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Remarks on the sexual dimorphism and taxonomy of *Fabia* Dana, 1851 (Crustacea, Brachyura, Pinnotheridae)

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Abstract

A study of the holotype of *Pinnotheres hemphilli* Rathbun, 1918, revealed it is an early post-hard female, not a male, of *Fabia* Dana, 1851. The morphology of *Pinnotheres emiliai* Melo, 1971 (based on a male specimen) and *Fabia insularis* Melo, 1971 (based on a female specimen) confirm earlier hypothesis that they belong to a sexually dimorphic species that should be known as *F. emiliai* (Melo, 1971). The redescription of the holotype of *Fabia felderi* Gore, 1986, supports its generic assignment and its relationship with *F. emiliai*. The implication of sexual dimorphism and intersexes in the taxonomy of *Fabia* is discussed.

Key words: Crustacea, Pinnotheridae, sexual dimorphism, intersex, taxonomy, *Fabia*

Resumen

El estudio del holotipo de *Pinnotheres hemphilli* Rathbun, 1918, reveló que éste es una hembra posdura, no un macho, perteneciente al género *Fabia* Dana, 1851. Las morfologías de *Pinnotheres emiliai* Melo, 1971 (basada sobre un espécimen macho) y *Fabia insularis* Melo, 1971(basada sobre un espécimen hembra) confirman una hipótesis previa que ellos pertenecen a una especie sexualmente dimórfica que debe ser conocida como *F. emiliai* (Melo, 1971). La redescripción del holotipo de *Fabia felderi* Gore, 1986, apoya su asignación genérica y su relación con *F. emiliai*. Se discuten las implicaciones del dimorfismo sexual e intersexos en la taxonomía de *Fabia*.

Introduction

The pinnotherid genus *Fabia* Dana, 1851, is composed of eight American species of symbiotic crabs: the Atlantic *Fabia byssomiae* (Say, 1818), *F. tellinae* Cobb, 1973, *F. emiliai* (Melo, 1971), and *F. felderi* Gore, 1986, and the Pacific *F. subquadrata* (Dana, 1851), *F. concharum* (Rathbun, 1893), *F. malaguena* (Garth, 1948), and *F. carvachoi* Campos, 1996 (see Campos 1996; Gore 1986; Campos & Manning 1998). Other nominal species, such as *F. sebastianensis* Rodrigues da Costa, 1970, and *F. obtusidentata* Dai, Feng, Song & Chen, 1980 (see Rodrigues da Costa 1970; Dai *et al*. 1980; Campos 1996; Becerra *et al.* 2006; Ng *et al.* 2008) were incorrectly placed in *Fabia* and their systematic status will need to be discussed in a forthcoming publications. Species of *Fabia* are sexually dimorphic and undergo remarkable morphological changes in their life history (Pearse 1966; Campos 1996). These developmental changes and coupled with sexual dimorphism have led to some authors describing the same species twice (see below; Campos 1996). Fenucci (1975) discovered one of these mistakes during a study of sexual pairs of specimens livings symbiotically with the bivalve *Glycimeris longior* (Sowerby, 1832). He found that the morphology of the female concurred with *F. insularis* Melo, 1971, while the male agreed with *Pinnotheres emiliai* Melo, 1971. Fenucci (1975) accordingly synonymized both species and his conclusions were later followed by Campos (1996). Martins & D'Incao (1998), as well as Melo (1998), Boschi *et al.* (1992) and Bezerra *et al.* (2006), subsequently revalidated both Melo's species. This study reassesses the conclusions of Martins & D'Incao (1998). *Fabia felderi* Gore, 1986, and *Pinnotheres hemphilli* (Rathbun, 1918), are re-described and the latter species is

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transferred to *Fabia* Dana, 1851. Abbreviations used include: cl = carapace length, cw = carapace width, P1 = pereopod 1 (cheliped), P2–P5 = pereopods 2–5 (walking legs 1–4), CARC = Colección de Crustacea, Instituto de Biología Marina, Mar de Plata, Argentina, FURG = Universidade do Rio Grande, Brazil, MZUSP = Museu de Zoologia, Universidade São Paulo, Brazil, UABC = Universidad Autónoma de Baja California, USNM = U.S. National Museum of Natural History (Smithsonian Institution).

Systematics

Order Decapoda Latreille, 1802

Infraorder Brachyura Linnaeus, 1758

Section Eubrachyura de Saint Laurent, 1980

Family Pinnotheridae De Haan, 1833

Fabia Dana, 1851

Type species. *Fabia subquadrata* Dana, 1851, by monotypy. Gender feminine.

Diagnosis. *Female* (after Campos 1996). Carapace widening posteriorly, broader than long, with 2 longitudinal sulci arising from upper margin of orbit, extending as far as gastric region. Third maxilliped obliquely placed on buccal cavity; ischium, merus indistinguishably fused; palp slender, 3 articles; propodus subtrapezoidal, subequal to or longer than carpus; dactylus digitiform, sublunated, inserting in angular notch placed in middle third on inner margin of propodus; exopod slender 2-segmented flagellum. Abdomen with 6 somites, telson well separated.

Male (after Campos 1996). Carapace dorsally convex, surface smooth shiny, porcelain-like. Anterolateral carapace margin with fringe of setae extending to hepatic region; longitudinal sulci present, ill-defined or absent in some cases. Third maxilliped similar to female. Abdomen with 2 or more somites fused, demarcation line sometimes visible.

Distribution. Western Atlantic: Florida, USA to Mar de Plata, Argentina; Eastern Pacific; Alaska, U.S.A. to Magdalena Bay, Baja California Sur, Mexico, San Felipe, Baja California (Gulf of California) and Málaga, Colombia (Campos 1996, Campos & Manning 1998).

Hosts (Campos 1996)**.** Mollusca-Bivalva: Arcidae (*Anadara* Gray, 1847); Carditidae (*Cyclocardia* Conrad, 1867), Donacidae (*Donax* Linnaeus, 1758), Glycimeridae (*Panopea* Ménard, 1807), Hiatellidae (*Hiatella* Bosc, 1801), Myidae (*Crypotomya* Conrad, 1849); Mytilidae (*Modiolus* Lamark, 1799, *Mytilus* Linnaeus, 1758); Phodalidae (*Barnea* Risso, 1826, *Parapholas* Conrad, 1848); Semelidae (*Semele* Schumacher, 1817) Tellinidae (*Tellina* Linnaeus, 1758); Veneridae (*Leukoma Römer, 1857, Tapes* Megerle von Mühlfeld, 1811, *Tivela* Link, 1807).

Sexual dimorphism of species of *Fabia* Dana, 1851. The species of *Fabia* are sexually dimorphic and both sexes are remarkably different in shape and size. Adult males are small (5 mm or less), with a hard, convex and porcelain-like carapace with the antero-lateral margin fringed with setae that extend to the hepatic region, and abdomen with two or more abdominal somites fused, although the suture line is sometimes observed between two fused somites (Figs. 4A, B, E; 5A, C). The most significant difference between the subadult male (pre-hard stage) and the adult males (hard stage) is the absence, in the former phase, of swimming setae on the meri, carpi and propodi of P3–P4, which are long and plumose in the adult phase. The female, like males, undergo a pre-hard and hard stage, but moult through several additional post-hard stages. The external morphology of both sexes is almost identical in the pre-hard and hard stages. Females with a masculine appearance can only be separated from males by the absence of gonopods and the presence of gonopores on thoracic sternite five. Females undergo several key morphological changes during the post-hard stages: the carapace become soft, fragile, with two dorsal sulci on the carapace and absence of traces of setae on its anterolateral margin, the abdomen gradually widens until it almost cover the entire sternal surface of the cephalothorax, and the P2–P5 became slender and feeble, losing the long and plumose swimming setae on P3–P4 (Fig 1; 2A; 3A, B). The P3 of adult females are asymmetrical in length and

shape, while male and pre-hard and hard female always have symmetrical P2–P5. Pearse (1966) provided a detailed description of the stages of development of *F. subquadrata* and detailed remarks of its life history and ontogeny.

FIGURE 1. *Fabia carvachoi* Campos, 1996, from San Felipe, Baja California, Mexico, UABC uncatalogued, A, live coloration of adult female in dorsal view. Carapace width = 11 mm.

Fabia hemphilli (Rathbun, 1918) new combination

(Figs. 2A–D)

Pinnotheres hemphilli Rathbun, 1918: 64–65, 99–100, pl. 23, figs. 1, 2.—Archer 1947: 12 (popular account).—Schmitt *et al.* 1973: 48 (list); Powers 1977:123 (listed).—Abele & Kim 1986: 65, 685, 703 (unnumbered figures a–b).— Ng *et al.* 2008: 249 (list).

Material examined. 1♀ holotype USNM 6420 (post-hard stage, probably II), Cedar Keys, Florida; between tides; "seems rare", cl = 2.3 mm, cw = 3 mm.

Distribution. Known only from the type-locality, Cedar Keys, Florida, U.S.A.

Redescription (modified from Rathbun 1918: 99)**.** Caparace suboctagonal, thin, transparent, depressed, wrinkled; with 2 ill-defined sulci arising posterior to orbits reaching gastric region; eyes dorsally visible; front subrectangular; posterior margin twice as long as anterior margin, mid-lateral margin subparallel to median line, as long as postlateral margins, anterolateral margins (to angles of front) longest, biconvex.

Third maxilliped short, wide *in situ*; partly overlapped by anterior portion of thoracic sternum; outer margin of ischium-merus broadly arcuate; palpus with first 2 joints short, broad, carpus slightly shorter than sub-trapezoidal propodus, dactylus digitiform, small, inserted in notch near middle of ventral margin of propodus.

P1 robust, tuft of setae at distal inner angle of merus, manus nearly as wide as superior length, slightly increasing distally in width , upper margin almost straight, lower convex, distal width greater than width across base of fingers; fingers basally broad, regularly tapering, denticulate on prehensile edges, tooth at base of right dactylus.

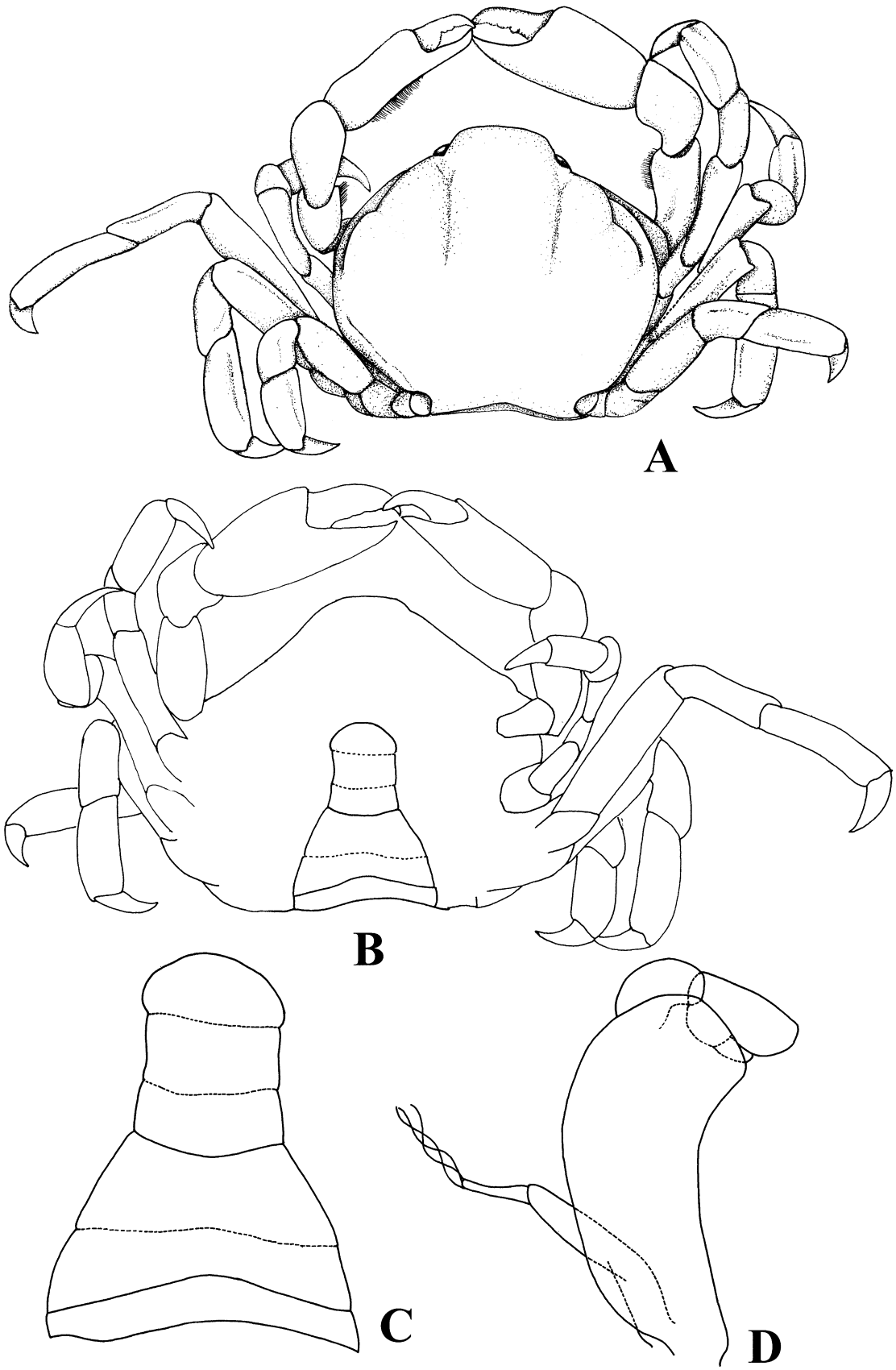

FIGURE 2. *Fabia hemphilli* (Rathbun, 1918) **new combination**, Cedar Keys, Florida, U.S.A., holotype (USNM 6420), caparace length 2.3 mm, width = 3 mm. A, dorsal view; B. ventral view, sterna details omitted; C, abdomen; D, third maxilliped, outer view.

P2–P5 slender, feeble, relative length P3 > P4 > P2 > P5, P2 subchelate, propodus widest medially slightly tapering distally, with fringe of setae on distal half of ventral margin; P3 substantially longer than the other walking legs, asymmetrical, left longer than right, all propodi dorsally convex, those propodi of P4–P5 slightly increasing in height to distal end; dactyli of P2, P4–P5 subequal in form, very stout at base, subconical, with short curved tip, those of P3 longer, less curved.

Thoracic sternum with a sharp obliquely transverse crest running inward from base of first, second, third pair.

Abdomen widest at somite 3, narrowing to somite 6 widening slightly at semicircular telson, suture between somites 3, 4 and 5, 6; telson faintly demarcated.

Remarks. The holotype of *Fabia hemphilli* is an atypical specimen since it possesses some masculine and feminine morphological features attributable to both sexes within the genus *Fabia*. The presence of two sulci, although ill-defined, on the carapace that arise behind the orbits and reach to the gastric region, the asymmetrical P3, and the anterolateral margins not protruding beyond the frontal margin are clearly feminine features, whereas the rectangular front, the dorsally visible eyes and the narrow abdomen with several somites giving the appearance of being fused, are masculine features. As previously pointed out, hard males and females are almost identical, and can only be separated by the presence of gonopods. After the hard stage, females undergo several post-hard stages that are characterized by the phased appearance of feminine features on the carapace and P2-P5 and by the gradual lateral enlargement of the abdominal somites (see Pearse 1966). The morphology of the very small (cw = 3 mm) holotype of *F. hemphilli* allow the conclusion that it is not a male as identified by Rathbun (1918), but an early post-hard female. Its morphology, including the narrow abdomen, compares well with the post-hard female stage II of *Fabia subquadrata* (Pearse, 1966). The morphology of this sub-adult female, especially the form of the chelipeds and P2-P5, actually agrees very well with *F. byssomiae* Say, 1818 (Campos 1996: fig 1), a species known from Tampa Bay, Florida, U. S.A., a locality close to Cedar Key, Florida, the type locality of *F. hemphilli*. Examination of additional specimens, including males and females in pre-hard, hard stage and females in post-hard stage, will be necessary to confirm if *F. hemphilli* is indeed an early post-hard stage and therefore a junior synonym of *F. byssomiae*. Both are regarded here as separate species for the time being. The masculine shape of the abdomen and third maxilliped of *F. hemphilli* do not match those of the known males of the Atlantic congeners (see Campos 1996). Instead, the third maxilliped and the abdomen of *F. hemphilli* actually resemble those of the male holotype of *F. malaguena* (Garth, 1948), a species that inhabits the Pacific coast of Colombia (Campos & Manning 1998).

Fabia emiliai **(Melo, 1971)**

(Figs. 3A–E, 4A–E)

Pinnotheres emiliai Melo, 1971: 198–200, fig. 1, pl. 1.—Fenucci 1975: 173, 175.—Martins & D'Incao 1998: 11, figs. 6, 14E.—Becerra *et al.* 2006: 1043.—Boschi 2008: unnumbered.—Ng *et al.* 2008: 249.

Fabia insularis Melo, 1971: 200–202, figs. 2, 3. pl. 2.—Fenucci 1975, 173–175.—Martins & D'Incao 1998: 6–8: figs. 3, 4.—Becerra *et al.* 2006: 1043.—Boschi 2008: unnumbered.—Ng *et al.* 2008: 249.

Fabia emiliai—Fenucci 1975: 173–175, pl. 2 A, pl. 3 F, M, P.—Boschi 1979: 139 (list); 2000: 82.—Campos 1996: 1162, 1168.—Spivak 1997: 79.—Melo 1996: 438; 1998: 496.

Material examined. Observations were based on photographs of the holotype of *Pinnotheres emiliai* (MZUSP 3480) and *Fabia insularis (*MZUSP 3688) provided by Gustavo Augusto S. de Melo and the redescription and illustrations of Fenucci (1975).

Type locality. Baia de Ilha Grande, Rio de Janeiro, Brazil.

Distribution. Western Atlantic, Brazil from Rio de Janeiro to Rio Grande do Sul and Mar del Plata, Argentina (Melo 1971; Fenucci 1975; Martins & D'Incao 1998).

Hosts. *Anadara brasiliana* (Lamark, 1819), *Glycimeris longior* (Sowerby, 1832), *Glycimeris* sp. (Melo 1971; Fenucci 1975; Martins & D'Incao 1998)

Remarks. During the taxonomic revision of the Argentinean pinnotherid crabs, Fenucci (1975) discovered a sexually dimorphic pair of symbiotic crabs inhabiting the mantle cavity of the bivalve *Glycimeris longior* (Sowerby, 1832). His study suggested that the adult hard stage male agreed with the holotype of *Pinnotheres emiliai* Melo, 1971, while the late post-hard stage adult female could be identified with *Fabia insularis* Melo, 1971. Fenucci (1975) accordingly synonymized both species, using the name *P. emiliai* and transferred it to *Fabia*,

creating a new combination, *F. emiliai* (Melo, 1971). Campos (1996) concurred with these changes during his revision of *Fabia*. Martins & D'Incao (1998), however, claimed they had discovered the "true" male of *Fabia insularis* and argued that it was different from *P. emiliai* restoring its original generic status. A comparative analysis between this putative male and those described by Campos (1996), Campos & Manning (1998) and herein, clearly show that the Martins & D'Incao´s (1998) specimen does not agree with the actual morphology of male *Fabia*. In fact, most of the described morphological characters agree with a sub-adult post-hard female of *Fabia* (*sensu* Pearce 1966). The Martins & D'Incao´s specimen (Fig. 3) shares the following features with other *Fabia* females 1) a soft and bare carapace with two sulci that arise from the orbits to the hepatic region, with no traces of setae on the anterolateral margin, (2) slender legs with the second pair asymmetrical, and (3) abdomen with six somites and telson all free. Martins & D'Incao (1998 fig 3-4) had figured what they labeled as a gonopod, but this appendage is so damaged that is difficult, at least on the basis of the original illustration, to recognize it as gonopod, unlike those figured by Campos (1996), Campos & Manning (1998) and herein (Figs 2C, 4E). Even assuming this appendage is a damaged or malformed gonopod, what Martins & D'Incao (1998) reported may only be an intersex individual. Intersex and gynandromorphs are generally uncommon among brachyuran crabs (see Zou & Fingerman 2000) and within the Pinnotheroidea in only four species have been recorded: *Nepinnotheres androgynous* Manning, 1993 (Senegal, Africa), *Nepinnotheres novaezealandiae* Filhol, 1885 (New Zealand), *Alain croisneri* Manning, 1998, and *Alain raymondi* Ahyong and Ng, 2008 (Philippines) (see Manning 1993, 1998; Ahyong & Ng 2008). Martins & D'Incao (1998) erroneously recognized an intersex female crab stage with a partially masculinized individual as the adult male of *Fabia insularis* and incorrectly concluded that this species is distinct from *Pinnotheres emiliai*.

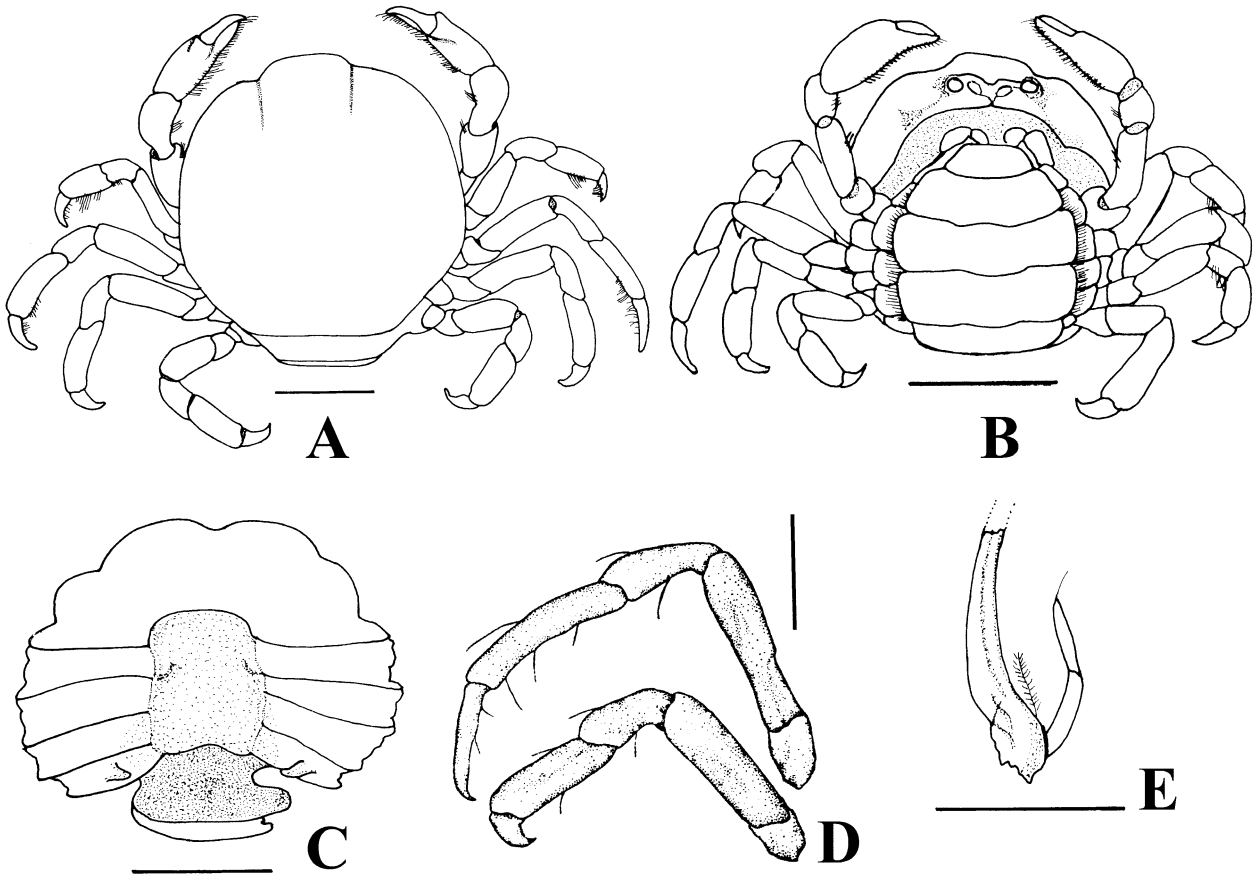

FIGURE 3. *Fabia insularis* Melo, 1971, A–C, E, from Rio Grande do Sul (FURG-1235), D, from Rio de Janeiro, Brazil (MZUSP 3688), sub-adult female; A, dorsal view; B, ventral view; C, ventral view of thoracic sterna; D, P3, longer left and shorter right; E, left gonopod. Scale A–C = 2mm; D = 1.7 mm; E = 1 mm. (A–C, E from Martins & D'Incao, 1998; D, from Melo 1971).

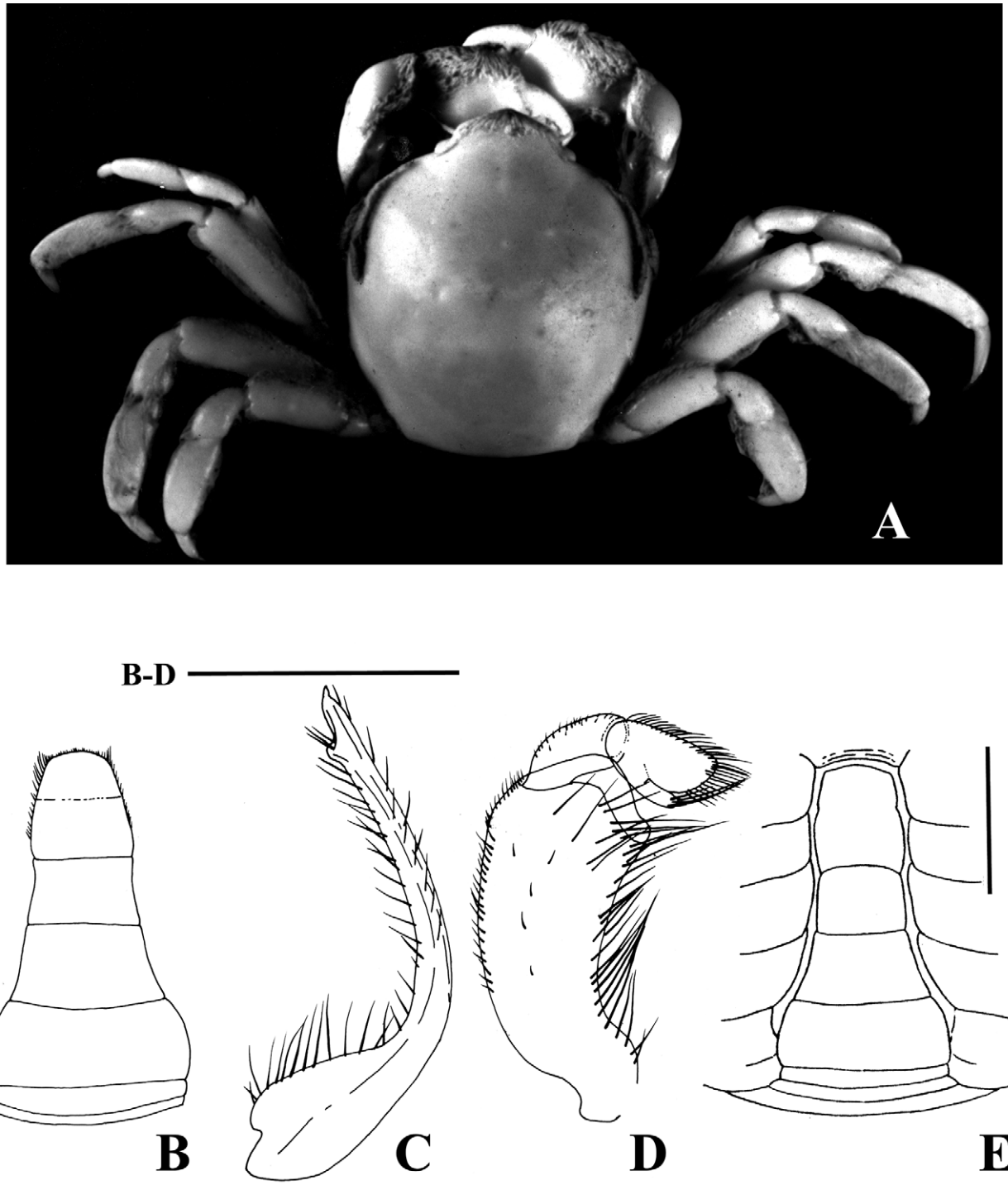

FIGURE 4. A, E, *Pinnotheres emiliai* Melo, 1971, A, E from Rio de Janeiro, Brazil (MZUSP 3480), B–D, from Mar del Plata, Argentina (CARC 1630), A, adult male in dorsal view, caparace width = 4.5 mm; B, Abdomen, dorsal view; C, left gonopod; D, third maxilliped; E, abdomen. A, E, from Melo 1971; B–D, from Fenucci 1975). Scale bar = 1 mm.

Melo (1971) had inadvertently named two species in two genera on the basis of two fully developed adult specimens occurring in different hosts, but in fact belong to one dimorphic species. This unfortunate mistake was corrected by Fenucci (1975) as discussed above. While the intersex female discovered by Martins & D'Incao (1998) is a very interesting finding, it does not refute Fenucci´s (1975) conclusion. Nevertheless, Fenucci´s argument in favor of precedence of *P. emiliai* over *F. insularis* was because the former species appeared published two pages before (p. 198) than the latter (p.200) in Melo´s paper, which was technically incorrect. The International Code of Zoological Nomenclature (ICZN, 1999, article 24.2.2) indicates that if two species are published in a same

paper both are nomenclaturally equal and there are no page priority. For this reason I am invoking the first reviewer rule (ICZN, 1999, article 24.2.1) of the Code in order to maintain the Fenucci´s selection of precedence in favor of *P. emiliai*.

Other American species that has been erroneously named based on different stages of development include, *Juxtafabia muliniarum* (Rathbun, 1918) [= *Pinnotheres jamesi* Rathbun, 1923 (male, hard stage), *Pinnotheres muliniarum* Rathbun, 1918 (male pre-hard stage), *Pinnotheres reticulatus* Rathbun, 1918 (female, post-hard stage)], *Tumidotheres margarita* (Say, 1818) [= *Pinnotheres margarita* Say, 1918 (adult female, post-hard stage), *Pinnotheres pubescens* (Holmes, 1895) (subadult female, post-hard stage] and *Opisthopus transversus* Rathbun, 1893 [= *Pinnotheres nudus* Holmes, 1895 (female, unknown stage)] (see Campos 1989; 1993; Campos & Manning 2000).

Campos (1996) and Ng *et al.* (2008) concluded that females of *Fabia emiliai* and *F. byssomiae* (Florida, USA) are morphologically similar and suggested both might be synonymous. A further comparative analysis between the descriptions and figures provided by Campos (1996), Melo (1971) and Fenucci (1975) for these species now show that they should be regarded as separate taxa. The carapace in *F. byssomiae* is sub-circular and the abdomen posteriorly curves gently to somites 3 and 4 before it folds towards the thoracic sternum, whereas in *F. emiliai* the carapace is sub-quadrate and the abdomen posteriorly extends to somite 3 and 4 before it folds towards the thoracic sternum. More specimens will be needed to ascertain if there are more differences; but they should be regarded as distinct species for the time being.

Fabia felderi Gore, 1986

(Figs. 5A–E)

Fabia felderi Gore, 1986: 143–148, figs. 1A–G.—Campos 1996: 1159 (discussion).—Ng *et al.* 2008: 249 (list).

Material examined. 1♂, holotype, USNM 228615, Sebastian Pinnacles, off Sebastian Inlet, Indian River County, 27°50.2'N, 78°58.0'W, Florida. U.S.A., 28 April 1981, Research Submersible *Johnson Sea Link 1*, R/V Johnson cruise 121, dive 1023, 80 m, within *Oculina* rubble.

Distribution. Known only from the type locality, Sebastian Pinnacles, off Sebastian Inlet, Indian River County, 27°50.2'N, 78°58.0'W, Florida, U.S.A

Measurements. Carapace length 2.2 mm, carapace width 1.9 mm, front-orbital width 1.08 mm.

Diagnosis (modified from Gore 1986: 143) Carapace longer than broad, smooth, subpentagonal, front noticeably produced, margin broadly truncate, oblique, with heavy fringe of anteriorly-directed setae extending backwards along anterolateral margin. MXP3 with ischium-merus indistinguishably fused, merus truncated; carpus longer than wide; propodus longer than carpus, subtrapezoidal, outer surface lacking transverse ridge as described and figured in original account, dactylus small, shorter than propodus, digitiform, inserted in angular notch in middle third of ventral margin of propodus, falling short of end of propodus. P2-P5 symmetrical, margins dorsally, ventrally hirsute, surface of merus, carpus, propodus of P3-P4 with additional long swimming setae. Abdomen with somites 2, 3, 6–telson fused, clear suture present between somite 6, telson.

Remarks. Gore (1986) was precise in his generic assignment of *Fabia felderi*, although his description and illustration of the third maxilliped and abdomen of his very small specimen was incorrect. The original description of some characters was for this reason inconsistent with the male diagnosis of *Fabia* provided by Campos (1996) and Campos & Manning (1998), particularly in the supposed structures of the third maxilliped and abdomen. A re-examination of the holotype male confirms that *F. felderi* agrees with our current understanding of *Fabia*. *Fabia felderi* is actually morphologically close to *F. emiliai* and might be the northern counterpart of this South Atlantic species, but differing in the fusion of the abdominal somites and shape of the first gonopods. In *F. felderi*, male abdominal somites 2, 3 and somite 6–telson are fused, instead of only somite 6-telson fused as in *F. emiliai* (Fig. 2B, 4C) and the first gonopods are relatively less curved in *F. felderi* (Fig. 2C, 4E). The female of *F. felderi* is still unknown.

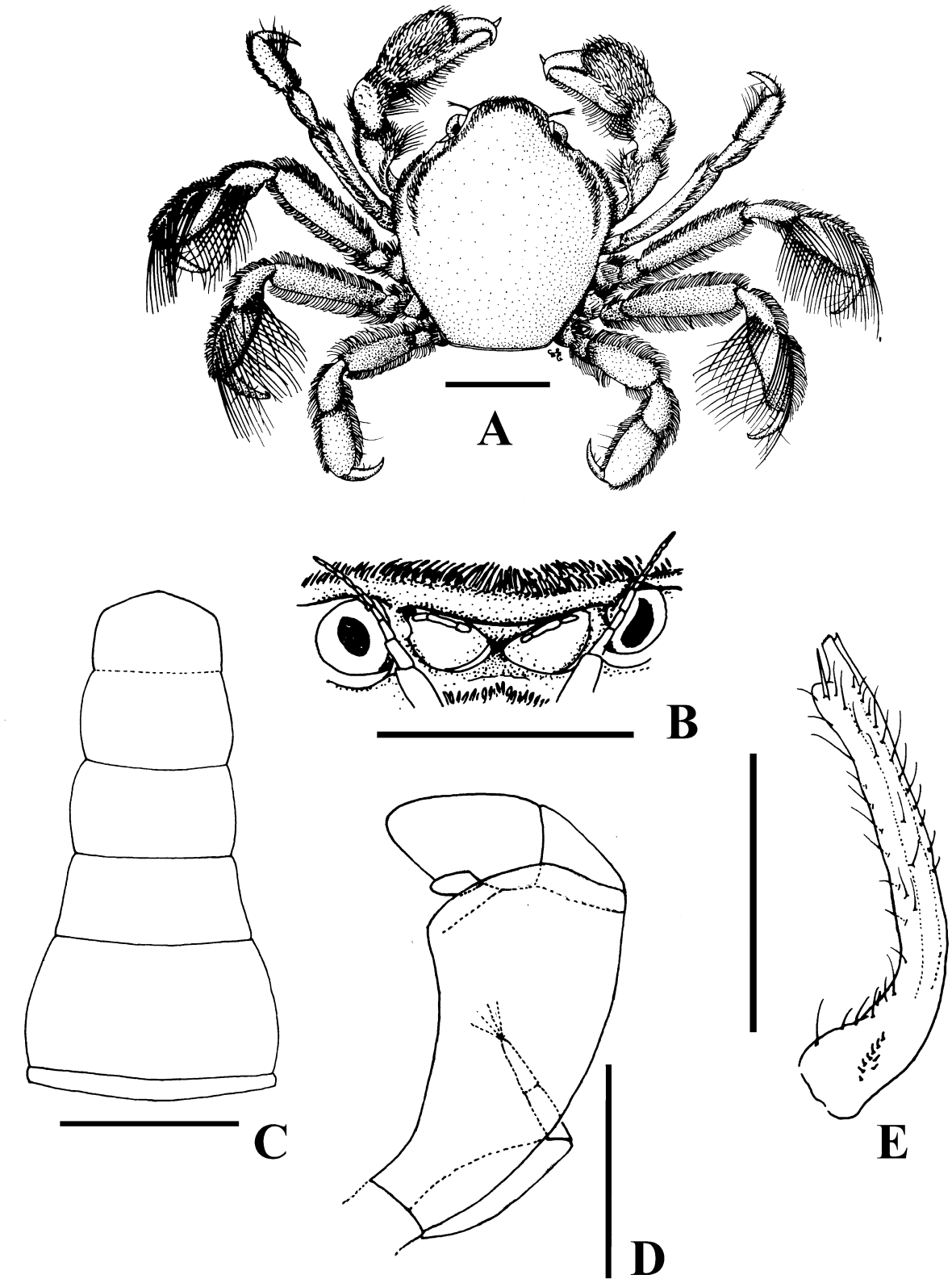

FIGURE 5. *Fabia felderi* Gore, 1986, from Sebastian Pinnacles, Florida. U.S.A holotype, (USNM 228615), adult male. A, dorsal view; B, frontal view; C, abdomen; D, third maxilliped; E, left first gonopod. A, B, E from Gore (1986); scale bars, A = 1 mm, B = 0.5 mm; C–E = 0.25 mm.

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