grooves.

Carpus of large cheliped with scattered tufts of setae forming discontinuous fringe on distal margin of lateral surface.

Lateral surface of palm with numerous scales, each scale with strong central tubercle, some with up to three smaller tubercles laterally. Tubercles very well developed, usually on center of scale, directed laterally.

Cornea narrow, length of eyestalks about 2.5 times greatest width of eyestalks.

Color.—Unknown in fresh material, color retained in preserved specimen basically orange rather than red, pereiopods broadly banded as in *D. venosus.*

Holotype.—British Museum of Natural History, London.

Type-Locality.—St. Helena.

Range.—Known only from St. Helena.

DISCUSSION

With the great morphological similarity of these three species, it is not difficult to understand how confusion might have arisen. Even now, it is still not possible to define the limits of variation for *D. imperator* due to an inadequate sample. Chace (1966) remarked on a few differences from the original description exhibited in his juvenile specimen, and it would appear, based on our reexamination of the type and of a specimen intermediate in size between the type and the juvenile, that he was, in fact,

noting subadult characteristics. The front in both specimens we examined is sinuous, with rounded prominences just lateral to the base of the eyestalks, but no slender spine was found. The ocular scales end distally in three or four acute denticles, three in the smaller specimen and four in the larger. The calcareous plates on the abdomen are present on both specimens, but they are much larger and more distinct on the larger male. The tuberculation on the palm and third pereiopod is more distinct in the holotype, which suggests that variation occurs similar to that described below for *D. venosus* and *D. fucosus*. Even so, the more prominent grooves and ridges on the third pereiopod would be sufficient to distinguish *D. imperator* from *D. venosus* or *D. fucosus*, and it is in identifying the latter two species that the greatest amount of difficulty will be met.

Evidence from the Larvae

Studies of glaucothoes of *Dardanus* provided one of the early clues that two species existed under the name *D. venosus*. The glaucothoe of *D. venosus* was described from live planktonic specimens which molted to crab stages and which were similar to specimens reared in the laboratory from a female of known identity (Provenzano, 1963a). Shortly thereafter, glaucothoes of three other species were described (Provenzano, 1963b), one of them attributed to *Petrochirus diogenes* (L.). Glaucothoes with the same identifying features as the "*Petrochirus*" specimens were later captured and maintained to crab stages in the laboratory. Since justification had been given previously for the identification of the "toothed-telson" glaucothoes as a *Petrochirus*, their molt into what appeared to be *D. venosus* was quite unexpected. The observation was repeated several times. Apparently two readily distinguishable glaucothoes could produce crab stages of "*D. venosus*." Meanwhile, the complete larval development of *Petrochirus diogenes* was studied from laboratory rearing (Provenzano, 1968), and the glaucothoes obtained were very distinct from those previously attributed to this species.

Observations of living juveniles and adults of "*D. venosus*" showed two types of corneal color patterns. All glaucothoes with a toothed telson, whether reared from plankton or from a "bar-eyed" female, produced first crab stages with the bar-eyed cornea characteristic of *D. fucosus*.

Corneal color or color pattern in living specimens is nearly always specifically distinct and, when utilized in combination with other characters, helps separate closely related species. Thus it was not surprising when other characters supporting the distinctness of these species became evident. For the glaucothoes, the most obvious and the most useful distinguishing features are the form of the telson and of the dactyl of the third left pereiopod. The telson in *D. venosus* has the posterolateral corners rounded, and the distal margin bears 16-20 setae; in *D. fucosus*,

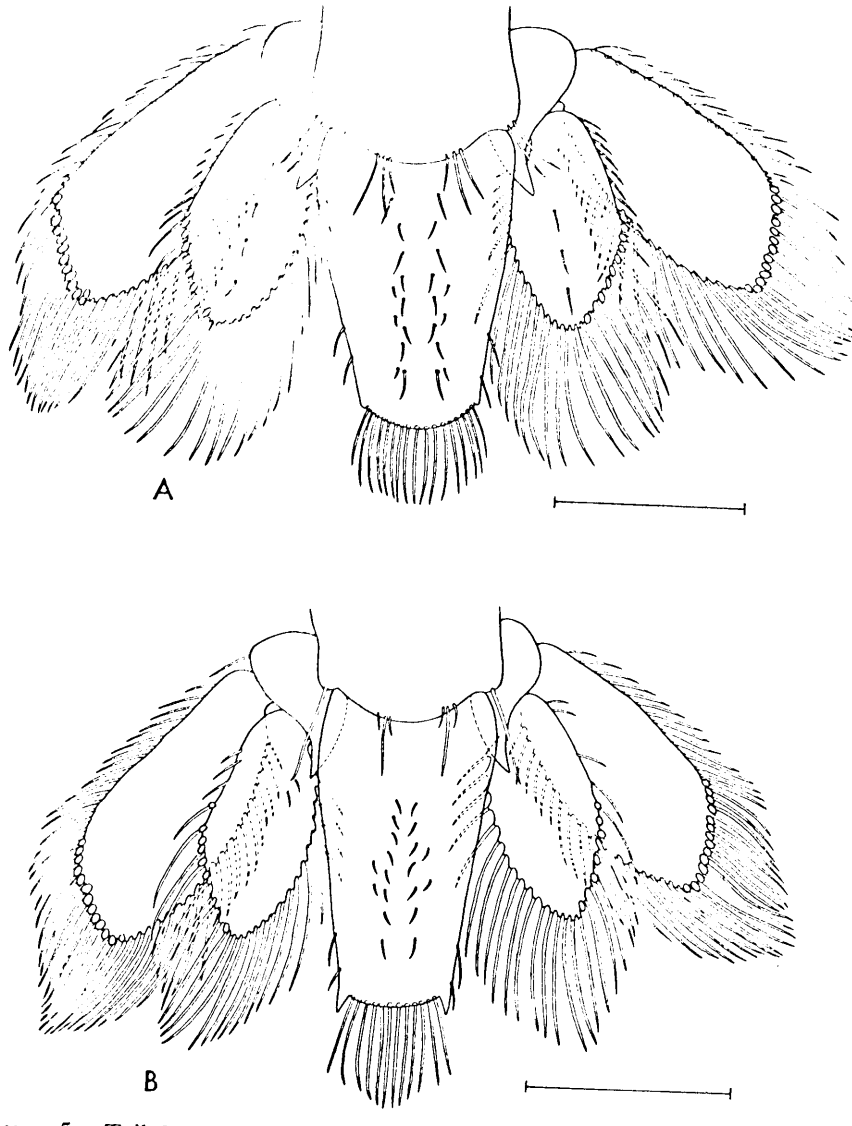


FIGURE 5. Tail fan of glaucothoe of: A, *Dardanus venosus*, specimen from GERDA Sta. G-47; B, *D. fucosus*, specimen from GERDA Sta. G-731. (Scales represent 1.0 mm.)

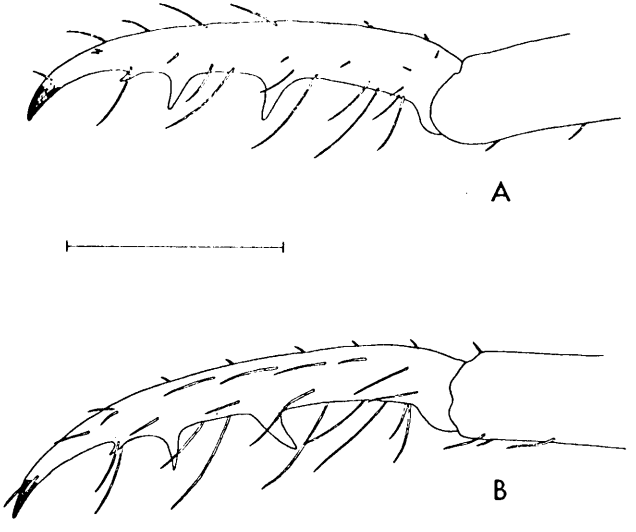


FIGURE 6. Dactyl of third left pereiopod of glaucothoe of: A, *Dardanus venosus*; B, *D. fucosus*. (Scale represents 1.0 mm.)

each of the posterolateral corners of the telson in the glaucothoe bears a large tooth and the distal margin of the telson between these teeth bears 11-12 setae (Fig. 5). The third left dactyl in *D. venosus* has the most proximal tooth on the ventral margin curving slightly distad; in *D. fucosus*, the proximal ventral tooth curves toward the body (Fig. 6).

VARIATION

Because of variation within the species, the presence or absence of a groove in the ventral margin of the dactylus of the third pereiopod on the left side is decidedly the best character that can be used in separating *Dardanus venosus* and *D. fucosus*. Except in very small specimens of *D. fucosus*, the character is extremely stable and easily seen or felt by running a probe down the length of the groove. The remaining characters are useful, but when using any single character, it is often difficult to decide to which species a specimen belongs, unless the observer has had experience in separating the species. However, the variation of these characters could not be adequately accounted for by intraspecific variation, and the wide occurrence of both *D. venosus* and *D. fucosus* suggested that we were not dealing with a single aberrant population. Examination of a series of specimens has shown that we are also not dealing with sexually dimorphic characters and that size has a limited effect on variation in all but the smallest specimens. With these considerations eliminated, it was

possible to describe the two species and to define the intraspecific variation.

The size of the available sample of *D. fucosus* (225 specimens) allows considerably more confidence in the statements about variation in that species. For example, the tuberculation of the palm falls within four categories; "normal," acute, strong, and *venosus*-like. The acute and strong tuberculations occur in 13 per cent and 4 per cent, respectively, of the specimens. The location of the tubercle on the scale and the number of tubercles per scale remains unchanged, and the chela would still be readily identified as belonging to *D. fucosus*. However, in 9 per cent of the specimens, the tuberculation is altered, either by reduction in the number per scale, or in the position of the tubercles, or both. In a few instances, the differences between the species with regard to this character can be very slight.

An additional complicating factor is the gross aspect of the tuberculation over the lateral surface of the palm. Scales situated proximally on the ventral half of the palm's surface are smaller and have fewer tubercles than those in the distoventral quadrant, and numerous small scales with a single tubercle are scattered among the larger scales. Scales on the dorsal half of the surface often have only a single strong tubercle. Thus it is difficult to describe this character adequately as it appears in *D. venosus*, because the same tuberculation can be found dorsally on the cheliped of *D. fucosus*.

The variation of the tuberculation of the palm has associated variation of other taxonomic characters in only one instance, the density of the fringe of setae on the third pereiopod. While presence of a dense or moderate fringe is almost equally common (45 per cent vs. 55 per cent of the total sample, respectively), 73 per cent of those specimens of *D. fucosus* having acute tuberculation on the palm also have a dense fringe. Of those specimens with *venosus*-like or strong tuberculation, 90 per cent and 100 per cent, respectively, have a moderate fringe. Other characters, including the form of the segments of the third pereiopods, carpal fringe, and the relative measurements of the eyestalks do not show associated variation.

The tuberculation on the palm of *D. venosus* exhibits similar variation. Of the total sample (27 specimens), 7 per cent showed strong tuberculation, none were found with acute tubercles, and 19 per cent showed tuberculation which might be mistaken for that of *D. fucosus*. Only one specimen was found with a dense fringe on the third pereiopod, and no other characters showed any variation correlated with the differences in tuberculation. Those specimens with a palm similar to that of *D. fucosus* have an increased number of tubercles per scale, but the tubercles are never located directly on the anterior margin of the scale.

The relatively high percentages of specimens having what might be termed nonspecific chelipeds (9 per cent *D. fucosus*, 19 per cent *D. venosus*) plus those specimens with strong tuberculation or acute tubercles (which raises the percentages even higher; 26 per cent *D. fucosus*, 26 per cent *D. venosus*) make specific identifications based on cheliped tuberculation alone rather tenuous. However, the position and orientation of the tubercules on the scale can afford a valuable clue to the correct identification of the species, and it is of considerable value when used in conjunction with other characters. Only in very small specimens is the development of the tubercles and scales rudimentary.

In contrast to the variation noted for the tubercles of the palm, the fringe of setae on the carpus seems to be quite stable in specimens of *D. venosus* and is consistently lacking in those of *D. fucosus*. In the latter species, the distalmost tubercles lack associated tufts of setae, and those tufts which are present are small and scattered. On the other hand, specimens of *D. venosus* have tufts both associated with tubercles and forming a fringe between tubercles. Together, these setae form a more or less continuous fringe along the distal margin of the carpus. The usefulness of this character in small specimens is unknown, since such specimens of *D. venosus* were unavailable.

As noted above, the groove on the third left pereiopod is probably the best character available for identification of preserved material. The remaining differences between the segments of the legs on these species are slight. It is possible, but difficult, to distinguish one species from the other by using leg segments alone (i.e., excluding consideration of the groove of the dactyl). The position and cross-sectional profile of the longitudinal propodal ridge may be distinctive; the ridge is nearer the ventral margin and is more rounded in *D. fucosus*. However, the shape does vary, and there are associated changes in the concavity of the dorsal portion of the surface.

The tuberculation of the vertical ridges presents much the same situation as is found on the palm. The tubercles are generally weaker, more numerous, and situated along the distal edge of the ridge in *D. fucosus*. In *D. venosus*, the tubercles are larger and situated more or less along the peaks of the ridges. Variation in the development of the tuberculation parallels that on the palm, including strong development and acute tubercles, although the occurrence of these types is less frequent. The row of strong ventral tubercles situated near or at the margin is often more ventral in *D. venosus* than in *D. fucosus*. In the latter species, a second row of tubercles may be present.

The concave area above the longitudinal ridge is usually wider in *D. fucosus* and contains more scattered scales. The width is often emphasized by the light color of the area in this species in contrast to the darker vertical

and longitudinal ridges. Although the general form and tuberculation of the propodus and dactylus were originally thought to be of considerable value for specific identification, the variation limits this value. On the other hand, used with other characters, the sculpturing of these segments can be useful.

The strength of the sculpturing in *D. fucosus* varies with the size of the specimen; smaller specimens have weaker transverse ridges and tuberculation on these ridges and less well developed longitudinal ridges. Very small specimens of *D. fucosus* may even lack a discernible groove ventrally. In these cases, the configuration of the tubercles and tufts of setae still defines a vacant area, as opposed to the tubercles and setae of *D. venosus*.

One specimen of *D. fucosus* with a malformed third left dactylus was seen. The form was that of the dactylus of the third right leg. No ventral groove or external ridge was evident.

Measurements of lengths and widths of dactylus and propodus of the left second pereiopods and the right and left third pereiopods did not reveal significant differences, nor did length-to-width ratios of the palm. For example, the cheliped may be longer than wide and moderately convex, or as long as wide and very convex, with all intergrades in each species.

Although it is a difficult character to use, the relative size of the eyestalk can be helpful. Careful measurement will usually confirm visual distinction. The most obvious difference is the widely rounded cornea of *D. fucosus* as opposed to the barely expanded, convex cornea of *D. venosus*. The more rounded cornea in the former species results in the extension of the lateral margins of the cornea beyond the lateral margin of the remainder of the eyestalk. The calcified portion of the eyestalk might be characterized as stubby in *D. fucosus*, with concave lateral margins flaring at both ends. In *D. venosus*, the eyestalk tends to be more straight-sided. A few specimens of *D. fucosus* from south Florida did not have a ratio of eyestalk length to corneal width below 2.0, and several abnormal specimens were noted. In the latter specimens, one eyestalk might be shorter than the other and asymmetrical, and the shape of the cornea might also be altered from the normal rounded shape to narrow, almost conelike corneas.

In summary, the two species are obviously very closely related morphologically, but are distinguishable. In all but the smallest specimens, the presence or absence of a groove on the dactylus of the third left pereiopod and the form of the tuberculation on the palm of the large cheliped will separate the species.

Related Species

The genus *Dardanus* contains a fairly large number of species; the total of described or ascribed species is more than 30. About 12 species of

Dardanus have been described from the Atlantic, but probably only half that many are valid. *Dardanus arrosor* (Herbst), for example, has been referred to as *D. errosor* Milne-Edwards, *D. incisus* Olivier, *D. striatus* Latreille, and *D. strigosus* Bosc. *Dardanus insignis* Saussure (= *D. arrosor* var. *petersi* A. Milne-Edwards) has been considered both a distinct species and more recently a subspecies of *D. arrosor* (see Forest & St. Laurent, 1967). In addition to *D. arrosor* and *D. insignis* (regardless of the status of the latter), other valid Atlantic species include *D. pectinatus* Ortmann, *D. calidus* (Risso), *D. venosus*, *D. fucosus*, and *D. imperator*. Gordan (1956) included several other species in *Dardanus*, which are now known to belong to other genera: *D. truncatulus* Rafinesque (= *Pagurus longicarpus* Say), *D. granulimanus* Miers (= *Pseudopagurus granulimanus* [Miers]), *D. loxochelis* Moreira (= *Loxopagurus loxochelis* [Moreira]), *D. fasciatus* (Bell) (= *Calcinus elegans* [H. Milne Edwards] *fide* Holthuis, *in litt.*), and *D. mediterraneus* (probably *Pagurus anachoratus* Risso, *fide* Holthuis).

One available name which requires some discussion is *Dardanus arrosor* var. *divergens* Moreira. Forest & St. Laurent (1967) were the first to synonymize this name with "*D. venosus*." Their judgment was based primarily on Moreira's original description (Moreira, 1906), which clearly indicates a *venosus*-type morphology. Moreira (1901) first referred to the specimens of this taxon under the name *D. arrosor*. In that publication and the subsequent one, he indicated a knowledge of two available names for western Atlantic species, *petersi* and *insignis*, both considered by him as varieties of *D. arrosor* and synonymized in a footnote (Moreira, 1906). Moreira obviously recognized that his specimens were distinct from the available specimen of *petersi* (= *insignis*), and when the "Annie" material provided additional specimens of *D. insignis*, a new taxon was definitely required. He did not appear to be aware of the description of *D. venosus*.

While it is possible that Moreira had a distinctive specimen, our present knowledge of the ranges of the species indicates that only *D. venosus* and *D. insignis* are found in the area of Moreira's record. Thus far, *D. fucosus* has not been found south of the Amazon River. Additional evidence came from correspondence with Dr. Lemos de Castro who was kind enough to compare specimens of *D. venosus* and *D. fucosus* with the type of *divergens*. The ventral margin of the third pereiopod is not grooved and the tuberculation of the palm is identical to that of *D. venosus*, for which reasons we synonymize *D. arrosor* Moreira and *D. arrosor* var. *divergens* with *D. venosus*.

Morphologically, *D. venosus*, *D. fucosus*, and *D. imperator* are distinct from other Atlantic species. They do have morphological affinities with an eastern Pacific species, *D. sinistripes*. Examination of the latter indicates

that, as with "*D. venosus*," two species are included under one name. While the situation requires further study, it appears that the degree of difference between them is comparable to that between *D. venosus* and *D. fucosus*.

In the Atlantic, *D. calidus* appears to be distinct enough to be excluded from the *venosus*-group, and it is clearly different from the group composed of *D. arrosor*, *D. insignis*, and *D. pectinatus*, all of which have spinous ridges rather than separate scales on the lateral surface of the palm. Of the species in the *venosus*-group, *D. imperator* shows greater morphological affinity with *D. venosus* than with *D. fucosus*, but *D. venosus* and *D. fucosus* seem to be more closely related.

Previous Citations

Considering the great morphological similarity between *Dardanus venosus* and *D. fucosus*, it is not surprising that previous descriptions rarely provided sufficient information to allow specific determinations based solely on published statements. In most instances, it was necessary to trace the material on which the statements were based and to examine each specimen. When this was impossible, the determination was based on all available information. For each citation, an indication of the method of identification is given.

Dr. Forest's examination showed that the entire type-series used by H. Milne Edwards (1848) consisted of one species (Forest, *in litt.*). Material described by Bouvier (1918) as *Pagurus insignis* and deposited in the Paris Museum was also examined by Forest and was determined to be *D. venosus*.

1. Stimpson (1859).—The two sentences describing a new record from St. Thomas do not allow an identification to be made. The site of the record and the scarlet color of the specimen suggest that it may be *D. venosus*, but the transverse striations on the right third pereiopod are rarely seen in this species and may indicate *D. insignis*.

2. Ortmann (1892).—It is impossible also to identify the specimen in this record. Since the author synonymized *D. insignis* with "*D. venosus*," he may have been referring to either of those or to *D. fucosus*.

3. Rathbun (1900).—Originally described or cited as *Petrochirus insignis* (an error which led to at least two others in subsequent literature), the material (USNM 25767 & 25768) is actually *D. venosus*.

4. Verrill (1900).—The specimen (YPM 3236) was misidentified as *Petrocheirus insignis*, corrected and redescribed as "*D. venosus*" (Verrill, 1908a), and referred again to *D. venosus* (Verrill, 1908b). The specimen from Bermuda is *D. venosus*, but the material from Dominica (YPM, unnumbered), which was also reported by Verrill (1908a), contains both *D. venosus* and *D. fucosus*.

5. Benedict (1901).—The specimens were misidentified as *Pagurias insignis* based on previous confusion. The material (USNM 42553) consists of one specimen of *D. venosus* and two of *D. fucosus.*

6. Schmitt (1924).—The single specimen (USNM 68963) is *D. venosus.*

7. Schmitt (1935).—The specimen from Guayanilla Harbor (AMNH 2245) is *D. venosus*, and it is the only specimen definitely located. There is a single specimen (AMNH 2171) labelled as from "Cayo Caribeto, Cayo Parguera" which is a *D. fucosus*, and there are three small specimens in the collection taken from "Puerto Rico" on the same day or within a week of the previous specimen. Two of these specimens (AMNH 2152 & 2831) are too small to identify, and the third (AMNH 2153) is a *D. fucosus.*

8. Schmitt (1936).—The specimen (USNM 67424) is a *D. venosus.*

9. Schmitt (1939).—The two adult specimens in the lot (USNM 78220) are *D. venosus.* The two juveniles could not be definitely named.

10. Provenzano (1959).—The first specimen listed in the Material section could not be located, but the second (UMML 32.322) is a *D. venosus.* The remaining specimens (USNM 101263; UMML 32.449, 32.2303 & 32.2304) are all *D. fucosus.*

11. Holthuis (1959).—The material deposited in Washington (USNM 103236-103241 & 103294-103300) is *D. fucosus.* The material in Leiden has not been reexamined critically, but, based on the homogeneity of available material, it seems reasonable to assume the same identification.

12. Provenzano (1960).—No specimen is available since this record is based on a sighting without examination, but, since only one species has been found in Bermuda, the specimen is assumed to have been a *D. venosus.*

13. Provenzano (1961).—The first and fourth lots noted in the Material section could not be located, but the remainder of the specimens (UMML 32.2307-32.2310, 32.2313 & 32.2315) are all *D. venosus.*

14. Provenzano (1963a).—The identification of the planktonic material as *D. venosus* has been confirmed by rearing of larvae from identified females.

15. Provenzano (1963b).—The original description of the planktonic glaucothoes as *Petrochirus diogenes* was found to be in error (Provenzano, 1968). Identical glaucothoes were reared from females of *D. fucosus.*

16. Cerame-Vivas, Williams & Gray (1963).—The specimen in question is no longer in the Duke University collection as they indicated, but there is a specimen in the collection of the Institute of Marine Sciences, Univer-

sity of North Carolina (UNC-IFR 1809), which could be the specimen they saw. The general location data and the date fit the record, but no more precise information is given. The specimen is a *D. fucosus*. In addition, there are no records of *D. venosus* from the eastern coast of the United States farther north than Miami, while *D. fucosus* has been collected from Miami to North Carolina.

17. Williams (1965).—No specific record was given, but it was learned in conversation that the general record was based on specimens in the UNC-IFR collection. These are all *D. fucosus*.

18. Forest & St. Laurent (1967).—The authors, aware of the existence of an undescribed species, examined their material critically for us. All specimens were found to be *D. venosus*.

19. Ross & Sutton (1968); Cutress & Ross (1969); Cutress, Ross & Sutton (1970).—The specimens preserved after use in these studies were kindly provided by Mr. Cutress. It is not known if these constitute all specimens used, but all 21 specimens are *D. venosus*.

20. Shoup (1968).—This color photograph illustrates *D. venosus*.

Sumario

Un Re-examen de *Dardanus venosus* (H. Milne Edwards) y *D. imperator* (Miers), con Descripción de una Nueva Especie de *Dardanus* del Atlántico Occidental (Crustacea, Decapoda, Diogenidae)

Por mucho tiempo se consideró bien conocida la especie de cangrejo hermitaño *Dardanus venosus* (H. Milne Edwards) pero hace algunos años empezó a acumularse evidencia que sugería que había realmente dos especies incluídas bajo este nombre. La primera indicación fue obtenida criando glaucotoes planctónicos, de los cuales dos formas distinguibles se transformaron en estados de cangrejo de *D. venosus*. Observaciones subsiguientes de adultos vivos mostraron diferencias consistentes en el color y finalmente diferencias morfológicas que podían ser utilizadas para definir dos especies.

En este trabajo *Dardanus venosus* y la nueva especie, *D. fucosus*, son descritas y parcialmente ilustradas y se revisan citaciones previas en la literatura en un intento por determinar a cuál especie se refieren. En la mayoría de los casos se pudo tomar una decisión después de extenso estudio de la referencia o examen del material en el cual estaba basada. *Dardanus imperator*, una especie estrechamente relacionada pero pobremente conocida de St. Helena, ha sido re-examinada y se encontró que

era distinta. Esta es descrita e ilustrada para proveer la información necesaria para su separación de *D. venosus* y *D. fucosus*.

Se da información general concerniente a la especie de *Dardanus* descrita procedente del Océano Atlántico. Doce nombres aparecen en la literatura, de los cuales seis o siete son válidos. Las especies válidas son: *D. venosus*, *D. fucosus*, *D. imperator*, *D. arrosor*, *D. pectinatus* y *D. calidus*. *Dardanus insignis* ha sido considerada como una especie independiente o una subespecie de *D. arrosor*. *Dardanus arrosor* var. *divergens* Moreira ha sido considerada sinónimo de *D. venosus*.

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