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REDESCRIPTION OF *HEXAPANOPEUS LOBIPES* AND ITS REASSIGNMENT TO *MILNEPANOPEUS* N. GEN. (DECAPODA: BRACHYURA: PANOPEIDAE)

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ABSTRACT

Milnepanopeus n. gen. is proposed to accommodate the western Atlantic brachyuran crab, *Hexapanopeus lobipes*. Characters of the carapace, sternal groove, carpus of the ambulatory pereiopods, and male first gonopod define this presently monospecific genus. Recent molecular analyses support removal of *H. lobipes* from *Hexapanopeus*, and segregate this genus as a distinct lineage of Panopeidae Ortmann, 1893. The species is redescribed as *Milnepanopeus lobipes*, n. comb., on the basis of the holotype and supplementary material from deep banks in the Gulf of Mexico. Variations in morphology are addressed along with morphological comparisons to related genera of the family.

KEY WORDS: Brachyura, *Hexapanopeus*, *Milnepanopeus lobipes*, Panopeidae

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INTRODUCTION

In the course of reviewing Panopeidae Ortmann, 1893, we have reexamined phylogenetic relationships among species presently assigned to *Hexapanopeus* Rathbun, 1898. The present study builds upon previous efforts (Schubart et al., 2000; Thoma et al., 2009) to clarify species composition of *Hexapanopeus* sensu stricto by molecular phylogenetic analyses. Here we undertake a comparative morphological study of the poorly known western Atlantic species *Hexapanopeus lobipes* (A. Milne-Edwards, 1880). Infrequently reported and easily confused with other taxa of similar habitus, it has proven to be a common component of benthic communities on deep banks in the Gulf of Mexico.

Hexapanopeus was erected by Rathbun (1898: 273) for "narrow, hexagonal species of *Panopeus* with rapidly converging posterolateral margins". Although numerous panopeid taxa have at some point been considered part of *Hexapanopeus*, the genus is by most accounts presently comprised of 11 species inhabiting both coasts of the Americas, ranging from Massachusetts to Uruguay in the Atlantic and from Mexico to Ecuador in the eastern Pacific. Despite several familiar species being commonly reported in environmental surveys or regional accounts from a variety of nearshore habitats (Rathbun, 1930; Felder, 1973; Williams, 1984; Sankarankutty and Manning, 1997; Felder et al., 2009), most representatives of the genus are rarely reported.

Recent examination of molecular phylogenetic relationships among *Hexapanopeus* and related genera of Panopeidae revealed this genus to be polyphyletic (Thoma et al., 2009). These analyses, based upon mitochondrial sequence data, also suggested that two commonly reported species, i.e., *Hexapanopeus angustifrons* (Benedict and Rathbun, 1891) and *Hexapanopeus paulensis* Rathbun, 1930, actually represent unrecognized complexes encompassing several undescribed taxa. Although only five species of the genus were included in the analyses, it revealed that several species assigned to *Hexapanopeus* were in fact rather distantly related to what might be regarded as *Hexapanopeus* s.s. In particular, *H. lobipes* appeared to represent a distinct lineage, prompting our current reexamination of its morphology.

Hexapanopeus lobipes has an unsettled taxonomic history. Originally described as a species of *Neopanope* A. Milne-Edwards, 1880 from deep waters off southern Florida, Rathbun later transferred it to *Lophopanopeus* Rathbun, 1898, with little comment. Menzies (1948: 23) subsequently pointed out that *H. lobipes* did not fit the diagnosis of *Lophopanopeus* and justified its transfer to *Hexapanopeus* by noting "it seems to fit the diagnosis of that genus better than that of any other American genus". In a recent review of extant Brachyura, Ng et al. (2008) reassigned *H. lobipes* to *Lophopanopeus* without comment. Although representatives of *Lophopanopeus* were not included in their analyses, Thoma et al. (2009) argued that morphology offered no support for reassignment of *H. lobipes* to *Lophopanopeus*, a position here reiterated.

Although recent sampling efforts on deep subtidal banks of the middle to outer continental shelf in the Gulf of Mexico have found *H. lobipes* to be common throughout the region (Felder et al., 2009; Thoma et al., 2009), only four specimens of *H. lobipes* had been reported prior to

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Wicksten's (2005) list of decapods from the Flower Gardens Banks in the northwestern Gulf (A. Milne-Edwards, 1880; Rathbun, 1898; Menzies, 1948). Most deep banks of that region were not heavily sampled until recently, but it is also likely that these small panopeids have been erroneously or incompletely identified in regional environmental surveys and impact assessments to date, including those preceding extensive oil and gas development in the region.

Morphologically, *H. lobipes* is distinctive and bears little resemblance to other members of *Hexapanopeus*. On the basis of morphology and molecular phylogenetic evidence it does not share a close relationship with *H. angustifrons*, type species of *Hexapanopeus* (Thoma et al., 2009). We redescribe it here on the basis of the incomplete holotype specimen, which retains only one ambulatory pereiopod, augmented by recently obtained materials from the Gulf of Mexico, and also designate this species as the type of a new monotypic genus. In the course of this redescription, we provide detailed illustrations and text accounts of its diagnostic features, with more expanded treatment of mouthparts and other features than is typical in most recent brachyuran descriptions. These are offered to facilitate identification and justify generic level separation, both for the present and to lay groundwork for detailed morphological comparisons in coming works on related taxa.

Materials and Methods

Materials examined include holdings from the Museum of Comparative Zoology at Harvard University, Cambridge, MA (MCZ), University of Louisiana at Lafayette Zoological Collection, Lafayette, LA (ULLZ), National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and Texas Cooperative Wildlife Collection at Texas A&M University, College Station, TX (TCWC). Specimen size (in mm) is noted as carapace width (CW), measured at the widest point including anterolateral teeth and carapace length (CL), measured from the anterior-most of the frontal lobes to the posterior-most margin of the carapace. All collection depths, where available, are given in meters (m).

Systematics

Infraorder Brachyura Linnaeus, 1758
Panopeidae Ortmann, 1893

Milnepanopeus, n. gen.

Type species.—*Neopanope lobipes* A. Milne-Edwards, 1880.

Diagnosis.—Carapace with surface granulate; frontal margin bilobed, median fissure distinct; anterolateral teeth well developed, arrayed in arc, first and second fused, giving appearance of four teeth. Ambulatory pereiopods two through five (walking legs) carpus extensor margin bearing two distinct elevations, proximal broadest, distal strongest. Male pleon anteriorly elongate, reaching beyond condyle of first pereiopod; seventh sternite distinctly exposed to either side of second pleomere; third segment lateral extremities unevenly rounded, slightly overreaching coxa of fifth pereiopod proximally. Male first pleopods (gonopods) distally of modified-panopeid, trifid arrangement, pair of strong subterminal microspinulous spines, spines directed posterolaterally and sternomesially, respectively; duct terminating within microspinulous cuspidate apex forming hood-like process.

Etymology.—The name combines the prefix "Milne", in honor of A. Milne-Edwards and his many contributions to our understanding of marine crustaceans, with a suffix derived from *Panopeus*, type genus of the Panopeidae, in recognition of its panopeid affinities.

Assigned species.—*Milnepanopeus lobipes* (A. Milne-Edwards, 1880), n. comb., formerly *Neopanope lobipes*.

Milnepanopeus lobipes, n. comb.
Figs. 1-4

Neopanope lobipes A. Milne-Edwards, 1880a: 331, pl. 61, fig. 3; A. Milne-Edwards, 1880b: 14.

Lophopanopeus lobipes Rathbun, 1898: 272; Rathbun, 1930: 320, text-fig. 50, pl. 155, figs. 3-5; Menzies, 1948: 3; Powers, 1977: 94; Ng et al., 2008: 190.

Hexapanopeus lobipes Menzies, 1948: 3, 23; Powers, 1977: 94, 96; Wicksten, 2005: tab. 1; Felder et al., 2009: 1082; Thoma et al., 2009: 552, tab. 2, figs. 1-2.

Material Examined.—Type material: MCZ 2911, holotype male 4.2 mm CW, 3.0 mm CL; SW Gulf of Mexico, SW of Dry Tortugas, Florida; 24°43′N, 83°25′W; Blake Station 10; 68 m depth; 2 Apr 1877. OTHER MATERIALS: USNM 88657, 1 male 3.6 mm CW, 2.7 mm CL, 2 females 3.9 mm CW, 2.8 mm CL and 3.5 mm CW, 2.6 mm CL; Bimini, Bahamas; dredge; 2 Nov 1948. ULLZ 8117, 2 males 6.3 mm CW, 4.3 mm CL and 4.5 mm CW, 3.3 mm CL, 3 females 3.9 mm CW, 2.9 mm CL, 4.7 mm CW, 3.4 mm CL, and 4.1 mm CW, 3.0 mm CL; NNW Gulf of Mexico, Ewing Bank, off Louisiana; NSF-III-080; 28°6.12′N, 91°1.33′W; box dredge; rubble; 61 m depth; 8 Jul 2006; coll. D. L. Felder. ULLZ 8213, 3 males 4.8 mm CW, 3.5 mm CL, 3.9 mm CW, 2.9 mm CL, and 5.4 mm CW, 3.9 mm CL, 1 female 3.9 mm CW, 2.9 mm CL; NNE Gulf of Mexico, Sackett Bank, off Louisiana; NSF-III-001; 28°37.87′N, 89°33.33′W; box dredge; rubble; 61-65 m depth; 28 Jun 2006; coll. D. L. Felder. ULLZ 4715, 1 male 6.1 mm CW, 4.5 mm CL; NNW Gulf of Mexico, Ewing Bank, off Louisiana; DOE Stn. 10-1; 28°05.561′N, 91°02.205′W; box dredge; 58-60 m depth; 27 May 2000; coll. D. L. Felder. ULLZ 4731, 1 male 4.5 mm CW, 3.2 mm CL; NNW Gulf of Mexico, Bouma Bank, off Louisiana; DOE Stn. 1-2; 28°03.606′N, 92°27.537′W; box dredge; 61.6-62.8 m depth; 30 Jun 2001; coll. D. L. Felder. ULLZ 6909, 2 males 4.2 mm CW, 3.2 mm CL and 4.1 mm CW, 3.1 mm CL; ESE Gulf of Mexico, NW of Dry Tortugas, Florida; NSF-1-019; 24°35.81′N, 83°28.49′W; box dredge; 61 m depth; 1 Jun 2004; coll. D. L. Felder. ULLZ 6686, 1 male 4.8 mm CW, 3.5 mm CL; NNW Gulf of Mexico, Bouma Bank, off Louisiana; NSF-II-029; 28°3.64′N, 92°27.72′W; box dredge; 61-66 m depth; 22 Jun 2005; coll. D. L. Felder. ULLZ 7828, 1 male 6.7 mm CW, 4.7 mm CL; NNW Gulf of Mexico, Ewing Bank, off Louisiana; NSF-III-078; 28°5.49′N, 91°1.96′W; box dredge; 57-66 m depth; 08 Jul 2006; coll. D. L. Felder. TCWC 2-

77691, 1 male 5.7 mm CW, 4.4 mm CL, 1 female 5.6 mm CW, 4.4 mm CL; NW Gulf of Mexico, Stetson Banks, off Texas; 23-26 m depth; 26 Jun 2001; coll. M. Wicksten.

Rediagnosis.—Carapace moderately convex, regions well-defined by shallow grooves, surface granulate, granules increasing in size and density anteriorly in each region; frontal margin bilobed, slightly thickened by dense granules, median fissure distinct; anterolateral teeth well developed, arrayed in arc, first and second fused, giving appearance of four teeth. Major chela (first pereiopod) dactylus with basal molariform tooth present, weakly developed. Ambulatory pereiopods two through five (walking legs) carpus extensor margin bearing two distinct elevations, proximal broadest, distal strongest. Male pleon anteriorly elongate, reaching beyond first pereiopod condyle; second segment narrowing distally, seventh sternite distinctly exposed to either side; third segment lateral extremities unevenly rounded, slightly overreaching fifth pereiopod coxa proximally; sixth segment slightly broader than long; telson rounded. Male first pleopods (gonopods) reaching well beyond suture between fourth and fifth sternites, not beyond anterior end of median sternal groove, distally of modified-panopeid, trifid arrangement, bearing pair of strong subterminal microspinulous spines, longer spine directed posterolaterally, shorter sternomesially, but deflected distally, duct terminating within microspinulous cuspidate apex forming hood-like process.

Redescription.—Carapace (Figs. 1A, 2A) moderately convex, regions well-defined by shallow grooves, surface granulate, granules increasing in size and density anteriorly in each region, occasionally forming weak rows or carinae; frontal margin bilobed, slightly thickened by dense granules, median fissure distinct, lobes broadly convex, antennal sinus distinct; supraorbital margin granulate, median fissure small, distinct, lateral fissure obsolete or as shallow notch. Pterygostomial and subhepatic regions (Fig. 2B) sparsely granulate; pterygostomial ridge weakly swollen, with irregular granules or single slightly raised ridge of granules. Endostomial ridge reduced to faint line, not distinct or raised. Branchiostegite below anterolateral teeth with ventral margin non-cuspate, nearly straight above coxa of each ambulatory pereiopod. Second pleurite anterolateral margin visible as small prominence below ventral margin of branchiostegite above second pereiopod coxa, full width of second pleurite sometimes narrowly visible. Anterolateral teeth well developed, arrayed in arc, first and second teeth with separation weak to obsolete, appearing indistinguishably fused, giving appearance of four teeth, teeth coarsely granulate to weakly tuberculate; lobe formed of fused first and second teeth broad forming acute to subacute outer orbital angle; depression between second and third teeth shallow, broad; third tooth (appearing as second, given fusion of preceding) largest, tip anteriorly directed; fourth tooth anterolaterally directed, often more coarsely granulate, more lobiform than preceding teeth; fifth tooth typically small, acute to subacute, less commonly tuberculiform as cluster of strong granules. Posterolateral margin sometimes bearing ill-defined low tubercle or slight elevation posterior to fifth tooth.

Eyestalk with distinct raised, coarsely granulate anterior crest. Mandible (Fig. 2C) with palp present; cutting edge nearly smooth, lacking mandibular process. First maxilla (Fig. 2D) with basal endite broadly lanceolate, lateral margins fringed by simple setae, distal margin with cluster of stout simple setae; distal endite obovate, lateral margins with sparse fringe of simple setae (longer on extensor margin than flexor), distal margin with several dense rows of mixed setae (thin, stout simple setae); endopod broadly subquadrate proximally, constricted distally over base of mandible, distal margin with several stout setae; exopod present as small protuberance on coxa, distal margin with small cluster of long simple setae. Second maxilla (Fig. 2E) scaphognathite broadly ovate, inferior margin nearly straight, proximoventral corner angled near 90°, margins densely fringed by simple setae, surface with sparse simple setae; endopod pyriform, distal process spire-like, lateral margin with row of simple setae, single long simple seta on distomesial margin near base of spire-like process; endites elongate, distal margins densely fringed by long setae.

First maxilliped (Fig. 2F-G) basal endite subobovate, external surface with several loosely-formed laterally-oriented rows of stout simple setae, internal surface bearing longitudinal ridge with row of simple setae, distal margin densely fringed by stout simple setae; distal endite oblong, lateral and mesial margins fringed by long simple setae, external and internal surfaces with field of simple setae originating basally, extending to distolateral margin. Endopod complex, dolabriform, lateral margin reflected externally, away from body, forming complexly convoluted ridge, distomesial margin with distinct flap directed towards body, mesial margin with fringe of long plumose setae, distal and distomesial margins with sparse fringe of short simple setae. Exopod vaguely lanceolate, tapering distally, base curved mesially, lateral margin with fringe of short plumose setae; flagellum long, recurved, strongly deflected mesially, distally multiarticulate with numerous long stout setae. Epipod broadly subquadrate proximally, distally constricted forming long thin posterolaterally directed process, margins fringed with long setae.

Second maxilliped (Fig. 2H-I) protopod largely uncalcified, bearing several calcified plates. Endopod of five articles, fused subtriangular basischium bearing small protuberance directed mesially near mid-length, several irregularly placed short simple setae in proximal half; merus oblanceolate, mesial margin with fringe of short simple setae, lateral margin with fringe of short to medium simple setae in proximal half, distally with small patch of medium to long simple setae, internal surface with single irregular longitudinal row of short simple setae near midline; carpus angled mesially at near 90°, broadening distally, distal margin with several long stout simple setae on internal surface, few short stout simple setae near distoextensor margin, external surface with a single short stout simple seta near distoextensor margin; propodus broadly oval with extensor margin distinctly enlarged, extensor margin with patch of medium to long stout simple setae on distal half, external surface with several medium to long stout simple setae near distal margin, setae increasing in length from flexor to extensor margins, internal surface with several widely scattered short simple setae near distoflexor margin, flexor margin with single medium simple seta distally; dactylus broadly oval, distal margin with dense fringe of stout setae continued onto flexor and extensor margins

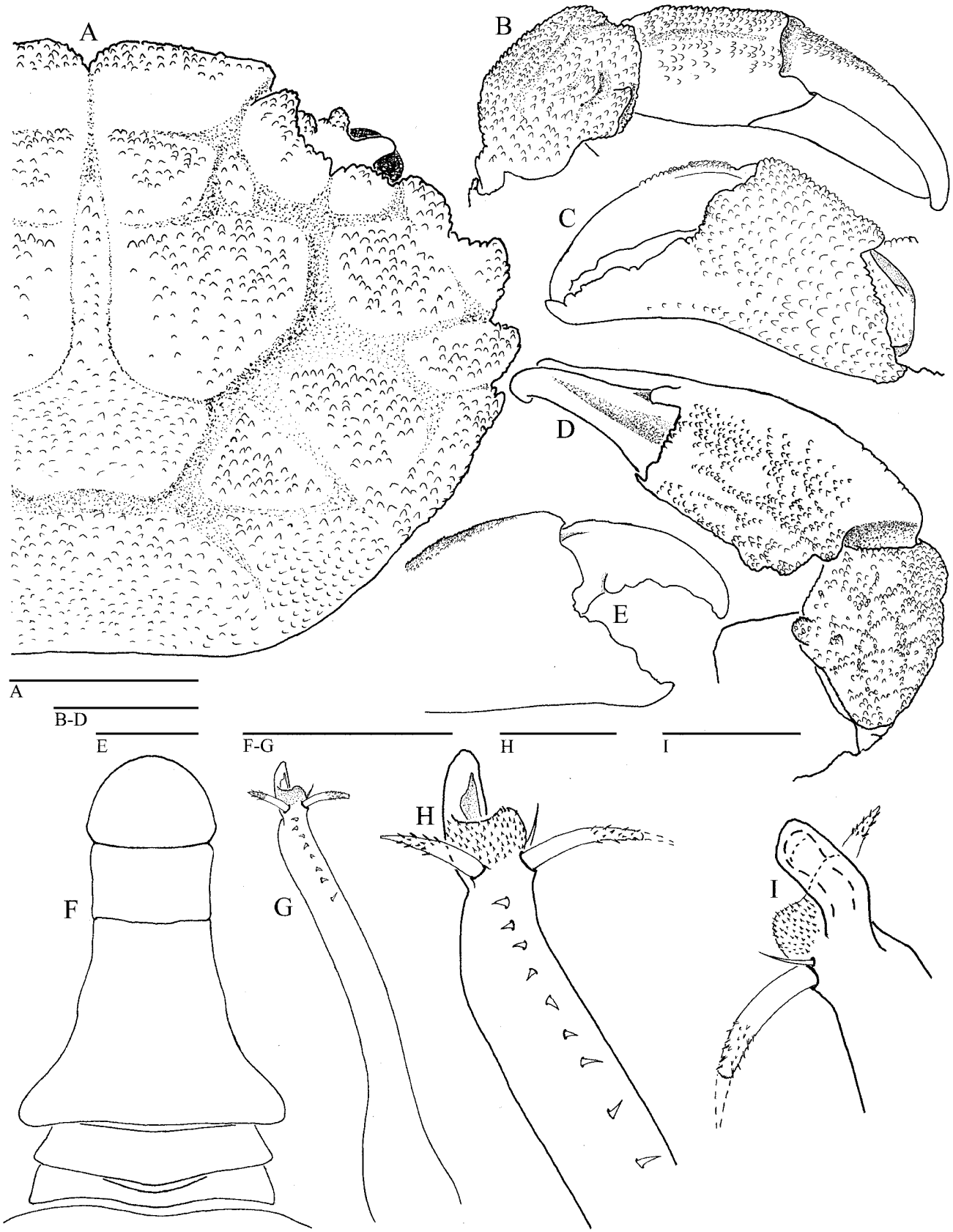

Fig. 1. *Milnepanopeus lobipes* n. comb. A-I = male holotype (MCZ 2911), SE Gulf of Mexico, NW of Dry Tortugas, 4.2 mm CW, 3.0 mm CL. A, carapace, right half only; B, left (minor) cheliped, superior surface; C, left (minor) chela, extensor surface; D, right (major) cheliped, superior surface; E, right (major) chela, extensor surface; F, pleon, external surface; G, left first gonopod, sternal surface (tip broken off one seta); H, left first gonopod, distal sternal surface; I, left gonopod terminus, pleonal surface. Scales A-F = 1 mm; G = 0.5 mm; H-I = 0.1 mm.

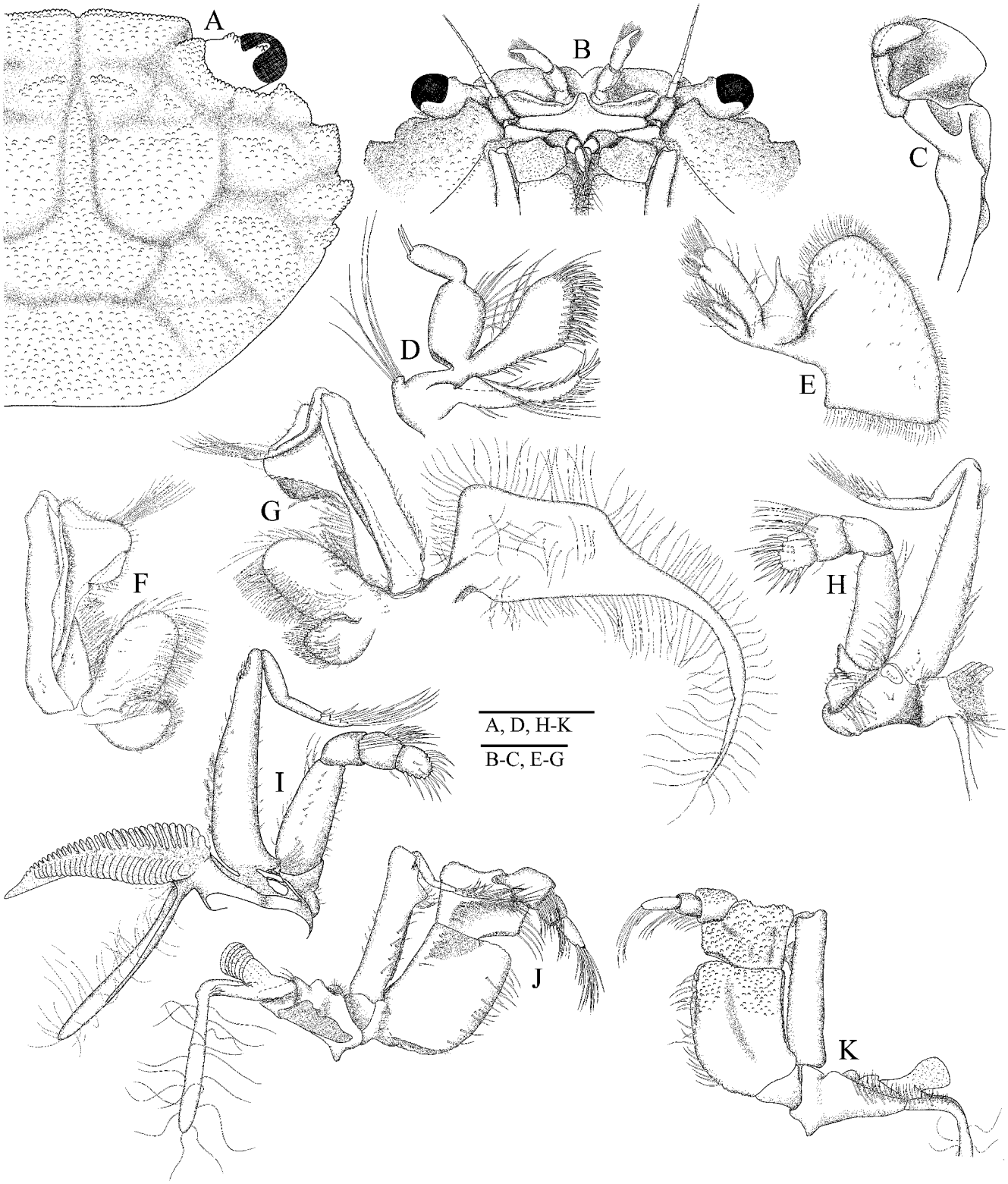

Fig. 2. *Milnepanopeus lobipes* n. comb. A, C-E, H-I = male (ULLZ 8117), NNW Gulf of Mexico, Ewing Bank, off Louisiana, 4.5 mm CW, 3.3 mm CL; B = female (ULLZ 8213), NNE Gulf of Mexico, Sackett Bank, off Louisiana, 3.9 mm CW, 2.9 mm CL; F-G, J-K = male (ULLZ 4715), NNW Gulf of Mexico, Ewing Bank, off Louisiana, 6.1 mm CW, 4.5 mm CL. A, carapace, right half only; B, buccal region; C, left mandible, internal surface; D, right first maxilla, external surface; E, left second maxilla, external surface; F, left first maxilliped, internal surface (excluding coxa and epipod); G, left first maxilliped, external surface; H, left second maxilliped, external surface (epipod and podobranch truncated); I, left second maxilliped, internal surface; J, left third maxilliped, internal surface; K, left third maxilliped, external surface (epipod truncated). Scales A-B, J-K = 1 mm; C-I = 0.5 mm.

in distal half, internal surface with several widely scattered simple setae, external surface with short transverse row of long simple setae near midlength. Exopod lanceolate, tapering distally, curving mesially near base, mesial margin with very sparse fringe of short simple setae, lateral margin with fringe of simple setae, short and plumose proximally, simple and becoming sparse distally, interior surface with distolateral patch of short simple setae, short longitudinal row of short simple setae near mid-length of lateral margin; flagellum recurved, multiarticulate distally with numerous long setae. Epipod thin, elongate, both margins with sparse fringe of very long simple setae; podobranch gill large, tapered to acute distal tip, either side bearing row of lamellae decreasing in size distally.

Third maxilliped (Fig. 2J-K) protopod subcuneate, narrowing laterally, bearing small subtriangular projection proximomesially, external surface with slight notch or groove near distomesial margin, patch of medium length simple setae distolaterally, continuing slightly onto epipod, distal surface deeply grooved to accept ventral edge of carapace, internal surface with three unequal projections on distal margin, larger projection near mid-length, distomesial margin with fringe of short simple setae, fringe continuing on mesial margin, slight groove or indentation near mid-length. Epipod strongly curved posteroventrally near one-third length, distally fringed with long simple setae; podobranch gill typically small, short, lamellae limited to tight terminal bundle or at most slightly bilobed proximally and subacute distally. Endopod with basis subtriangular, external suture between basis and ischium distinct, internal distal extensor margin with few short simple setae, continuing as irregular line onto flexor margin of ischium, basis suture with ischium nearly fused, indistinct; ischium broadly subrectangular with proximal portion deflected laterally, distomesial corner slightly expanded, external surface with distomesial margin excavated, appearing as irregular shelf bearing fringe of medium-length simple setae, external surface with distal sparsely granulate in distal half, mesial margin with irregular fringe of short to medium length simple setae, continued for short distance on internal surface, internal surface with short irregular row of short simple setae near distomesial margin, subtriangular uncalcified region at articulation with merus; merus subquadrate, thin strip of proximomesial margin excavate to accept distomesial swelling of ischium, distal margin expanded near corner of lateral margin, with indentation mesially, distomesial corner excavated to accommodate carpus, external surface densely granulate, internal surface deeply excavate to accept endopod of second maxilliped, excavation with fringe of short simple setae, internal surface with deep distomesial notch to accept carpus, mesial margin with sparse fringe of medium length simple setae; carpus appearing subcylindrical externally, subobovate internally, external surface granulate especially near extensor margin, internal surface with fringe of medium-long stout simple setae on distal margin; propodus cylindrical, internal surface with short row of medium-length stout simple setae near midlength; dactlyus subcylindrical, tapering distally, nearly twice as long as propodus, flexor margin proximally with short fringe of medium-length stout simple setae extending about half dactylus length, tip bearing dense tuft of long stout simple setae. Exopod sublanceolate, nearly linear, slightly tapering distally, internal surface with mesial margin produced forming subtriangular projection in distal third, projection fringed with several short to medium length simple setae, external surface mesial margin subtly crenulate, lateral margin with sparse fringe of very short simple setae in proximal one-half, internal surface with short irregular row of short to medium-length setae near mesial margin in proximal one-half; flagellum recurved, multiarticulate distally, bearing numerous long, simple setae.

Chelipeds (first pereiopods) (Figs. 1B-E; 3A-D) moderately unequal, sparsely setose, dense granules covering superior and extensor surfaces often forming ridges or rugosities on superior surface of carpus and propodus, especially on major chela; merus flexor surface smooth to weakly granulate, proximo-inferior margin typically fringed with short plumose setae, extensor surface densely granulate, distal margin beaded; carpus densely granulate, distinct distal tooth on flexor side of superior surface, occasionally appearing as cluster of enlarged tubercules, superior and superolateral surfaces often with weak rugosities formed by dense aggregations of granules, with few sparse simple setae, superodistal margin often with distinct fringe of plumose setae; propodus superior and superoextensor surfaces densely granulate with few sparse simple setae, superior surface often weakly rugose, with, distinct longitudinal groove, flexor surface of palm smooth or microscopically punctate; fixed finger of major chelae short, stout, smooth on both flexor and extensor surface, extensor surface often with shallow groove, inferior margin weakly sinuous, tip distinctly curved upwards, opposable margin bearing two to three prominent teeth, often with several smaller teeth between, teeth occasionally worn to low rounded lobes; fixed finger of minor chela noticeably longer and more slender than that of major, opposable margin forming slender cutting edge, often with several small teeth proximally, occasionally worn to appear like two distinct platforms or steps; dactylus of major chela curved, slightly longer than fixed finger, superior surface irregularly granulate, granulations strongest proximally, shallow, longitudinal groove on external side of superior midline, groove widest and deepest proximally, several medium length simple setae on proximal half, external surface with several short simple setae near cutting edge on distal half, cutting edge with small patch of very short thin simple setae proximally, hidden when gape closed, cutting edge with single large molariform tooth proximally, followed immediately by a single sharp, triangular tooth, remainder of cutting edge with three to four subtriangular teeth, teeth decreasing in size distally, tip strongly curved downwards, forming coniform tooth; dactylus of minor chela curved, longer than fixed finger, dorsal surface smooth or nearly so, not densely granulate as in major chela, with shallow narrow groove on external side of superior midline, groove much shallower and narrower than on the major chela, single, simple setae near base of groove, cutting edge dentition much weaker than in major chela, with three to four small, irregular, subtriangular tooth in distal two-thirds, tip strongly curved downwards to form strong, sharp, coniform tooth.

Ambulatory pereiopods two through five (Fig. 3E-H) generally similar in form, third pereiopod largest, fifth pereio-

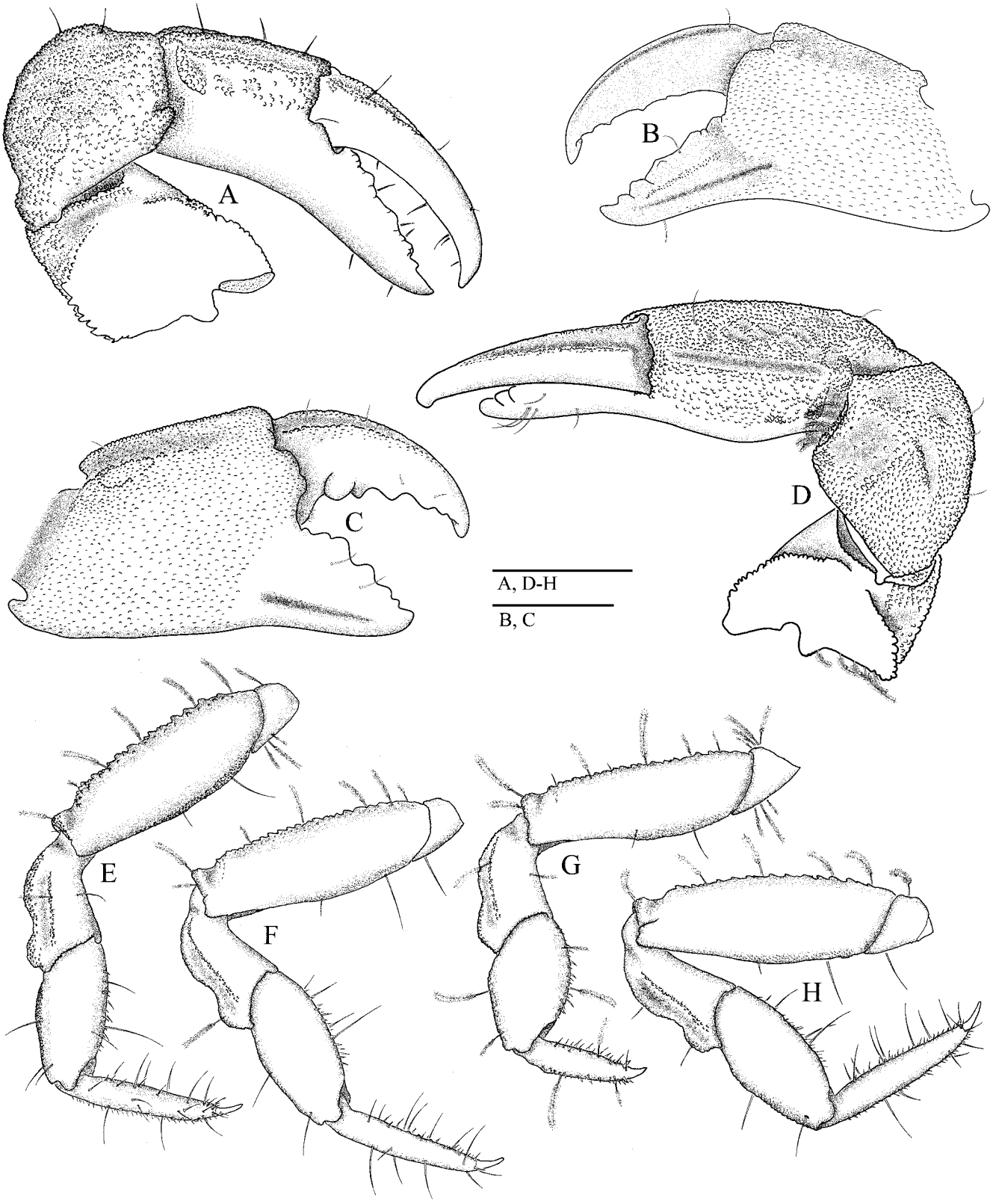

Fig. 3. *Milnepanopeus lobipes* n. comb. A-H = male (ULLZ 8117), NNW Gulf of Mexico, Ewing Bank, off Louisiana, 4.5 mm CW, 3.3 mm CL. A, left (minor) cheliped, superior surface; B, left (minor) chela, extensor surface; C, right (major) chela, extensor surface; D, right (major) cheliped, superior surface; E, second pereiopod, posterior surface; F, third pereiopod, posterior surface; G, fourth pereiopod, posterior surface; H, fifth pereiopod, posterior surface. Scales = 1 mm.

pod smallest; ischium with extensor margin approximately one-half length of flexor margin, extensor margin usually bearing one to three medium to long densely plumose setae, flexor margin with one to three setae, plumose or simple; merus length slightly less than three times width at widest point, extensor margin bearing multiple small teeth or acute granules along with four or five long densely-plumose setae, excavate distally by smooth transverse depression or groove, margin terminating beyond groove as swollen minutely granulate distal lobe bearing several plumose setae, flexor margin granulate in proximal three-fourths with several simple setae, longest proximal; carpus strongly bent in flexor plane at near right angle, extensor margin densely granulate, strongly sinuous, broad marginal depression or sulcus giving the appearance of two large lobes, broadest lobe proximal, narrower more erect lobe distal, posterior surface with single raised longitudinal ridge of raised granules parallel to extensor margin, creating elongate sulcus between ridge and extensor margin; propodus extensor margin granulate with one to three plumose or simple setae, granules continued onto posterior surface above midline, flexor margin with fringe of mixed short stout setae and long thin setae; dactylar-propodal locking mechanism not developed; dactylus subcylindrial, tapering distally, flexor and extensor margins with short dense pubescence intermixed with long simple setae, corneous tip falciform.

Sternum of male (Fig. 4A-B) narrow, anteriorly projected, length from apex to suture of fourth and fifth sternites (at the edge of the pleon) 0.65-0.68 sternal width at anterior-most point of fifth sternite; fourth sternite midline visible from just anterior to sternal groove to suture with fifth sternite; suture between sixth and seventh sternites uncalcified, membranous-region widest near outer angle; fourth through sixth episternites acutely angled posteriorly; seventh episternite broad, round, margin scalloped; eighth sternite visible between lateral margin of flexed second abdominal somite and fifth pereiopod condyle; midline visible on seventh and eighth sternites; large anteriorly projecting uncalcified region mesially at suture of sixth and seventh sternites; large, star-shaped, weakly calcified area at union of fourth through sixth sternites; press-button on anterior-most reaches of fifth sternite.

Pleon of male (Figs. 1F, 4C) with third through fifth somites fused; first somite lateral margins rounded, widest at articulation with carapace, narrowest at articulation with second somite; second somite lateral margins forming a sharp angle proximally, slightly wider than first somite at their articulation, distally narrowing sharply; third somite widest, slightly wider than first somite at widest point; fused third through fifth somites narrowing distally, width at articulation with sixth somite half or less that at articulation with second somite, sutures between fused somites evident only as slight indentations on lateral margins; sixth somite lateral margins nearly parallel, swelling slightly near articulation with telson to accept press-button internally; telson terminally rounded, as broad as widest point of sixth somite. Pleon of female (Fig. 4D) with first somite rounded, narrowing distally, widest at articulation with carapace, narrowest at articulation with second somite; second somite narrowest at articulation with first somite, slightly expanded distally; third somite widest, lateral margins rounded, disto-lateral corners near right angles; fourth through sixth somites each tapering to articulation with the next, narrowest point at the articulation between sixth somite and telson; telson subtriangularly rounded.

Male first gonopod (first pleopod) (Figs. 1G-I; 4F-H) long, reaching well beyond suture between sternites four and five, not reaching beyond sternal groove; terminal apparatus of complex, modified-panopeid, trifid arrangement, including two sub-apical microspinulous spines, posterolaterally projected spine typically longer, sternomesially directed spine deflected somewhat distally; tract terminating within microspinulous, cup-like apparatus of apex that forms hood-like process over-reaching terminus. Male second gonopod (second pleopod) (Fig. 4E) less than one-third length of first gonopod; basis subreniform, proximally truncate to accept insertion of coxa; lateral margin commonly with several stout simple setae; distal margin with several long plumose setae; endopod slender, upcurved, inserted on mesial margin of basis, apex cuspidate.

Color.—Color in life highly variable, carapace commonly off-white to light brown or rust, marked dorsally with flecks, spots, or broad patterns of orange to brown, pigment occasionally forming broad irregular median bar centered on symmetrical pattern of blotches and reticulations, sometimes very wide and dominating most of dorsum (especially in young); chelipeds of similar color and pattern to carapace and ambulatory pereiopods or of contrasting lighter or darker overall pigmentation, fingers light to dark brown, color of fixed finger extended proximally well onto distal part of palm in mature males; pigmentation of ambulatory pereiopods similar to that of carapace or darker, commonly appearing darker due to broad, slightly darker, diffuse or weakly reticulated ill-defined bands on distal three articles, merus commonly darkened slightly by broad, diffuse or weakly reticulated band over most of length, usually with lighter narrow band distally; third maxilliped ischium commonly bearing striking slightly oblong spot of scarlet red pigment on proximolateral corner of internal surface in either sex, fading quickly after preservation.

Habitat.—Abundant on offshore reefs and banks in hard substrate interstices and among sponges, bryozoans, and encrusting algae of epifaunal fouling communities; also in or under rubble and shell debris of low relief on varied continental shelf bottoms. Confirmed depth records range from 23-68 m, though also reported simply from "shallow water" (Rathbun, 1930).

Distribution.—Bahamas Banks through Florida Straits (Rathbun, 1930); southeastern, northeastern, and northwestern Gulf of Mexico (Felder et al., 2009, present study).

Remarks.—In regard to variations in adult morphology, representatives of *M. lobipes* display variation in the granulation of the carapace (Figs. 1A, 2A) and chelipeds (Figs. 1B-E; 3A-D), with smaller-bodied specimens typically being more profoundly granulate than larger specimens. Although larger specimens usually maintain at least some granulation laterally on the carapace at the base of the anterolateral teeth (Figs. 1A, 2A) and dorsally on the chelae (Figs. 1B, D; 3A, D), large specimens occasionally will be almost smooth

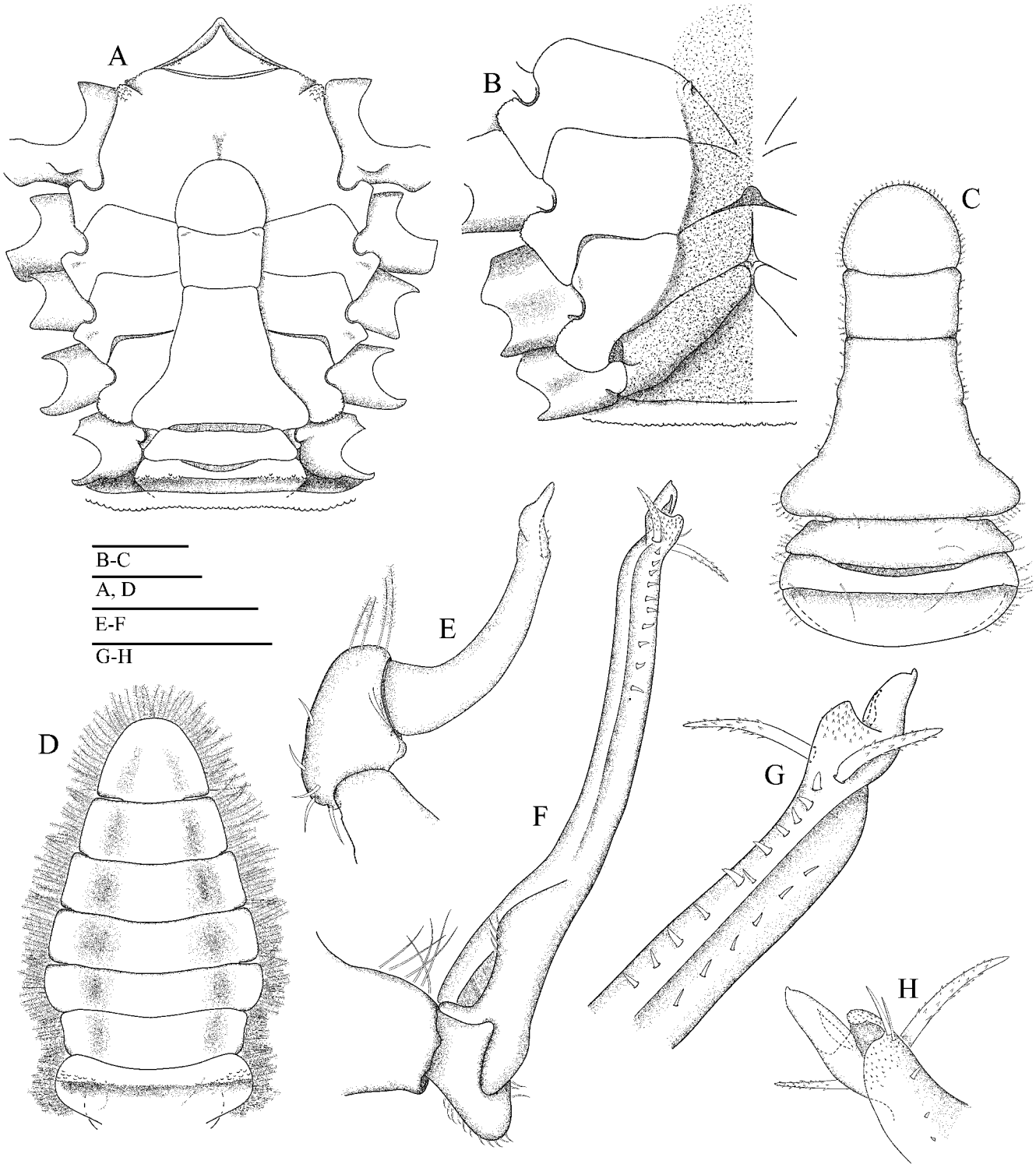

Fig. 4. *Milnepanopeus lobipes* n. comb. A-B = male (ULLZ 8213), NNE Gulf of Mexico, Sackett Bank, off Louisiana, 5.4 mm CW, 3.9 mm CL; C, E-H = male (ULLZ 8117), NNW Gulf of Mexico, Ewing Bank, off Louisiana, 4.5 mm CW, 3.3 mm CL; D = female (ULLZ 8213), NNE Gulf of Mexico, Sackett Bank, off Louisiana, 3.9 mm CW, 2.9 mm CL. A, sternum overlain by flexed pleon, ventral surface; B, posterior somites of sternum, pleon removed, ventral surface; C, male pleon, external surface; D, female pleon, external surface; E, left second gonopod, pleonal surface; F, left first gonopod, sternal surface; G, distal one-third of right first gonopod, sternomesial surface; H, apex of right first gonopod, posterolateral surface. Scales A, D = 1 mm; B-C, F = 0.5 mm; E, G-H = 0.2 mm.

and bear only a few scattered granules. In addition, dentition on the dactylus of the chelipeds (Figs. 1C, E; 3B-C) varies considerably, with larger, well-worn specimens frequently having lost nearly all dentition on the cutting-edge.

The overall morphology of the male first gonopod (Figs. 1G-I; 4F-H) is generally well conserved, however the length of the lateral spines and the acute process on the cuspidate apex vary slightly. In particular, the few specimens available from the Bahamas have noticeably longer lateral spines than the type-specimen or other materials from the Gulf of Mexico. While the acute process on the apex of the gonopod is generally nothing more than a reduced knob, it can occasionally be noticeably elongate. In addition, the sternomesially directed spine is often deflected distally, in an anteriorly direction, to varied degrees. Despite this variation, all of the specimens examined display the same general gonopod morphology with the distinct sub-distal, microspinulous spines and microspinulous cup-shaped process, along with a distinct apical cuspidate hood.

Discussion

Phylogenetic Analysis

While the molecular phylogenetic analyses of Panopeidae by Thoma et al. (2009) showed that *M. lobipes* (as *Hexapanopeus lobipes*) was not a member of the genus *Hexapanopeus* s.s., they did not reveal conclusively to which taxon *M. lobipes* was most closely related. *Milnepanopeus lobipes* was recovered as both the sister-taxon to *Panopeus americanus* Saussure, 1857 (16S rDNA) and sister-taxon to *Panopeus* s.s. H. Milne Edwards, 1834 (12S rDNA); however, neither arrangement had strong support from either bootstrap analyses or posterior probabilities. Furthermore, no representatives of the genus *Lophopanopeus* were included in their analyses making it impossible to clarify what, if any, relationship exists between *Milnepanopeus* and *Lophopanopeus*.

Despite the inclusion of additional taxa, including species of *Lophopanopeus*, a more recent phylogeny of the group by Thoma et al. (in preparation) does little to clarify the identity of the closest living relative of *M. lobipes*. However, the relationship between *M. lobipes* and the member of the genus *Lophopanopeus* proposed by Rathbun (1898) and later by Ng et al. (2008), is not supported, as *Lophopanopeus bellus* (Stimpson, 1860), the type species of the genus, showed little affinity to *M. lobipes* in this most recent molecular phylogenetic analysis (Thoma et al., in prep.). Thus, the affinities remain ambiguous, but at the very least, no molecular phylogeny has indicated *M. lobipes* to be a member of the *Hexapanopeus*, *Lophopanopeus*, or any other known panopeid genus.

Systematic Affinities of *Milnepanopeus*

Morphologically, *M. lobipes* is grossly similar to a number of small-bodied panopeid genera including representatives of *Glyptoplax* Smith, 1870 and *Acantholobulus* Felder and Martin, 2003. *Milnepanopeus* n. gen. can be distinguished from these and all other panopeid genera by the unique morphology of the first gonopod and its strongly bilobate extensor margin on the carpus of the ambulatory pereiopods. In the male first gonopod, two distinct subterminal, microspinulous spines and the terminal, microspinulous cup-shaped process, with its distal cuspidate process, appear to be unique to *Milnepanopeus* n. gen., with only superficial resemblance only to the arrangement in *Glyptoplax*. In *Milnepanopeus*, the extensor margin of the carpus of the ambulatory pereiopods is distinctly bilobate rather than being gently arched, nearly straight, or broadly and shallowly excavate as in other panopeid genera with similar distributional ranges. While a distal or terminal lobe is variably developed on this margin in those species of *Hexapanopeus*, *Glyptoplax*, and *Micropanope* Stimpson, 1871, in which the margin itself is shallowly concave, and the appearance of marginal bilobation can be enhanced by a weak transverse band of dark pigmentation at midlength, the sinuosity of the margin and strength of the lobes is never as strong.

Milnepanopeus can be further distinguished from *Hexapanopeus* s.s. by the morphology of the carapace and how far the sternal groove of the male extends anteriorly. In *Milnepanopeus*, the first and second anterolateral teeth of the carapace are indistinguishably fused while in *Hexapanopeus* the first and second teeth are each still evident. Furthermore, in *Milnepanopeus*, the sternal groove of the male extends to well beyond the condyles of the first pereiopods while in *Hexapanopeus*, the sternal groove, at most, barely reaches the posterior margin of the condyle of the first pereiopod.

Acantholobulus can be separated from *Milnepanopeus* not only by the distinct morphology of the gonopod and the extensor margin of ambulatory pereiopod carpus in *Milnepanopeus*, but also by the morphology of the carapace and sternal groove of the male. In *Acantholobulus bermudensis* (Benedict and Rathbun, 1891), the type species of the genus, the first and second anterolateral teeth of the carapace are indistinguishably fused as in *Milnepanopeus*, but in *Acantholobulus schmitti* (Rathbun, 1930) and *Acantholobulus caribbaeus* (Stimpson, 1871) the first two anterolateral teeth remain readily visible as they are incompletely fused. In addition, most species of *Acantholobulus* have a male sternal groove that rarely reaches beyond the condyle of the first pereiopod (except in *A. bermudensis*, in which it extends at most, slightly beyond the condyle of the first pereiopod), while in *Milnepanopeus* it extends well beyond the condyle of the first pereiopod.

Although representatives of *Glyptoplax* can be separated from *Milnepanopeus* by the shape of the gonopod and morphology of the carpus of the ambulatory pereiopods, other characters used to separate *Milnepanopeus* from panopeid genera are variable within *Glyptoplax*. For example, in *Glyptoplax smithii* A. Milne-Edwards, 1880, the sternal groove of the male, at most, barely reaches the condyle of the first pereipod, while in specimens of the type-specimens, *Glyptoplax pugnax* Smith, 1870, the sternal groove extends beyond the condyle, especially in larger specimens. In addition, the first and second anterolateral teeth are indistinguishably fused in *G. smithii*, while in *G. pugnax*, the first and second teeth are incompletely fused. Martin and Abele (1986) in their review of panopeid gonopod morphology pointed out several differences between the morphology of *G. pugnax* and *G. smithii*; however, as no recent material of *G. pugnax* has yet become available to us for genetic analysis, it is un-

clear if the level of morphological variation evident between these two species of *Glyptoplax* is significant enough to recognize them as different genera. Regardless, both species can clearly be excluded from *Milnepanopeus* by the distinctive gonopod morphology as well as the complex morphology of the carpus of each ambulatory pereiopod. The gonopod in *Glyptoplax* does superficially resemble that of *Milnepanopeus* and could lead to confusion in separation of small specimens of *M. lobipes* from *G. smithii* in areas of sympatry.

Milnepanopeus lobipes can be separated from *L. bellus*, the type species of *Lophopanopeus*, by differences in the male gonopod, the anterolateral teeth of the carapace, the carpus of the ambulatory pereiopods, and the extent to which the sternal groove extends anteriorly. In *L. bellus* the first and second teeth are indistinguishably fused and form a broad, subquadrate tooth, unlike the large, rounded tooth of *M. lobipes*. In addition, the sternal groove of *L. bellus* extends to the condyle of the first pereiopod but does not extend beyond. Finally, although the carpus of the ambulatory pereiopods on *L. bellus* are among the more similar to those of *M. lobipes*, the lobes on the extensor margin are lower and separated by a much wider sulcus than in the new genus; in this configuration, the distal lobe in *Lophopanopeus* is much more restricted to the distal end of the margin, often overreaching the propodus.

In contrast, *Lophopanopeus leucomanus* (Lockington, 1877) shares little in common with its congeners and is, in some ways, morphologically similar to *M. lobipes*. Perhaps most pronounced are similarities of the carpus of the ambulatory pereiopods, which appear to share the same bilobed extensor margin and similar granulate ridges laterally; but the extensor margins of the propodus of the ambulatory pereiopods of these two species are markedly different. *Milnepanopeus lobipes* has the propodus of the ambulatory pereiopods with the extensor margin gently arched, while in *L. leucomanus*, the extensor margin has a distinct lobe proximally. Even though the male first gonopods of these two species are clearly different (see Menzies, 1948, pl. 2, fig. 9), they do share some similar characteristics, both taxa having a first gonopod with at least one distinct lateral microspinulous spine and a distal microspinulous cup-shaped process. However, the lateral spines of the first gonopod in *M. lobipes* are slenderer, more acutely tipped, and set farther from the apex than that of *L. leucomanus*. In addition, the hood-shaped process of the apex of *L. leucomanus* is much broader and rounder than the narrow to subacute, acute, cuspidate process of *M. lobipes*. Finally, the sculpture of the carapace is much more pronounced in *L. leucomanus* than in *M. lobipes*. Although the inclusion of *L. leucomanus* in *Lophopanopeus* remains questionable, distinct differences in morphology and the absence of molecular phylogenetic data on this species lead us to exclude *L. leucomanus* from *Milnepanopeus*.

Previous phylogenetic analyses by Thoma et al. (2009) showed a potential sister relationship between *P. americanus* and *M. lobipes*, but this relationship has not been previously examined on the basis of morphology. These taxa can be distinguished not only by their distinct male gonopods and strongly bilobed extensor margin of the carpus in the four ambulatory pereiopods of *Milnepanopeus* but also by the morphology of the carapace and male pleon. *Panopeus americanus* has the first and second anterolateral teeth separate or at least incompletely fused and the sternal groove in males of *P. americanus* rarely reaches the condyle of the first pereiopod, further separating it from *M. lobipes*. While we defer the eventual generic reassignment of *P. americanus*, we exclude it from *Milnepanopeus*.

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