AMERICAN SPECIES OF THE DEEP-SEA SHRIMP GENUS
BYTHOCARIS (CRUSTACEA, DECAPODA, HIPPOLYTIDAE)

Lawrence G. Abele and Joel W. Martin

ABSTRACT

The American species of the deep-sea hippolytid shrimp genus *Bythocaris* are reviewed. *Bythocaris nana* is redescribed, and three new species—*B. floridensis*, *B. gorei*, and *B. miserabilis*—are described from material collected along the east and southeast coasts of the United States. A key to the known species of *Bythocaris* is given, and their distribution in American waters is discussed.

The hippolytid shrimp genus *Bythocaris* G. O. Sars, 1869, consists of eleven described species: *B. biruli* Kobjakova, 1964 (given specific status by Bowman and Manning, 1972); *B. cosmetops* Holthuis, 1951; *B. cryonesus* Bowman and Manning, 1972; *B. curvirostris* Kobjakova, 1957; *B. gracilis* Smith, 1885; *B. grumanti* Burukovskii, 1966; *B. irene* Retovskiy, 1946; *B. leucopis* Sars, 1879; *B. nana* Smith, 1885; *B. payeri* (Heller, 1875); and *B. simplicirostris* G. O. Sars, 1869 (the type-species of the genus). Three additional species are described herein.

The genus is best represented in fairly deep (shelf to 3,000 m) waters of the Arctic and North Atlantic, where 10 species occur. An additional species (*B. cosmetops*) occurs in the eastern Atlantic off Sierra Leone (Holthuis, 1951). All species except *B. cosmetops* are geographically sympatric with at least one other species in the genus, although the species appear allopatric with respect to both temperature and depth. Of the previously known species listed above, three (*B. gracilis*, *B. payeri*, and *B. nana*) are distributed along the eastern coast of the United States south to Florida, and one (*B. nana*) extends into the Gulf of Mexico. Worldwide distribution of the genus has been dealt with by Burukovskii (1966) and is summarized in his figure 1. The present paper reviews the distribution of the genus *Bythocaris* in the western Atlantic. Additionally, we redescribe *B. nana* and provide descriptions of three new species collected on the east coast of the United States off Jacksonville, Florida, thus increasing to six the number of species known from eastern North America and increasing to 14 the number of known species of *Bythocaris*.

MATERIALS AND METHODS

All American material of *Bythocaris* in the Smithsonian Institution's National Museum of Natural History, Washington, D.C., and in the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands, was examined. The material in the Rijksmuseum was collected by vessels of the Rosenstiel School of Marine and Atmospheric Science, University of Miami. Additional material from the northwestern Atlantic, collected by the Virginia Institute of Marine Science, was examined. Measurements were made with an ocular micrometer or Helios dial calipers. Illustrations of key characters were made with the aid of a Wild M-5 stereomicroscope equipped with camera lucida. The abbreviation *cl* stands for carapace length excluding rostrum. Material is deposited in the National Museum of Natural History, Washington, D.C.

Terminology.—There is some variation in the use of terms describing the spines and angles of the anterior carapace in the genus *Bythocaris*. Holthuis (1955: 3, fig. A), in his schematic figure of a caridean shrimp, illustrated three spines on the anterior margin of the carapace (the antennal, branchiostegal, and pterygostomial) plus the lateral hepatic spine, which is located behind the branchiostegal. The dorsal antennal spine arises from the area of the suborbital angle and is often coalesced with this angle to form an acute projection (Chace, 1972: 125, key to *Lysmata*). Below the antennal spine, and also on the anterior margin, is the branchiostegal spine, behind which is the hepatic spine.
only one of the latter two spines is present, assignment to type depends on the anterior-to-posterior location of the spine and thus is somewhat arbitrary, although if the spine has its origin on the anterior border it is considered branchiostegal. The third spine, the pterygostomial, is ventral to the branchiostegal and is an acute extension of the angle between the anterior and ventral carapace borders (see also Williams, 1984, fig. 2 and glossary). Previous authors have referred to these anterior carapace spines by various names. For example, the spine of B. cryonesus that Bowman and Manning refer to as a "submarginal antennal spine" we would refer to as a branchiostegal spine. For consistency, we have followed the diagrams of Holthuis (1955) and Williams (1984).

The spines or teeth referred to in the present paper as "supraorbital" appear, in some species, to arise from the lateral borders of the rostrum. These flanking teeth could be termed "rostrolateral" if the entire tridentate frontal protrusion is considered the rostrum. Because these teeth are often (but not always) in a different plane from that of the rostrum, we have adopted the precedent use of "supraorbital teeth" for these structures in Bythocaris; this usage is consistent with that of most previous workers on the genus.

Bythocaris G. O. Sars, 1869


Diagnosis.—Rostrum usually reduced, depressed, broadly triangular in dorsal view, always unarmed. (In B. grumanti rostrum compressed and much longer than in any other known species.) Well-developed supraorbital tooth on either side of and slightly higher than rostrum. Antennal spine or acute ventral orbital angle (these often coalesced) present on all species. Branchiostegals or hepatic spine present or not; former, when present, may approach pterygostomal position. Dorsal median carina present, often reduced, sometimes with anterior short tooth.

Eyes well developed and pigmented, or reduced, or well developed and without pigment.

Stylocerite of antennular peduncle well developed; basal antennular segment with small spine on distal margin. Basal antennular segment longer than penultimate; penultimate longer than ultimate.

Scaphocerite of antenna well developed and far overreaching antennular peduncle.

Mandible simple, lacking incisor process and palp. Maxillule with lower endite narrow, upper endite much wider than lower; palp truncate and slightly wider than lower endite. Maxilla with upper endite distinctly bilobed and well developed, lower endite reduced to small lobe; palp short. Scaphognathite well developed. First maxilliped with endites of coxa and basis distinct; palp present, caridean lobe and epipod distinct. Second maxilliped with endopod composed of five distinct segments; penultimate segment considerably expanded; ultimate segment narrow and attached with its longer margin to penultimate segment. Third maxillipeds pediform and well developed; ultimate and antepenultimate segments much longer than penultimate; ultimate segment slightly spatulate and armed with strong, amber-colored spines along interior distal margin; ultimate and penultimate segments with horizontal rows of setae along concave inner surface. Branchial formula:

<table>
<thead>
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<tr>
<td>1 2 3</td>
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<tr>
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<td>exopod</td>
<td>1 1 1 1 1</td>
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</table>
First pereiopods short, equal, robust, chelate. Second pereiopods long, slender, chelate, with subdivided carpi. Third through fifth pereiopods long, strong; meri each armed ventrally in about distal third with movable spines; propodi each armed on posterior ventral margins with 4–7 pairs of spines, each spine pair originating near same location giving appearance of single bifid spine; dactyli each armed ventrally with 5–7 (rarely to 10) spines; meri and propodi subequal, at least twice length of remaining segments.

Endopod of female first pleopod reduced, ovate; appendix interna absent; remaining pleopods each with appendix interna. Appendix masculina present on second pleopod of male.

Eggs few and large where known; development apparently direct.

Known from West African region (off Sierra Leone); eastern Arctic from 50 to 3,500 meters; from southern and western Florida on the east coast of the United States to off Greenland.

**KEY TO THE KNOWN SPECIES OF *BYTHOCARIS***

The following key is based on our examination of the species treated in this paper and of *B. payeri* and on accounts of other species in the literature.

1a. Rostrum dorsally compressed, broadly triangular in dorsal view, lying below or at same level as supraorbital teeth 2

1b. Rostrum laterally compressed, narrow in dorsal view, rising above level of supraorbital teeth

    B. grumanti Burukovskii, 1966

2a. Rostrum slightly upturned distally or extending more or less straight out in front of carapace; eyes with or without dark pigment 3

2b. Rostrum strongly downcurved distally; eyes without dark pigment

    B. curvirostris Kobjakova, 1957

3a. Carapace with distinct branchiostegal, pterygostomial, or hepatic spine present below lower orbital angle 4

3b. Carapace devoid of spines below lower orbital angle

    B. cosmetops Holthuis, 1951

4a. Scaphocerite (antennal scale) truncate distally, distolateral tooth extending almost to distal border; eyes reduced and without dark pigment 5

4b. Scaphocerite (antennal scale) produced distally, distolateral tooth falling far short of distal border; eyes well developed and with or without dark pigment 8

5a. Rostrum extending to just beyond cornea 6

5b. Rostrum never extending beyond cornea

7a. Dorsal carina of carapace terminating anteriorly in short sharp spine

8a. Eyes with dark pigmentation

    B. gorei new species

8b. Eyes without dark pigment

    B. simplicirostris Sars, 1869

9a. Rostrum slender in dorsal view, long, extending beyond cornea; dorsal carina with two sharp teeth anteriorly

    B. gracilis Smith, 1885

9b. Rostrum broad in dorsal view, short, never extending beyond cornea; dorsal carina without teeth or with at most one tooth or projection anteriorly

    B. miserabilis new species

10a. Dorsal carina terminating in small anterior tooth or projection 11

10b. Dorsal carina lacking anterior tooth or projection

11a. Fourth abdominal somite with posterolateral angle acute

    B. floridensis new species

11b. Fourth abdominal somite with posterolateral produced but rounded, not acute

12a. Branchiostegal spine strong, originating posterior to carapace border and therefore "hepatic" in location; carapace with slight ridges on dorsal surface

    B. gracilis Smith, 1885

12b. Branchiostegal spine weak, originating on anterior carapace border, never "hepatic" but rather "pterygostomial" in location; carapace without dorsal ridges

    B. miserabilis new species

13a. Rostrum rather acute, exceeding tips of supraorbital teeth by ¼ length of rostrum
13b. Rostrum very broad, somewhat obtuse, shorter than or even with tips of supraorbital teeth; if longer than teeth then never by as much as ¼ length of rostrum.

14a. Branchiostegal spine strong, originating posterior to carapace border and therefore almost "hepatic" in location. 

14b. Branchiostegal spine weak, originating on anterior carapace border, never "hepatic" but rather "pterygostomial" in location.

**Descriptions**

*Bythocaris floridensis* new species

**Figure 1**

*Material examined.*—Table 1.

*Holotype.*—Ovigerous female, $cl = 3.5$ mm.

*Type-Locality.*—Florida, east of Jacksonville, 31°09'N, 79°33'30"W; 644 m; dredge; ALBATROSS station 2669; 5 May 1886.

*Measurements.*—Males, $cl = 3.1$ to 3.9 mm; females, $cl = 3.3$ to 3.5 mm; ovigerous female, $cl = 3.5$ mm.

*Description.*—Rostrum (Fig. 1a–c) unarmed, depressed and triangular in dorsal view, ending in long acute tip reaching almost to base of antennules. Rostrum flanked by pair of acute supraorbital teeth, slightly higher than level of rostrum; distance between these spines about one-sixth to slightly more than one-fourth carapace length. Strong dorsal median carina present beginning at about middle of carapace and ending anteriorly in small, acute forwardly directed tooth at base of or just anterior to base of supraorbital teeth. Lower margin of orbit (Fig. 1c) rounded; antennal spine (coalesced with lower orbital projection) present below orbit. Weak branchiostegal spine present below antennal spine, extending anteriorly as far as antennal spine. Carapace smooth; no other spines present.

Abdomen smooth. Pleura one, two, and three rounded; four and five acute (Fig. 1d). Second pleuron in ovigerous females very wide, almost completely covering first and third pleura. Sixth segment about 1.6 times length of fifth segment.

Telson (Fig. 1e, f) about 1.6 times length of sixth segment. Six pairs of dorsal spines present, distal four pairs on lateral margin. First pair located one-fourth distance from base; second pair closer to first pair than to third; third through sixth pairs increasingly closer distally. Posterior tip of telson (Fig. 1f) truncate and armed with three pairs of spines; medial and lateral pair shorter than submedial pair.

Eyes large; cornea rounded and well pigmented.

Stylocerite (Fig. 1g) with small medial lobe on inner margin, tapering rapidly to acute tip reaching to about three-quarters of distance to distal margin of basal antennular segment. Basal segment about 1.5 times length of penultimate segment and about three times length of ultimate segment and with spine small present on inner margin just below distal border.

Scaphocerite (Fig. 1h) extending far beyond antennular peduncle, about 2.4 times longer than wide. Outside margin straight, ending in strong tooth that does not extend to distal margin of lamella. Basal segment with tooth present on lateral margin; this tooth absent on right side of holotype presumably as result of damage.

Epistome with pair of strong, acute, incurved spines on center region (Fig. 1i).

Third maxillipeds extending beyond scaphocerite by distal fourth of ultimate segment. Ultimate segment about three-fourths length of antepenultimate and twice length of penultimate. Segments about equal in width throughout length. Antepenultimate segment armed on distal margin with one distinct and two small
Figure 1. *Bythocaris floridensis*, new species. a, dorsal view of carapace; b, lateral view of carapace; c, frontal region of carapace, appendages removed; d, fourth through sixth abdominal somites; e, telson and uropods; f, distal tip of telson; g, antennule; h, scaphocerite; i, epistome spines; j, first pereiopod; k, propodus and chela of first pereiopod; l, second pereiopod; m, chela of second pereiopod; n, third pereiopod; o, dactylus of third pereiopod. Figures a, b, c, from same ovigerous female, GERDA station 44, figure i from different female in same lot (G-44); all others from ovigerous female holotype (ALBATROSS 2669). All scale bars = 1.0 mm: • = a, b, d, e, g, h, j, l, n; ○ = c; ■ = f, i, k, m, o.
ABELE AND MARTIN: AMERICAN SPECIES OF BYTHOCARIS

indistinct spines. Ultimate segment armed with six strong, amber-colored spines on distal fourth of interior margin. Small triangular spines alternate with these amber spines.

First pereiopods (Fig. 1j, k) equal, reaching to distal third of scaphocerite. Fingers of chela somewhat less than half length of palm. Chela and merus subequal and slightly longer than carpus. Carpus with tuft of stout setae bordering slight groove on distoventral margin. Ischium armed with small spine on distal medial margin. Second pereiopods (Fig. 1l, m) slender, overreaching scaphocerite by half length of carpus. Length of ischium and merus combined slightly longer than carpus. Merus longer than ischium. Carpus subdivided into eight segments; first longer than last; last longer than remaining subequal segments. Fingers slightly shorter than palm. Third through fifth pereiopods (Fig. 1n, o) long and strong. Merus and propodus of third pereiopod subequal. Ischium and carpus subequal. Dactylus about half length of carpus; carpus about half length of merus. Merus and propodus of third pereiopod subequal. Ischium and carpus subequal. Dactylus armed on distal third with two or three small spines. Distal upper margin of carpus extending beyond propodus, forming small lobe. Propodus armed with six pairs of spines, each spine pair originating near same location giving appearance of single bifid spine. Spines increasing slightly in strength distally. Dactylus very slightly curved and armed ventrally with six or seven spines.

Endopod of first pleopod of female reduced and rounded distally. No distal lobe present. Appendix interna absent from first pleopod but present on remaining pleopods. Appendix masculina present on male second pleopod and shorter than appendix interna. Appendix masculina rounded on distal margin and armed with three long and one very long setae. Three setae present on inner distal margin; four setae on outer distal margin.

Median branch of telsosomal uropod (Fig. 1e) lanceolate; lateral branch longer than medial branch and with weak spine on outer distal margin reaching to end of somewhat truncate lamella.

Eggs large (1.8 × 1.4 mm). Present ovigerous female (cl 3.5 mm) bore six eggs.

Distribution.—Eastern and southern Florida from 570 to 815 m.

Remarks.—In having dark pigment in the cornea and a produced (rather than truncate) scaphocerite, Bythocaris floridensis resembles B. nana, B. gracilis, B. payeri, B. simplicirostris, and B. miserabilis n. sp. (see below). However, B. floridensis is easily distinguished from B. simplicirostris and B. nana by rostral morphology. The distinctions between B. floridensis and the other above-named species are less obvious. The acute posterolateral angle of the fourth abdominal somite will distinguish B. floridensis from B. payeri and B. gracilis, both of which have this angle rounded. Bythocaris floridensis is perhaps most similar to B. miserabilis n. sp. (see below). Based on the present material, the two species can be distinguished by the following characters. The epistome region is armed with two spines in B. floridensis, whereas it is armed with three spines in B. miserabilis; the telson of B. floridensis is armed with six pairs of dorsal spines, whereas it is armed with four pairs in B. miserabilis; the fingers of the first pereiopods are slightly less than half the length of the palm in B. floridensis, whereas they are slightly greater than half the length of the palm in B. miserabilis; the carina of the carapace ends in a distinct spine in B. floridensis, whereas it is unarmored or has a small tubercle in B. miserabilis. Although these differences do not seem great, they are constant in the available specimens, which include ovigerous females of both species.

Etymology.—After the type-locality.
Table 1. Locality data for the material examined of *Bythocaris*

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<td>1,460</td>
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**B. gracilis**

1 ovigerous ♂ | Massachusetts, off Martha's Vineyard 39°35'N, 71°24'30"W | 1,096 | 20 August 1884 | Dredge, ALBATROSS 2206 |

1 ovigerous ♀ (Holotype) | North Carolina, off Cape Hatteras 35°45'23"N, 74°31'25"W | 1,624 | 11 November 1883 | Dredge, ALBATROSS 2116 |

**B. miserabilis**

1 ♂ (Holotype) | Southeast Florida 27°11'N, 79°30'W | 677 | 29 June 1963 | OT, GERDA 170 |

1 ovigerous ♂ | East Florida 33°44'N, 79°26'W | 805 | 1 April 1885 | Dredge, ALBATROSS 2415 |

1 ovigerous ♂ | South Florida 24°19'N, 81°39'45"W | 220 | 26 February 1902 | Dredge, FISH HAWK 7298 |

**B. nana**

1 ♂, 2 ovigerous ♀♂ | Massachusetts, off Martha's Vineyard 40°05'N, 70°23'W | 119 | 4 September 1880 | Dredge, FISH HAWK 865 |

1 ovigerous ♀ (Syntype) | Massachusetts, off Martha's Vineyard 40°05'39"N, 70°23'52"W | 157 | 4 September 1880 | Dredge, FISH HAWK 872 |

1 ♂ (Syntype) | Massachusetts, off Martha's Vineyard 40°00'N, 70°57'W | 155 | 13 September 1880 | Dredge, FISH HAWK 874 |
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*B. paveri*

| 2 ♂, 1 ovigerous ♀ | North Atlantic Faeroe Channel | 1,149 | 1882 | A. M. Norman |

Table 1. Continued
Bythocaris gorei new species

Figure 2

Material examined.—Table 1.

Holotype.—Ovigerous female, cl 5.6 mm.

Type-locality.—Florida, east of St. Augustine, 29°41’N, 79°55’W; 682 m; dredge; ALBATROSS station 2664; 4 May 1886.

Measurements.—Males, cl 4.2 to 7.2 mm; females, cl 4.4 to 7.2 mm; ovigerous females, cl 5.4 to 7.5 mm.

Description.—Rostrum (Fig. 2a–c) short and unarmed, apex ranging from acute and extending to base of cornea to broadly rounded and not extending to base of cornea. Pair of supraorbital teeth dorsal to and flanking rostrum, extending to about same level as or just posterior to rostrum; distance between these teeth about one-sixth carapace length. Dorsal median carina present from anterior third of carapace to base of supraorbital teeth, strongest in anterior part of carapace. Antennal spine (coalesced with lower orbital angle) (Fig. 2b, c) present just below orbit. Strong hepatic spine present. No branchiostegal spine. Carapace slightly constricted just posterior to hepatic spines (Fig. 2a). Carapace smooth, with no other spines.

Abdomen (Fig. 2d) smooth. First three pleura broadly rounded; fourth and fifth acute with posterolateral margins ending in small spines. Second pleuron in ovigerous females very wide, almost completely covering first and third pleura. Sixth segment almost twice length of fifth.

Telson (Fig. 2e, f) long and narrow, slightly longer than sixth segment. Dorsal surface usually with four pairs of spines closer to the midline distally; first pair located about one-third distance from anterior margin, second pair slightly anterior to midline, third pair about five-eighths, and fourth pair about seven-eighths distance from anterior margin; occasionally spines unpaired (as illustrated). Posterior tip (Fig. 2f) truncate and armed with three pairs of spines.

Eyes (Fig. 2a, b) large. Cornea rounded, lacking pigmentation or with very light pigmentation. Peduncle widening distally.

Stylocerite (Fig. 2g) wide medially, tapering to acute tip extending to distal margin of basal antennular segment. Basal segment with small spine present on inner margin about one-third distance from distal margin. Basal segment slightly less than twice length of penultimate; penultimate about 1.5 times length of antepenultimate. Two simple flagella present; outer one broad, longer than narrow inner one.

Scaphocerite (Fig. 2h) extending beyond antennular peduncle, length about 2.5
times width, increasing in width distally. Outer margin almost straight, ending in strong tooth overreached by lamella.

Epistome with two straight or incurved teeth in center region (Fig. 2i).

Third maxilliped (Fig. 2j, k) extending beyond scaphocerite by approximately distal half of ultimate segment. Ultimate segment spatulate, widening distally, with six or seven strong amber-colored spines along distal interior margin (Fig. 2k). Amber spines alternating with small triangular spines. Antepenultimate segment with three small spines on distal margin. Ultimate segment about 2.5 times length of penultimate, slightly shorter than antepenultimate segment.

First pereiopods (Fig. 2l, m) short, equal, robust, reaching to about base of scaphocerite. Fingers of chela somewhat longer than half length of palm. Chela about 1.5 times length of carpus, slightly longer than merus. Ischium armed with small spine on disto-interior margin (not illustrated). Second pereiopods (Fig. 2n, o) slender, extending beyond scaphocerite by at least chela. Fingers about equal in length to palm. Merus and ischium subequal, their combined length about equal to that of carpus. Carpus subdivided into 11 segments. Third through fifth pereiopods (Fig. 2p, q) long and slender. Merus and propodus of third pereiopod subequal. Ischium slightly longer than carpus; carpus slightly longer than dactylus. Merus armed distally with five spines, increasing in strength distally. Distal dorsal margin of carpus extends beyond propodus, forming small lobe. Propodus armed with five pairs of subequally spaced spines increasing in strength distally. Each spine pair originates near same location, giving appearance of single bifid spine. Dactylus slightly curved and armed with five to ten ventral spines.

Endopod of first female pleopod (Fig. 2r) ovate, often with very small lobe on outer distal margin. Appendix interna absent on first pleopod of female, present on remaining pleopods. Appendix masculina of male second pleopod (Fig. 2s) longer than appendix interna and armed with six to eight distal strong setae.

Medial branch of telsonal uropod (Fig. 2e) narrow and lanceolate. Lateral branch longer than medial with outer margin straight, ending in strong spine extending almost to distal margin of somewhat truncate lamella.

Eggs large (1.8 mm x 1.2 mm) and few. Holotype female carried only six eggs.

**Distribution.**—Eastern and southern Florida from 531 to 1,460 m.

**Remarks.**—All previously known species with non-pigmented eyes (i.e., lacking the dark pigment associated with "normal" decapod eyes, but often with some slight brown or tan pigment) also have in common a scaphocerite that is distally truncate (Bowman and Manning, 1972; 189, key). An exception is the deep-water form of *Bythocaris nana*, some specimens of which have pale or non-pigmented eyes (see under *B. nana*). *Bythocaris gorei* is therefore unique in having non-pigmented eyes and a distally produced and rounded (not truncate) scaphocerite. If one ignores eye pigmentation, *Bythocaris gorei* is similar to both *B. gracilis* and *B. payeri* but can be distinguished from both species in that the fourth and fifth pleura of *B. gorei* have the posterolateral angle acute. Both *B. gracilis* and *B. payeri* have pigmented eyes and the posterolateral angles of pleura four and five blunt.

A single ovigerous female (cl 8.6 mm; 23°35.7'N, 77°10.7'W; 1,348 m; 6 April 1975; R/V COLUMBUS ISELIN st. 312) is close to *B. gorei* but differs from it sufficiently that we do not include it with that species. The eyes of this specimen are pigmented, and the posterolateral angles of pleura four and five are acute. There are ten carpal segments on the second pereiopod. The supraorbital teeth are set farther apart than in *B. gorei*. Thus in eye pigmentation, number of carpal segments, and form of the supraorbital teeth, this specimen differs from those
referred by us to *B. gorei*. Although it may represent a variant of that species, we hesitate to identify it as *B. gorei* at this time.

Mature females of *B. gorei* were collected during January, April, May, June, September, and November; those collected during January, May, June, September, and November were ovigerous.

**Etymology.** —After our friend and colleague Robert H. Gore, for his many excellent contributions to crustacean systematics.

*Bythocaris gracilis* Smith, 1885

*Bythocaris gracilis* Smith, 1885: 497.—Smith, 1886, pl. 12, figs. 3–4.—Kemp, 1910: 117, pl. 18, figs. 1–3.—Sivertsen and Holthuis, 1956: 32, fig. 22.—Burukovskii, 1966: 536.

**Material Examined.** —Table 1

**Type-Locality.** —North Carolina, off Cape Hatteras, 1,628 m.

**Measurements.** —Ovigerous female, cl 8.4 mm.

**Description.** —Smith, 1886: 658, pl. 12, figs. 3–4.

**Distribution.** —The species has been recorded off western Greenland, off the Faeroe Islands, off southwest Ireland, and off Massachusetts and North Carolina on the eastern coast of the United States. It is known to occur between depths of 550 and 1,906 m (Sivertsen and Holthuis, 1956).

**Remarks.** —Various authors beginning with Smith (1885, 1886), Kemp (1910), and Sivertsen and Holthuis (1956) have dealt with relationships between *B. gracilis* and *B. payeri*. The differences enumerated by Sivertsen and Holthuis (1956) were found to hold in the material examined in the present study. However, the ridges on the carapace of *B. gracilis* were very difficult to see, possibly because the specimens have undergone some decomposition in the 100 years since they were collected. The most striking difference in the present material, which is the same material examined by Smith (1885, 1886), is in the strength of the supraorbital teeth. There is also a difference in the form of the female first pleopod; it is broadly rounded with a distal emargination in *B. payeri*, whereas in *B. gracilis* the distal portion is relatively more acute with the margins smooth and lacking any emargination. Kemp (1910) also noted a difference between the telsons of the two species and a difference between the endopod of the first male pleopod that may be due to age differences (i.e., between immature and mature specimens).

*Bythocaris miserabilis* new species

**Figure 3**

**Material Examined.** —Table 1.

**Holotype.** —Male, cl 1.8 mm.

**Type-Locality.** —Southeast Florida, 27°11'N, 79°30'W; 677 m; otter trawl; GERDA station 170; 29 June 1963.

**Measurements.** —Male, cl 1.8 mm; ovigerous females, cl 1.8 to 2.6 mm.

**Description.** —Rostrum (Fig. 3a–c) depressed, broadly triangular in dorsal view, unarmed, tapering to acute slightly upturned tip extending to cornea when eyes are in horizontal position. Rostrum flanked by acute supraorbital teeth dorsal to (higher than) rostrum; distance between these teeth slightly less than one third carapace length. Slight dorsal median carina present, sometimes with very small
Figure 3. *Bythocaris miserabilis*, new species. a, dorsal view of carapace; b, lateral view of carapace; c, frontal region of carapace, appendages removed; d, fourth through sixth abdominal somites; e, antennule; f, scaphocerite; g, epistome spines; h, first pereiopod; i, chela and subdivided carpus of second pereiopod; j, third pereiopod; k, dactylus of third pereiopod; l, appendices masculina and interna of male second pleopod. Figures a, b, c, e, f, g, l, from Holotype male (GERDA station 170); all others from ovigerous female, ALBATROSS station 2415. All scale bars = 1.0 mm: • = a, b, f, g; ○ = c, e, g, k, l; no scale exists for other figures (taken from pencil sketches of specimens no longer intact).

tubercle anteriorly (Fig. 3c); carina begins in posterior half of carapace and ends slightly posterior to level of tips of supraorbital teeth. Antennal spine (coalesced with lower orbital angle) (Fig. 3c) present just below orbit. Weak branchiostegal spine present below (ventral to) antennal spine, not extending anteriorly as far as antennal spine; this spine just as easily termed pterygostomial as carapace bends posteriorly just ventral to spine. Carapace smooth, lacking any other spines.

Abdomen (Fig. 3d) smooth. Pleura one through four rounded; fifth produced and subacute. Second pleuron in ovigerous females very wide, almost completely covering first and third. Sixth segment about 1.8 times length of fifth and about three-fourths length of telson. Telson long and narrow, with three or four pairs of small dorsal spines near lateral margin. Posterior margin of telson truncate, armed with three pairs of small spines; center pair shorter than submedial pair but longer than lateral pair.

Eyes (Fig. 3a, b) very large and well developed; cornea rounded, pigmented,
and well developed; peduncle very narrow proximally, rapidly increasing in width distally.

Stylocerite (Fig. 3e) tapering more or less smoothly to subacute tip, slightly wider medially in smaller female, and reaching to just over half length of first antennular segment. Small spine present on inside margin about one-fourth distance from distal margin of first antennular segment. First antennular segment over twice length of second; second about 1.5 times length of third. Two simple flagella present; outer one broad, inner one narrow.

Scaphocerite (Fig. 3f) far overreaching antennular peduncle, about 2.3 times longer than wide, widening slightly distally and widest just over half distance from base. Outer margin straight, ending in strong tooth far overreached by lamella. Basal segment with reduced tooth on outer margin.

Epistome (Fig. 3g) with three teeth in center; median tooth longest, submedian teeth shorter and blunt.

Third maxillipeds reaching almost to distal margin of scaphocerite. Ultimate segment about 2.3 times length of penultimate and just shorter than antepenultimate. Antepenultimate segment widening slightly distally, exceeding ultimate segment in width, armed on outer distal margin with small spine. Ultimate segment with six strong amber-colored spines on distal fourth of mesial margin and with small amber-colored spine on lateral distal margin. Small triangular spines alternating with strong amber spines.

First pereiopods (Fig. 3h) short, equal, robust. Fingers of chela about 0.6 times length of palm. Chela slightly longer than merus; merus slightly longer than carpus. Ischium about half length of chela and armed with two spines on disto-inferior margin. Second pereiopods (Fig. 3i) slender, extending beyond scaphocerite by chela and last four carpal segments. Fingers of chela longer than palm. Carpus divided into eight segments; first and last segments longest. Merus and ischium combined about equal in length to carpus. Third through fifth pereiopods (Fig. 3j, k) long and strong. Propodus of third longer than merus. Ischium and carpus about equal in length, each about twice length of dactylus. Carpus about half length of propodus. Merus armed with two or three spines, increasing in strength distally, on distal third. Distal dorsal margin of carpus overreaching propodus and forming small lobe. Propodus armed with five or six pairs of spines about equally spaced except for last two pairs; last two closer together than other pairs. Spines increasing in strength distally and each spine pair originating near same location, creating appearance of single bifid spine. Dactylus very slightly curved and armed ventrally with six spines.

Endopod of first pleopod of female somewhat oblong with very small lobe on distal exterior margin. Appendix interna lacking on first pleopod but present on remaining pleopods. Appendix masculina of male second pleopod (Fig. 3l) longer than appendix interna and armed distally with up to ten spines or setae.

Telson with medial uropod lanceolate and narrowing at both ends. Lateral uropod longer than inner one. Lateral margin of lateral uropod straight, ending in small tooth; tooth overreached by somewhat truncate lamella of distal margin.

Eggs large (1.2 x 0.86 mm). One female (cl 1.8 mm) carried only eight eggs.

Distribution. — Eastern and southern Florida from 220 to 805 m.

Remarks. — Bythocaris miserabilis is another species with fully pigmented eyes and a produced scaphocerite margin and as such is similar to the species discussed under B. floridensis. We hesitate to erect this species, not because of the distinctness of the characters but because few specimens are at hand (three, of which two are badly damaged) and because the extent of variation in this genus cannot yet be
fully appreciated. The tubercle on the dorsal carina is present only in the holotype male. Sivertsen and Holthuis (1956) noted that the presence of this tubercle varied in \textit{B. payeri} as well. In specimens lacking this tubercle, \textit{B. miserabilis} resembles \textit{B. nana} and \textit{B. payeri} but can be distinguished by the weak nature of the branchiostegal (=pterygostomial) spine. In specimens where the tubercle is present (the holotype male), \textit{B. miserabilis} resembles \textit{B. gracilis} and \textit{B. floridensis} but again can be distinguished by the weak nature of the branchiostegal tooth. \textit{Bythocaris miserabilis} is most similar to \textit{B. floridensis} but can be distinguished by characters listed under the latter species.

\textit{Etymology}.—After the diminutive size and poor condition of the available specimens.

\textit{Bythocaris nana} Smith, 1885

\textit{Figure 4}

\textit{Bythocaris} sp. indet.: Smith, 1881: 437.—Smith, 1882: 55. \textit{Bythocaris nana} Smith, 1885: 449.—Smith, 1886: 660, pl. 12, fig. 2.—Burukovskii, 1966: 536.—Bowman and Manning, 1972: 188.

\textit{Material Examined}.—Table 1.

\textit{Type-Locality}.—Massachusetts, off Martha’s Vineyard, 263 m.

\textit{Measurements}.—Males, \textit{cl} 3 to 5.4 mm; females, \textit{cl} 2.5 to 5.4 mm; ovigerous females, \textit{cl} 2.5 to 5.4 mm.

\textit{Description}.—Smith (1885, 1886) described this species but provided only a single figure of the dorsal anterior region of the carapace and frontal appendages. We redescribe it below.

Rostrum (Fig. 4a–c) depressed, broadly triangular in dorsal view, unarmed and ending in a slightly upturned subacute apex that fails to reach base of cornea. Rostrum flanked on either side by supraorbital tooth, at higher level than and slightly advanced beyond or at same level as rostrum; distance between these teeth about one-third carapace length. Slight dorsal median carina present, usually beginning in anterior third of carapace and terminating before (posterior to) base of rostrum; this carina in large specimens sometimes reduced to short low ridge, in small specimens sometimes stronger and beginning in posterior third of carapace. Carapace with small downturned lobe at lower margin of orbit extending beyond anterior margin of carapace and terminating before (posterior to) base of rostrum; this carina in large specimens sometimes reduced to short low ridge, in small specimens sometimes stronger and beginning in posterior third of carapace. Carapace with small downturned lobe at lower margin of orbit extending beyond anterior margin of carapace (Fig. 4c); antennal spine arising from this lobe. Well developed branchiostegal spine present just below antennal spine, in large specimens almost “hepatic” in location, being distinctly removed from anterior margin of carapace but still extending beyond it. Carapace smooth; no other spination present.

Abdomen (Fig. 4d) smooth. Pleura rounded; second pleuron in ovigerous females very broad, almost completely covering first and third; fourth and fifth extended posteriorly; fifth narrower than fourth. Male fourth and fifth pleura not extending so far posteriorly; lower margins truncate, giving pleura rectangular form. Fifth pleura broader in ovigerous females. Sixth segment about 1.7 times length of fifth. Telson (Fig. 4e, f) about 1.2 times length of sixth segment, long and narrow (length about 3.7 times width), with slight constriction about one-half distance from base. Distal half may bear three or four pairs of spines; number and spacing of spines variable. Posterior telson margin (Fig. 4f) truncate with three pairs of spines, medial pair shorter than submedial pair but longer than lateral pair.

Eyes (Fig. 4a, b) large; cornea rounded and well pigmented (with some excep-
Figure 4. *Bythocaris nana* Smith, 1885. a, dorsal view of carapace; b, lateral view of carapace; c, frontal region of carapace, appendages removed; d, fourth through sixth abdominal somites; e, telson and uropods; f, distal tip of telson; g, antennule; h, scaphocerite; i, epistome spines; j, third maxilliped; k, first pereiopod; l, chela and carpus of first pereiopod; m, second pereiopod; n, chela of second pereiopod; o, third pereiopod; p, dactylus of third pereiopod; q, endopod of female second pleopod; r, appendix masculina and appendix interna of male second pleopod. Figures a–d, g, h, j–p, from female, GERDA station 649; figures e, f, r, from different specimen in same lot (G-649); figure i from female, GERDA station 415. All scale bars = 1.0 mm: • = a, b, d, e, h; ◯ = g, m, o; ■ = b, j, k; □ = f, l, n, p, q, r.
tions; see Remarks). Peduncle sometimes with slight lobe present on inner margin just below cornea.

Stylocerite (Fig. 4g) wide medially and tapering distally, extending to about distal fourth to distal margin of basal antennular segment. Basal antennular segment with small spine on inner margin about one-third distance from distal margin (not shown); basal segment about three times length of penultimate; penultimate about 1.6 times length of ultimate and bearing two simple flagella; inner flagellum much narrower and slightly longer than outer.

Scaphocerite (Fig. 4h) extending far beyond antennular peduncle, equal in width throughout length; width about three times length. Outer margin very slightly concave and ending in distinct tooth; tooth far overreached by lamella. Basal segment with weak lateral tooth. Epistome region with pair of straight acute teeth (Fig. 4i), not visible in dorsal view.

Third maxillipeds (Fig. 4j) reaching to about distal fourth of scaphocerite, in small specimens extending almost to distal margin. Ultimate segment more than twice length of penultimate and just shorter than antepenultimate; ultimate segment spatulate, almost hollowed, and armed along inner distal third with six or seven strong, amber-colored spines, these spines with small triangular spinules between them. Antepenultimate segment armed with small spine on outer distal margin and also on opposite side (not shown).

First pereiopods (Fig. 4k, l) short, equal, robust. Fingers of chela about three-fourths length of palm. Chela longer than merus. Carpus and ischium subequal, shorter than either chela or merus. Ischium with small spine on disto-interior margin. Second pereiopods (Fig. 4m, n) slender, overreaching scaphocerite at least by chelae. Chela fingers slightly shorter than palm. Carpus subdivided into eight segments, first and last segments longest. Merus somewhat more than half length of carpus and slightly longer than ischium. Third through fifth pereiopods (Fig. 4o, p) long and strong; merus and propodus of third pereiopod about equal. Ischium longer than carpus; carpus about equal in length to dactylus. Merus armed with four to six spines on distal two-thirds, these spines increasing in strength distally. Distal margin of carpus overreaching propodus and forming small lobe. Propodus armed with five to eight pairs of equally spaced spines; each pair originating from nearly same location, giving appearance of single bifid spine; pairs of spines increasing in strength distally. Dactylus slightly curved and armed with five to seven ventral spines.

Endopod of first pleopod of female (Fig. 4q) somewhat rectangular, with distinct lobe on outer distal margin. Appendix interna lacking on first female pleopod, present on all other pleopods. Appendix masculina (Fig. 4r) present on second male pleopod, longer and stronger than appendix interna; distal margin rounded and armed with about eight to twenty strong setae extending from about half distance from distal margin.

Medial branch of uropod (Fig. 4e) narrow, lanceolate; lateral branch longer than medial. Distal margin of lateral branch rounded and extending beyond spine of outer margin.

Eggs large (1.2 × 0.8 mm), numbering up to 18 (on one 4-mm el female).

Distribution.—The species is known from off Martha's Vineyard, Massachusetts, to southern Florida and the northeastern Gulf of Mexico, from 79 to 1,175 m.

Remarks.—Size and sexual variation is evident in the material examined. In small specimens (Fig. 4b, c) the branchiostegal spine is relatively small and set toward the anterior margin of the carapace; larger specimens have the spine set farther back on the carapace so that it appears almost "hepatic" in location. The spine,
however, even in large specimens, still extends beyond the anterior margin of the carapace. The posterolateral margins of the fourth and fifth pleura and the antennular flagella are sexually dimorphic. In females the fourth and fifth pleura extend posteriorly and are rounded; in males the posterolateral pleuron margins do not extend so far posteriorly and are truncate, giving the pleura a rectangular form. The lateral antennular flagellum of females is broad; that of males is distinctly narrower.

Differences exist between deep (>200 m) and shallow (<200 m) forms of this species, and two species may be involved. The shallow-water form (Fig. 5) is usually smaller and more pigmented and seems to have a shorter sixth abdominal segment relative to the length of the telson (compare Fig. 5c, d). The deep-water form is usually pale in comparison, and the eyes are occasionally without pigment (e.g., the 5 males and 2 females from BLM-003-J1-SBT2). Various statistical analyses on several characters, including relative length of the sixth abdominal segment, were inconclusive in separating the two forms.

Mature males were collected during January, February, March, April, May, July, August, and September; only those females collected during February were not ovigerous.

_Bythocaris payeri_ (Heller, 1875)

_Hippolyte payeri_ Heller, 1875: 26, pl. 1, figs. 1–4.


_Material Examined._—Table 1.

_Type-Locality._—Franz Josef Land (Zemlya Frantsa Iosifa), Arctic Ocean, 185 m.

_Description._—Sars, 1885: 33, pl. 3, fig. 27. See also Sivertsen and Holthuis, 1956: 34, figs. 23–24.

_Distribution._—This species has the widest distribution of any in the genus (Burukovskii, 1966). It has been reported from the Atlantic along the coast of Newfoundland, from the Skandian Basin, and from the Arctic Ocean. The species is included here on the basis of the record of Sivertsen and Holthuis (1956) and is known from 160 to 2,000 m.

Remarks. —The relationship of this species to _B. gracilis_ has already been discussed under _B. gracilis_. In addition to the problems of differentiating _B. payeri_ from _B. gracilis_, there is another regarding the status of the three “populations” of _B. payeri_. As noted by Sivertsen and Holthuis (1956), specimens from American waters, the Barents Sea, and the Faeroes all differ from one another in small but consistent characters. A re-examination of all material is needed to determine the limits of variation in this species.

**DISCUSSION**

The rareness of specimens of _Bythocaris_ is evident from an examination of the numbers of specimens upon which the various species are based. Three species (_B. cryonesus_, _B. curvirostris_, and _B. irene_) are known from single specimens; _B. grumanti_ is known from two specimens, one of which was damaged; _B. miserabilis_ is known from three specimens, two of which are badly damaged; several other species are represented by only a few extant specimens. In contrast, a few species are considered common. However, in those common species (e.g., _B. leucopis_ and
Figure 5. *Bythocaris nana*, specimen from relatively shallow (<100 m; BLM station A1) water and abdomen from a deep-water form (BLM station J1). a, dorsal view of carapace and eyes; b, lateral view of frontal region of carapace; c, abdomen; d, last several segments of abdomen of deep-water form; e, scaphocerite; f, cheliped; g, second pereiopod; h, chela of second pereiopod. All scale bars = 1.0 mm: • = a–e, g; O = f, h.

*B. payeri* almost no information is available either on intraspecific variation or on the biology of the species. Our examination of western Atlantic material has convinced us that variation is marked in several species. In *B. nana* there is ontogenetic variation in the placement of the hepatic spine, sexual dimorphism in the form of the abdominal pleura, and some variation in the length of the sixth abdominal somite (the latter possibly a function of depth of the population; see Remarks under *B. nana*). In *B. miserabilis* the presence of the anterior tubercle of the dorsal carina is variable as it is also for known series of *B. payeri* (see discussion by Sivertsen and Holthuis, 1956: 32–33). Other characters of purported taxonomic significance are also unreliable. For example, the number and location of spines on the dorsal surface of the telson varied within a species, and the number of carpal segments on the second pereiopod differed from side to side in a single individual. Further examination of larger series will probably disclose additional variable characters, possibly resulting in synonymy of presently accepted species. A further morphological trend, the striking increase in size with higher latitudes, should also be considered as a possible source of intra- and interspecific variation in future studies.

Development in *Bythocaris* is almost certainly direct or strongly abbreviated. Sars (1885: 32, pl. 3, figs. 24–26) noted large eggs in *B. leucopis* and commented that “it could be fully substantiated, that the young in this genus, contrary to what is the case in all other known Caridians [sic], undergo their transformation in the
egg itself, from which they emerge as perfect decapods, with the number of their limbs complete.” Subsequent findings confirm that other members of the genus have similar development; Burukovskii (1966) cites Thorson (1955) as having
found large eggs in four species of the genus and argues for a deep-sea origin of the group on the basis of this character. Females of the species described herein carried few large eggs (e.g., a female *B. nana* with a carapace length of 4 mm carried 18 eggs each about 1.2 mm × 0.8 mm). Direct development in other deep-water carideans is well documented (Martin, 1986). Occurrence of direct development and brooding of few large eggs may favor establishment of local populations capable of responding differently to local and random conditions. This is a possible explanation for morphological variations observed between local populations of the same species (e.g., variation in *B. payeri* described by Sivertsen and Holthuis, 1956).

Bowman and Manning (1972) published photographs of live *B. cryonesus* taken at about 3,500 m in the Arctic Ocean. They suggested, on the basis of morphology and the available photographs, that *B. cryonesus* is a strong swimmer and that the eyes, although lacking pigment, are probably sensitive to bioluminescence. Other species are probably similar in their habits, although we do not know whether there is a functional difference between those species lacking eye pigmentation and those with dark eyes.

The presence of a thick tuft of setae on the distal end of the carpus of the first pereiopod suggests that these shrimp clean their antennae in the manner described by Bauer (1975, 1978) for various carideans. This character has not previously been noted for *Bythocaris*, probably because of the small size of most of the species and the small relative size of the cheliped. However, we would not be surprised to find that it is shared by all members of the genus.

The present study significantly extends the number of species and localities known from the western Atlantic (Fig. 6). Previous to this study the western Atlantic was known to harbor *B. gracilis*, *B. nana*, and *B. payeri* (actually in the northwest Atlantic) (Burukovskii, 1966). In addition, the range of *Bythocaris* is extended south below latitude 35°N, a range that previously included only *B. cosmetops* from the far eastern Atlantic off Sierra Leone (Holthuis, 1951). It is probable that the concentration of collecting sites shown in the straits of Florida in Figure 6 reflects the efforts of the R/V *GERDA* in this region.

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NOTE ADDED IN PRESS: The following paper was brought to our attention while our manuscript was in press: Zarcnkov, N. A. 1986. On the fauna of decapods in the Chuckchee Sea. Zool. Zh. 65(5): 796–798 (in Russian). (Includes first records of *Bythocaris curvirostris* and *B. payeri* from the Chuckchee Sea).