# The megalopa stage of the hydrothermal vent crab genus *Bythograea* (Crustacea, Decapoda, Bythograeidae)

**Joel W. MARTIN**
Natural History Museum of Los Angeles County,
Research and Collections Branch,
900 Exposition Boulevard, Los Angeles, CA 90007 (USA)
jmartin@nhm.org

**Ana DITTEL**
University of Delaware, Graduate College of Marine Studies,
700 Pilottown Road, Lewes, DE 19958 (USA)

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**ABSTRACT**
The megalopa larva stage of the hydrothermal vent crab genus *Bythograea* Williams, 1980, is described and illustrated based on larval stages attributed to *B. thermydron* Williams, 1980, from vents on the East Pacific Rise. The megalopa of *Bythograea* is a large and generalized developmental stage, with virtually no obvious morphological adaptations that would indicate either an unusual habitat or clues as to the phylogenetic placement of bythograeid crabs within the Brachyura. Aspects of larval development and natural history of the megalopa and postlarval stages of vent crabs are summarized.

**KEY WORDS**
Crustacea,
Decapoda,
Bythograeidae,
hydrothermal vents,
crabs,
megalopa,
morphology,
development.

**RÉSUMÉ**
*Le stade mégalope des crabes hydrothermaux du genre* Bythograea *(Crustacea, Decapoda, Bythograeidae).*
La larve mégalope des crabes des sources hydrothermales du genre *Bythograea* Williams, 1980, est décrite en se basant sur des stades larvaires de *B. thermydron* Williams, 1980, récoltés au voisinage de sources de la dorsale est-pacifique. La mégalope de *Bythograea* est de grande taille et commune ; elle ne présente aucune adaptation morphologique qui indiquerait soit un habitat exceptionnel, soit des indices concernant la place phylogénétique des Bythograeidae parmi les Brachyura. Les aspects du développement larvaire et l'histoire naturelle des mégalopes et des stades postlarvaires des crabes des sources hydrothermales sont résumés.

**MOTS CLÉS**
Crustacea,
Decapoda,
Bythograeidae,
sources hydrothermales,
crabes,
mégalope,
morphologie,
development.

## INTRODUCTION

One of the most exciting carcinological finds of the last century was the discovery of a new family of crabs from hydrothermal vents in the deep sea (Williams 1980). Williams (1980) placed the first described vent crab species in its own genus (*Bythograea*), family (Bythograeidae), and superfamily (Bythograeoidea). Since that time, vent crabs have been discovered at a variety of vents around the world, and there are currently five known genera and approximately 14 species (see Martin & Haney 2005) of bythograeid crabs endemic to hydrothermal vents.

Our knowledge of larval development in vent crabs remains sketchy. The original description by Williams (1980) included observations on the megalopa stage of *Bythograea thermydron* Williams, 1980, and a single zoeal larval stage attributed to that species was described by Van Dover *et al*. (1984). Williams (1980) included characters of the megalopa stage in his diagnosis of the new family, making this one of very few, if not the only, brachyuran family for which the family diagnosis is based in part on megalopal characters. Subsequently, one species of *Bythograea*, *B. intermedia* de Saint Laurent, 1988, was described based only on the megalopa larval stage and on some juveniles of questionable parentage (Saint Laurent 1988; see also Guinot & Hurtado 2003; Martin & Haney 2005), in a paper that also briefly described the megalopa stage of *B. microps* de Saint Laurent, 1984. Yet little is known concerning larval development in the genus, and almost nothing is known about larval morphology. Although the description of the megalopal stage of one shallow water "vent crab" has been published (Jeng *et al*. 2004a), that species is currently classified as a varunid (former grapsid) adapted to life in relatively shallow volcanic systems (Jeng *et al*. 2004b) and not a "true" vent crab (the endemic family Bythograeidae).

To date, it remains unclear how larvae of bythograeid crabs are transported and how new vents are located, and the duration and number of larval stages is unknown. Anecdotal evidence, mostly in the type of visual receptors found in larvae vs. adult, would seem to indicate that the larvae can survive as part of the plankton in mesopelagic waters, in some cases as much as 1000 m above active vent sites (Jinks *et al*. 2002). Megalopa larvae of bythograeids also survive at surface pressures and temperatures, whereas adult crabs do not, supporting the idea that larvae of these crabs might reach upper (mesopelagic) waters (e.g., see Epifanio *et al.* 1999; Jinks *et al*. 2002; Dittel *et al.* 2005). If so, this would be in contrast to the "along-ridge" dispersal at depth that appears responsible for larval transport in some other vent invertebrates (e.g., Marsh *et al*. 2001). Conclusive evidence for the mode of dispersal in vent crabs, in the form of identifiable larvae collected from surface or mesopelagic waters, remains elusive, perhaps in part from the lack of morphological descriptions that would allow for ready identification. Apart from the somewhat brief descriptions of the zoeal stage and the inclusion of some illustrations of the megalopa stage in the papers noted above, we are aware of no morphological descriptions of vent crab larvae.

There are several reasons why a thorough description of a bythograeid megalopal stage is important. First, the description would facilitate field identification of larval and postlarval crabs belonging to this family, allowing observations and deductions about the natural history of these crabs in the field. This is important not only at vent sites but at distances from vents, either on the sea floor or in the water column, as larval transport in these crabs still is poorly understood (as noted above). Second, new species of bythograeid crabs occasionally have been proposed on the basis of megalopal characters alone, and without a thorough knowledge of the morphology of this stage in all species of the family, subsequent work along these lines will be seriously impeded. Third, megalopal stages have been used to deduce or support phylogenetic relationships in several groups of crabs (e.g., see Rice 1981, 1988; Martin *et al.* 1984; Felder *et al*. 1985; Martin 1988), and because we still know so little about the relationships of vent crabs to other brachyuran families, any additional evidence along these lines would be welcomed. Fourth, a more thorough description of the megalopal stage

of vent crabs might reveal sensory structures that aid in locating suitable adult habitat, which is the primary function of this important larval stage (Martin *et al*. 1984; Felder *et al*. 1985; Epifanio *et al*. 1999); such information might in turn shed light on how larvae of vent-associated invertebrates locate vent sites toward the end of the larval phase of their lives.

In this note, we describe the megalopa stage of the vent crab genus *Bythograea* based on collections made at hydrothermal vent sites in the Eastern Pacific.

## MATERIALS AND METHODS

In August of 2003, a remarkable collection (19 vials) of megalopae and juvenile crab stages, consisting of a combination of molts and dead specimens, was sent by AD to JWM. Details for where and how each of these specimens was collected are not available, but in general they were part of ongoing behavioural studies being conducted by C. Epifanio and A. Dittel based on collections of crabs from vents fields of the East Pacific Rise (EPR) (e.g., see Epifanio *et al*. 1999; Jinks *et al*. 2002). The collections included several megalopal stages; two specimens selected for SEM and illustrations were large, with carapace widths (CW), measured across the widest region of the carapace, and lengths (CL), measured from either side of the slight indentation of the "rostrum" to the centre of the posterior margin of the carapace, of 7.5 mm/6.1 mm and of 7.4 mm/6.2 mm, respectively. The specimen used for Figure 1 and for most of the other illustrations was the above-mentioned large megalopa with CW 7.4 and CL 6.2 mm, collected on DSV *Alvin* Dive 3177, East Pacific Rise, 09°46.2'N, 104°16.589'W, 2515 m depth.

Another fine collection of young vent crab specimens was lent to us by Paul Clark (Natural History Museum, London); this collection contained 15 vials of juvenile and megalopal crabs collected on the following cruises, all with IFREMER-CENTOB labels: HOPE 99 dives 1330, 1361, 1362, 1366, 1369, 1373, 1377, 1383; HOT 96 dives 5 (2 vials), 20, 22, 25; HERO 91 dives 06; HERO 92 (no dive number indicated). Megalopal stages in this collection were slightly smaller; two selected megalopal stages measured CW 7.5 mm/CL 5.7 mm and CW 3.2 mm/CL 3.1 mm.

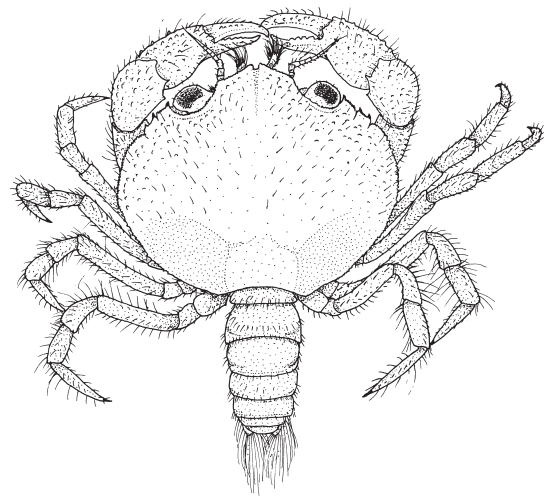

FIG. 1. — Megalopa larval stage of a vent crab (*Bythograea*), entire specimen, dorsal view, based on a relatively large (carapace width 7.4 mm, carapace length 6.2 mm) specimen from the Epifanio and Dittel collection from the East Pacific Rise (*Alvin* Dive 3177). Scale bar: 10 mm.

Finally, we also examined a collection of vent crab specimens collected by Tim Shank (Woods Hole Oceanographic Institution) from DSV *Alvin* dives at the 9°N site on the EPR on 28 May 2002. The seven megalopal stages in this collection ranged from CW/CL 2.5 mm/1.8 mm to 6.8 mm/5.5 mm.

Illustrations, all of which were based on specimens from the Epifanio & Dittel collection, were made using a Wild M5APO dissecting stereoscope with camera lucida. The two specimens selected for SEM use also came from the Epifanio & Dittel collection. These were dried in a stepwise series of ethanol and subsequently transferred to HMDS (hexamethydisilazane; see Nation 1983), mounted on stubs with carbon tape, sputter coated with gold, and observed in a Cambridge 360 on the campus of the University of Southern California. Description follows more or less the suggestions of Clark *et al.* (1998), borrowed in turn largely from Rice (1979) though the latter referred only to zoeal stages.

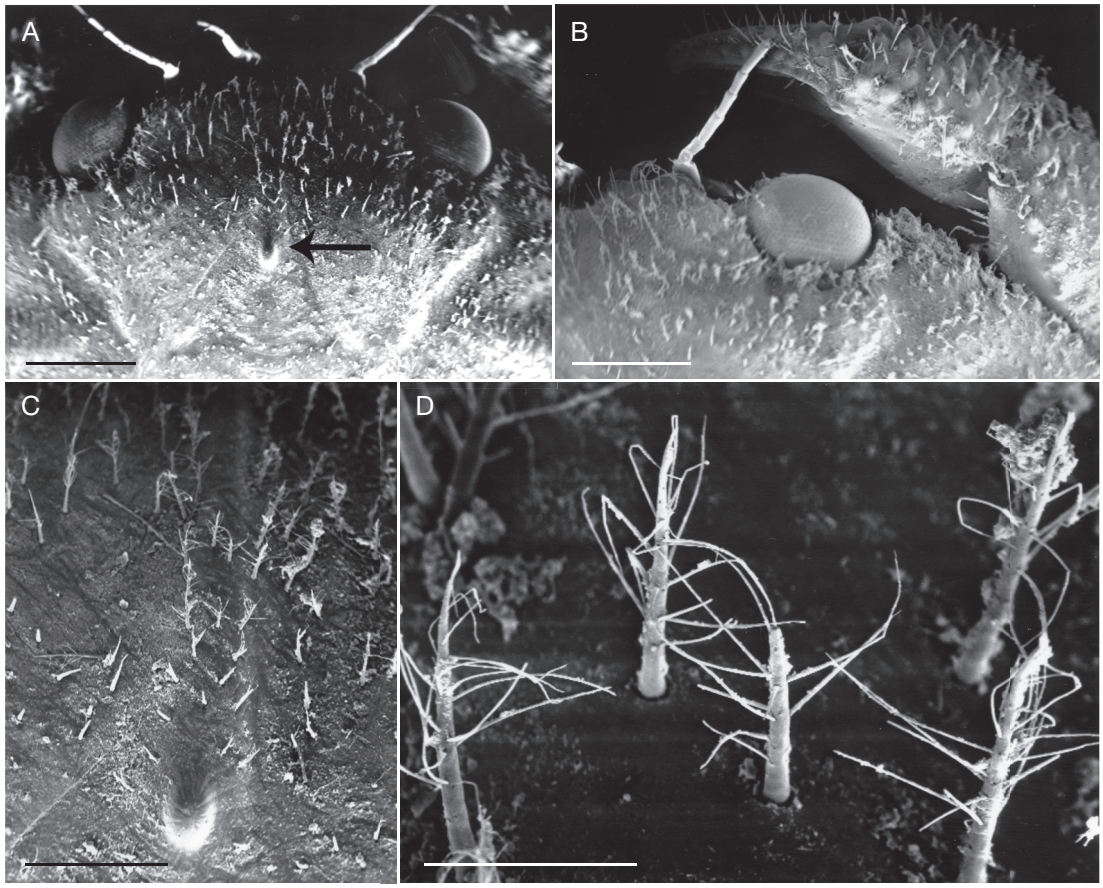


FIG. 2. — Megalopa stage of *Bythograea*, selected SEM photographs of the carapace: **A**, anterior two thirds of carapace showing relative size of eyes, setal covering, and central protrusion (arrow); **B**, dorsal view of right anterolateral region of carapace and right chela; **C**, higher magnification of central carapace protrusion indicated by arrow in A; **D**, higher magnification of pappose setae from anterior dorsal region of carapace. Scale bars: A-C, 0.5 mm; D, 100 µm.

## RESULTS

### "MEGALOPAL" CHARACTERS

As noted by Williams (1980), and in contrast to many other families of brachyuran crabs, there are few characters that differentiate the megalopal stage from the subsequent juvenile crab stages in bythograeid crabs. Our description is restricted to those specimens deemed "true" megalopae, as opposed to similar-sized specimens that appeared to be juveniles. "True" megalopae were recognized by the following characters: 1) abdomen extended (although juveniles may carry the abdomen in a more or less extended state, and some megalopae have a slight ventral bend to their abdomen); 2) well developed pleopods bearing appendices internae; 3) well developed uropods on the sixth abdominal somite; and 4) relatively large eyes as compared to the carapace and especially as compared to later juvenile stage crabs.

### SIZE

CW from 2.5 up to 7.5 mm; CL from 3.8 to 6.2 mm (Fig. 1 is of a specimen that measures CW 7.4 mm, CL 6.2 mm).

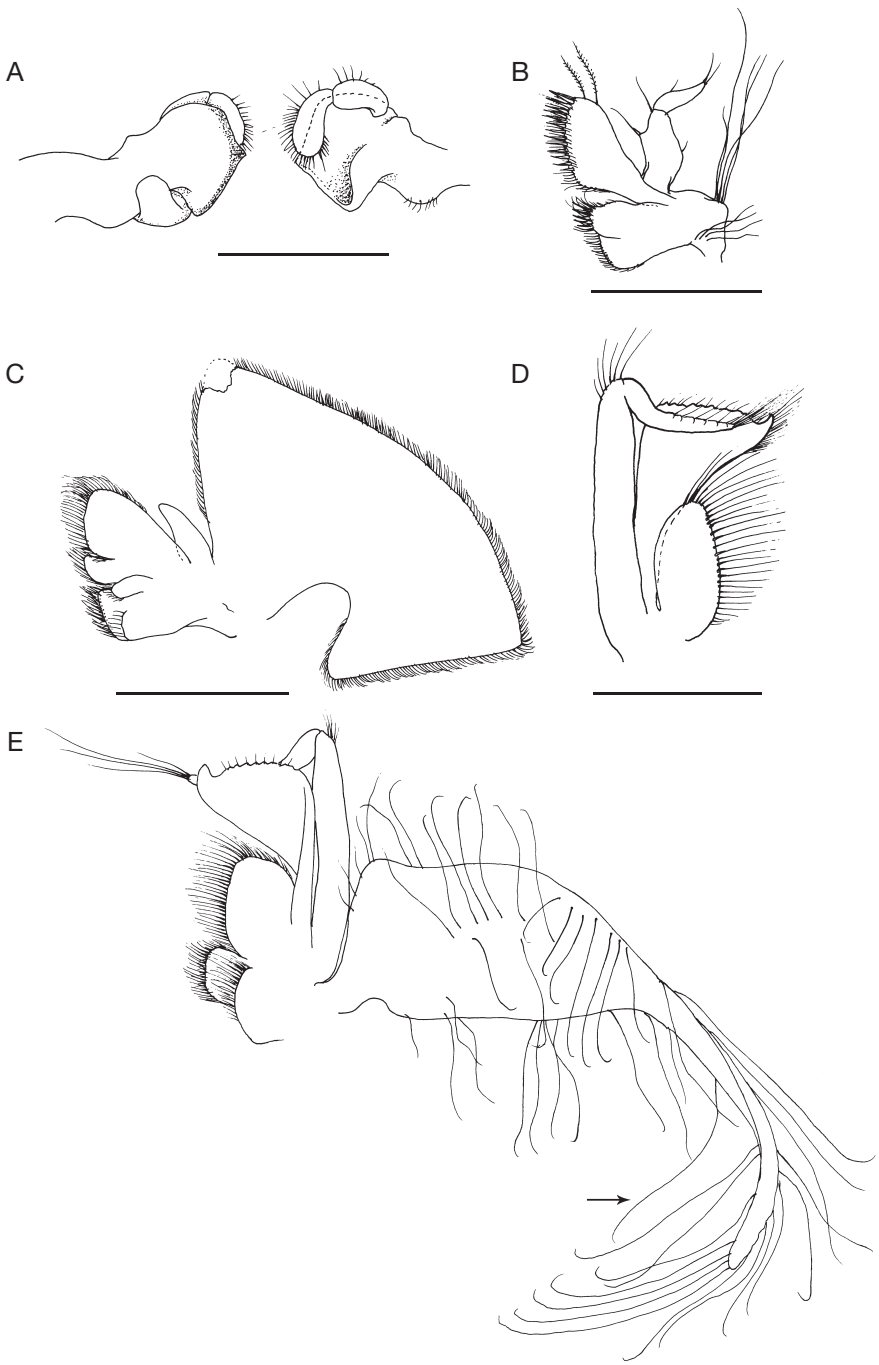


FIG. 3. — Megalopa stage of *Bythograea*, mandibles, maxillae, and first maxilliped: **A**, outer (anterior) view (figure on left) and inner view of right mandible; paragnath shown only in outer view; **B**, first maxilla (maxillule), left side; **C**, second maxilla, left side; **D**, first maxilliped, inner view, left side; **E**, same appendage as D, outer view; arrow denotes serrate cleaning seta shown at higher magnification in Figure 5C and E. Scale bars: A-D, 1 mm; E not to scale.


FIG. 4. — Megalopa stage of *Bythograea*, second and third maxillipeds: **A**, second maxilliped, outer view, left side; **B**, third maxilliped, inner view; **C**, third maxilliped and gill (detached), outer view. Scale bar: A, *c.* 1.5 mm; B, C, 2 mm.

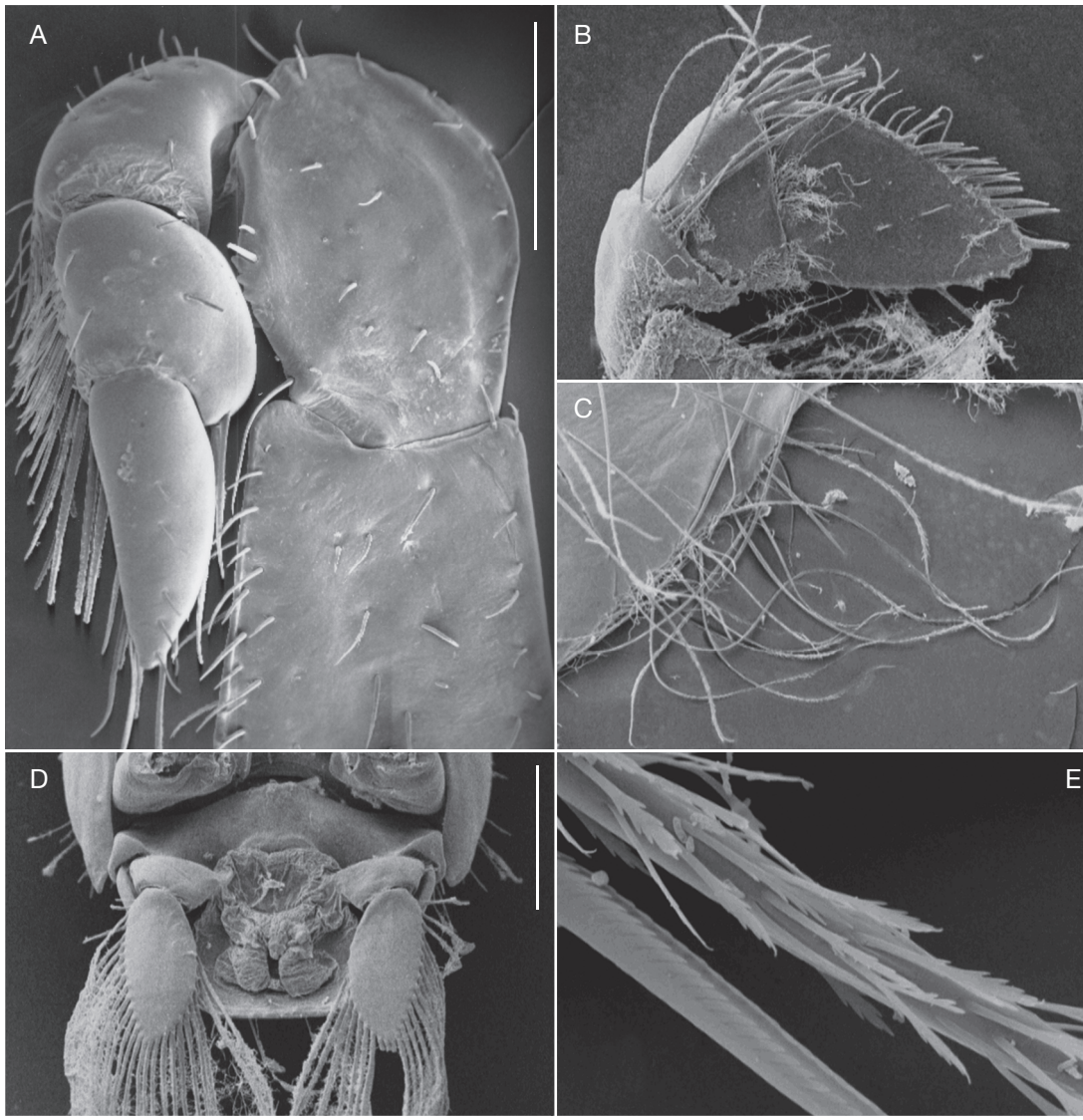


FIG. 5. — Megalopa stage of *Bythograea*, selected SEM photographs of mouthparts and abdomen: **A**, outer view of distal 4 articles and part of ischium of left third maxilliped; **B**, dactylus of left second maxilliped, inner view; **C**, setae of the epipod of the first maxilliped (arrow in Fig. 3E); **D**, ventral view of telson and uropods; **E**, higher magnification of serrate cleaning setae (shown in C and indicated in Fig. 3E). Scale bars: A, D, 500 µm; B, C, E, photographs at higher magnifications, no scale bar available.

CARAPACE (Fig. 1)

Broadly oval, with slight rostral protrusion extending beyond eyes and appearing bilobed in dorsal view. Rostral protrusion deflected ventrally at distal end. Slight median dorsal indentation arising from within rostral protrusion and extending from anterior of rostrum to approximately 1/5 to 1/4 length of carapace. Posterior of carapace with small, curved indentation where abdomen meets body. Anterolateral margins with three to five small teeth in smooth arc, giving way to smaller spines and spinules along posterolateral margins. Small, centrally located

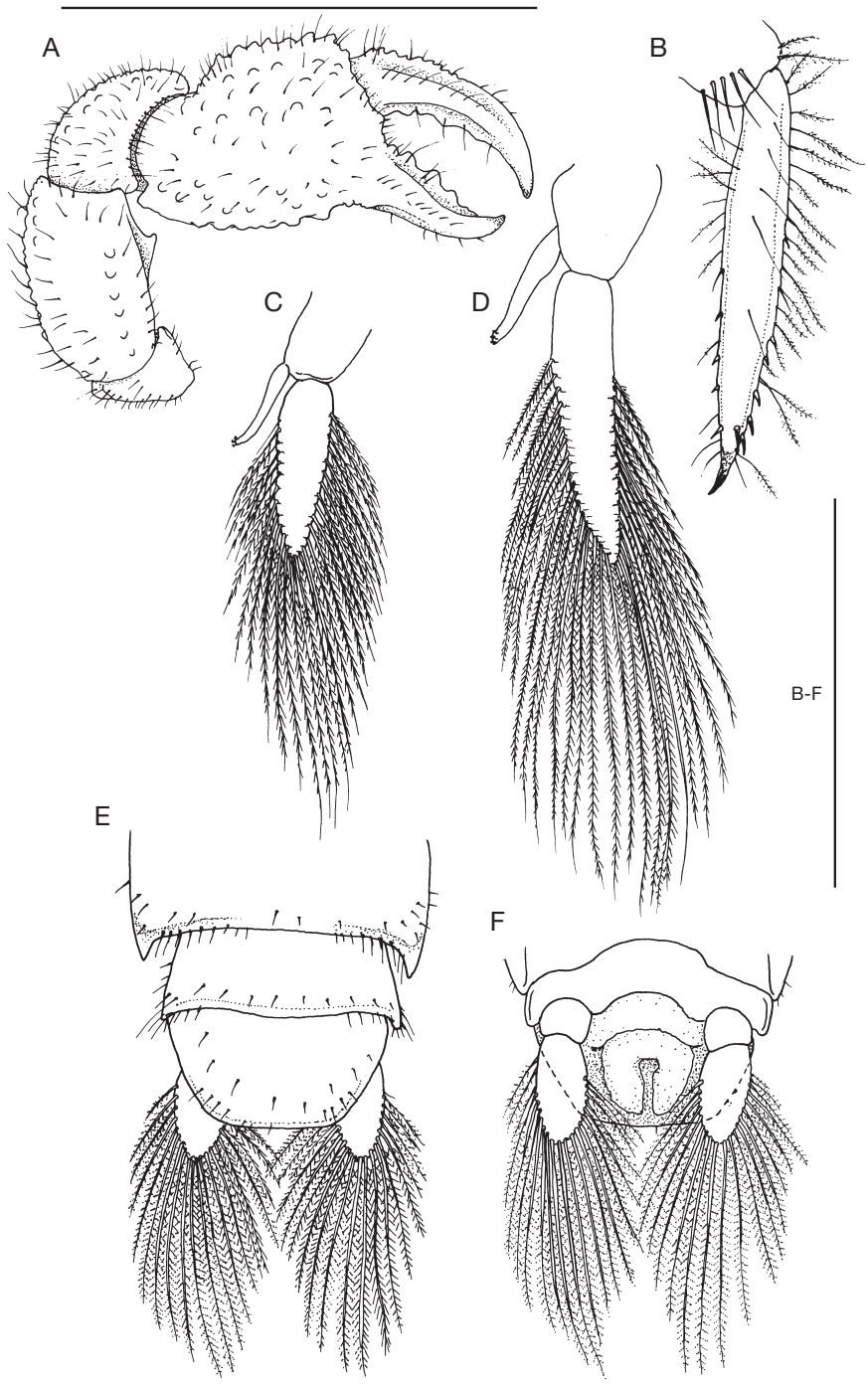


FIG. 6. — Megalopa stage of *Bythograea*, same individual as in Figure 1, selected appendages, abdomen, and telson: **A**, right cheliped, external view; **B**, dactylus of third pereopod, dorsal view; **C**, first pleopod, anterior view; **D**, fourth pleopod, anterior view; **E**, posterior two abdominal somites, telson, and uropods, dorsal view; **F**, ventral view of same region shown in E. Scale bars: A, 5 mm; B-F, 2 mm.

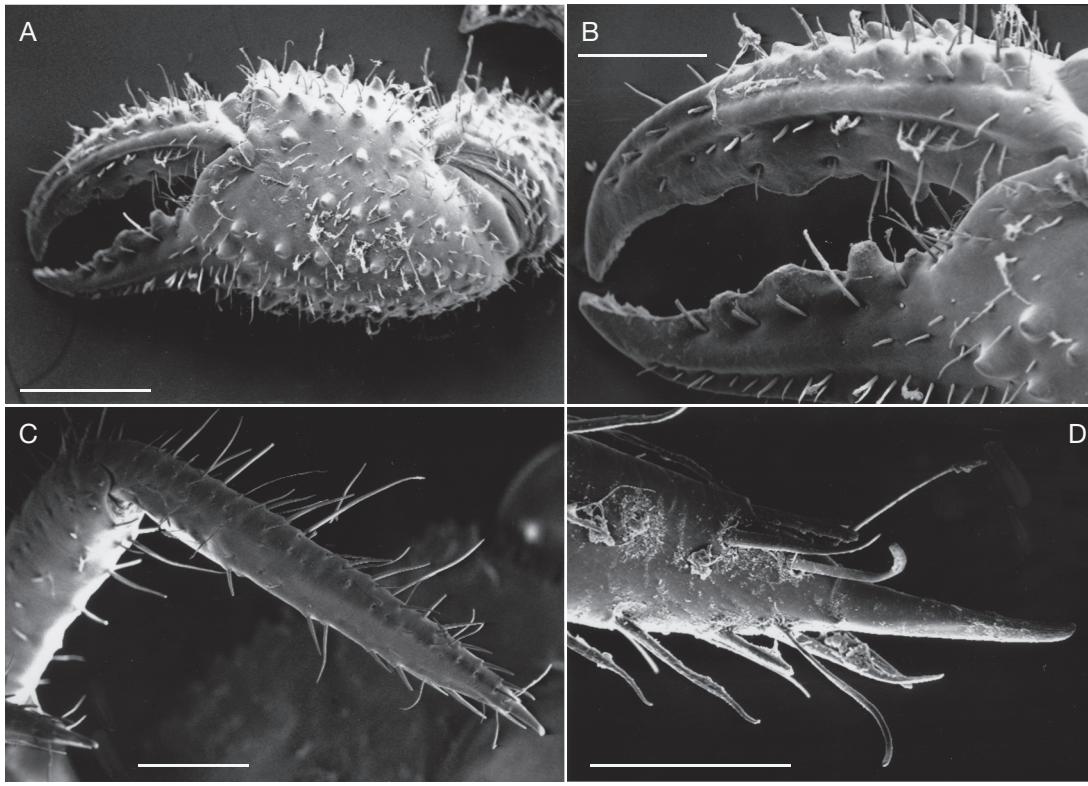


FIG. 7. — Megalopa stage of *Bythograea*, SEM photographs of chela and pereopods: **A**, anterior (outer) view of left chela; **B**, higher magnification of same appendage as in A showing details of chelipedal fingers; **C**, dactylus and distal region of propodus of fifth pereopod (walking leg); **D**, higher magnification of distal part of dactylus shown in C; note absence of curved serrate setae and serrate spines found in many other brachyuran megalopae. Scale bars: A, 1.0 mm; B, C, 0.5 mm; D, 200 µm.

bump, possibly homologous to dorsal spine in zoeal stages, between eyes and approximately 1/4 to 1/3 distance from front along midline. Scattered setae, some of which are plumose or pappose, present especially on anterior third of carapace. Posterodorsal region of carapace slightly transparent, appearing darker than other regions.

### ANTENNAE

First antenna (antennule) (Fig. 9A) short, peduncle with three articles, sharply flexed between second and third; basal article inflated, second article cylindrical with distal setae, third article with conical process extending at right angle from distal end; flagellum consisting of 4 short, stout articles with aesthetasc setae only on distal 3 articles. Second antenna (Fig. 9B) with peduncle of three articles and flagellum of nine articles (though distinction between peduncle and flagellum indistinct), most articles bearing two or three distal setae.

### MOUTHPARTS

Mandible (Fig. 3A) spade-shaped, with slight point at midlength of medial margin; palp two-segmented, distal article distally rounded; scattered setae on both articles becoming more dense on distal half of distal article. Maxillule (Fig. 3B) with stout spines and setae along medial endites; basial endite slightly bilobed; palp two-segmented with setation as illustrated; protopod with five or six long setae on posterodorsal margin. Maxilla (Fig. 3C) with complex medial endites and broad, posteriorly

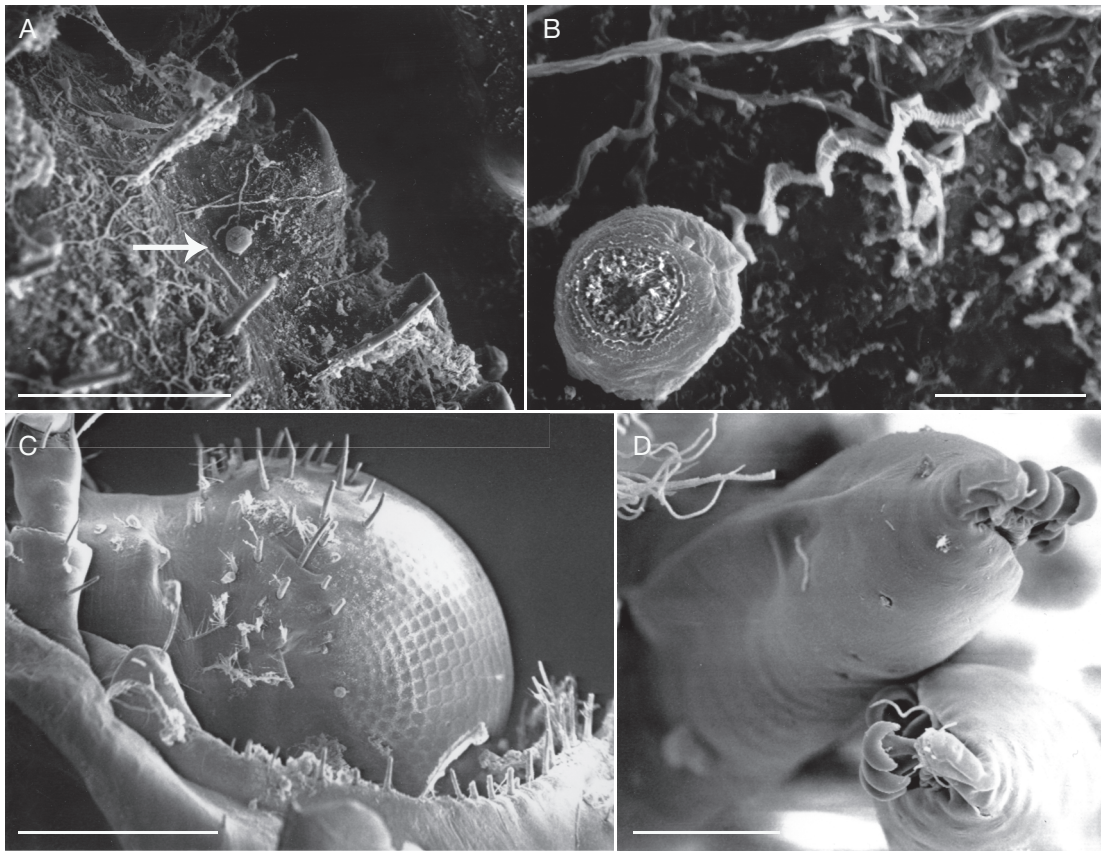


FIG. 8. — Megalopa stage of *Bythograea*, miscellaneous images: **A**, anterolateral region of carapace in dorsal view, white arrow indicating peritrichous ciliate (one of several found on carapace); **B**, higher magnification of ciliate marked by arrow in A; **C**, ventral view of left eyestalk and base of antenna; **D**, tip of endopod of second pleopod showing curved, interlocking serrate spines (cincinulli), disassociated in this view for clarity. Scale bars: A, 200 µm; B, 20 µm; C, 500 µm; D, 50 µm.

angled scaphognathite bordered with short plumose setae; endopod short and unarmed. First maxilliped (Figs 3D, E; 5C, E) with two-segmented exopod; endopod slightly twisted and expanding distally to end in broad, scalloped border that bears medial up-turned tooth or projection; coxal endite complex, with overlapping lobes; basial endite quadrate, nearly rectangular, bordered with long plumose and simple setae; epipod greatly expanded proximally, becoming long, narrow, and curved distally, covered throughout with long, minutely serrate setae (Fig. 3E, arrow; Fig. 5C, E) that aid in branchial grooming. Second maxilliped (Figs 4A; 5B) with endopod composed of four articles, distal article heavily spinose and setose on dorsodistal region (Fig. 5B); exopod two-segmented and much longer than endopod when both are extended; gill (arthrobranch) well developed, extending about 4/5 length of epipod; epipod long and strap-like, slightly widening distally and bearing approximately 25 long, minutely serrate cleaning (grooming) setae. Third maxilliped endopod with five articles, first of which is longest and widest and is scalloped along medial border, dactylus elongate-triangular, strongly tapering distally and bearing numerous short setae; propodus short, nearly spherical; carpus bearing distinct tuft of long setae on inner distal border (Fig. 4B) that extend well past propodus (Fig. 4C); exopod generally similar to

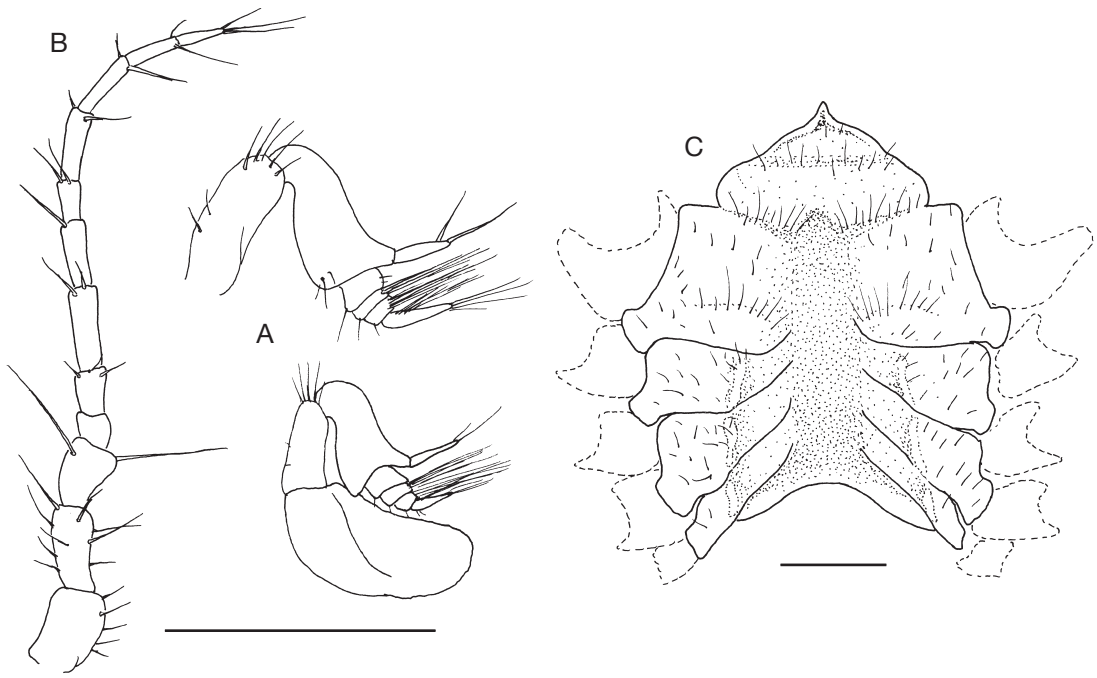


FIG. 9. — Megalopa stage of *Bythograea*, first and second antennae and sternal region: **A**, first antenna (antennule); **B**, second antenna; **C**, sternal region, anterior toward top of figure, with pereiopodal coxae indicated by dashed lines. Scale bars: 1 mm.

that of second maxilliped; gill (arthrobranch) well developed and longer than appendage (in resting position, not when extended); epipod not observed (possibly not present).

### CHELIPEDS

Large relative to body size (Figs 1; 2B; 6A; 7A, B) and overall covered with small tubercles and scattered short setae. Dactylus smoothly curving, with indistinct teeth along cutting edge and with numerous tubercles along dorsal border, larger toward base of dactylus. Outer face with strong central rib bearing scattered setae (Figs 6A; 7A, B). Tip of dactylus lightly cornified; tips of chelae crossing when closed. Propodus (Figs 6A; 7A) heavily tuberculate; fixed finger with low teeth along cutting edge and with strong rib similar to that of dactylus. Propodus lacking patch of setae on internal face, as seen in adults. Carpus short, thick, heavily tuberculate. Merus nearly cylindrical, with ventral row of small tubercles and with small anteroventral protrusion (Fig. 6A).

### PEREIOPODS 2-4

Dactylus (Figs 1; 6B; 7C, D) long and narrow, conspicuously pointed but not strongly curved at tip, longer than propodus and carpus but slightly shorter than merus. Dactylus with short spines on ventral and dorsal margins and scattered plumose and simple setae.

### PEREIOPOD 5

Dactylus with small, regularly-spaced spines on distal half of flexor margin and with irregularly-spaced spines on distal half of dorsal margin, but lacking any long, serrate setae and the stout, serrate spines so often associated with this appendage in brachyuran megalopae. Other articles of fifth pereiopod similar to those of pereiopods 2-4.

### ABDOMEN AND PLEOPODS

Abdomen (Figs 1A; 6E) composed of six somites and extending posteriorly behind carapace when at rest, slightly bent ventrally and appearing widest

across somites 2 and 3. Somites 1 and 6 much shorter than other somites. Pleopods (Figs 6C, D; 8D) two-segmented; protopod lacking setae. Exopod increasing in length from anterior to more posterior pleopods and bearing numerous long, plumose, natatory setae, the number increasing with length of the appendage. Endopod narrow, approximately half length of expopod (and becoming relatively shorter on more posterior [longer] pleopods), bearing two to four recurved serrate spines (cincinulli) terminally (Fig. 8D).

STERNAL REGION (Fig. 9C)
Sternal region broadly triangular anteriorly with slight transverse groove just posterior to apex; sternal plates corresponding to first pereopod larger than others; central longitudinal groove deep and extending anteriorly to slight bifurcation just anterior to sternal plate of P1; coxae of pereiopods attached and articulated with sternum as illustrated.

TELSON AND UROPODS
Telson (Figs 5D; 6E, F) bearing scattered simple setae and widest anteriorly, with posterior border approximately half width of anterior border. Posteriorly border truncate, straight across. Lateral borders straight, converging from approximate width of sixth abdominal somite to posterolateral "corners" of telson. Uropods (Figs 5D; 6E, F) two-segmented, proximal segment very short, wider than long, and lacking setation; distal segment oval to lanceolate and bearing approximately 20 long, dense plumose (natatory) setae on distal 4/5 of appendage.

COLOUR
Colour of live specimens is usually bright red (Fig. 10). This coloration is probably due to high concentrations of carotenoids, which are known to be present in bythograeid eggs (DeBevoise *et al.* 1990). Adults are almost uniformly white or "bone coloured".

## DISCUSSION

In terms of known genera and species of vent crabs, the EPR is the most diverse region on earth (Martin & Haney 2005). Known EPR genera include *Bythograea*, *Cyanagraea* de Saint Laurent, 1984, and *Allograea* Guinot, Hurtado & Vrijenhoek, 2002. Of these, *Cyanagraea praedator* de Saint Laurent, 1984 (the only species in the genus to date) is a much larger and morphologically very different crab from species of *Bythograea*, and *Allograea* currently is known only from the 31°S EPR site. Within the genus *Bythograea*, six species are known from various eastern Pacific vent sites. Thus, it is conceivable that the megalopae forming the basis of this study came from any of those six species. However, dissected and illustrated larvae used in this study all were from the 9°N site on the EPR, where to date only *B. thermydron* and *B. microps* de Saint Laurent, 1984 (a far smaller and somewhat rare species; see Martin & Haney 2005) have been reported, and where by far the most commonly encountered species is *Bythograea thermydron* (Martin & Haney 2005). Furthermore, results of genetic analyses of megalopae from these collections showed similarities to adults of *B. thermydron*, and several megalopae were reared through juvenile stages in which the characters resembled those of adult *B. thermydron* (Epifanio *et al.* 1999). Thus, it is certain that our larvae are from the genus *Bythograea* and very nearly certain that they are all from the species *B. thermydron*. This is somewhat surprising in light of the large size range of these megalopae, ranging from CW 2.5 to 7.5 mm.

Most brachyuran megalopae are recognizable as such by a unique combination of characters. Some characters tend to be specific for certain groups of crabs, such as the strong posteriorly-directed sternal spines found in some portunid megalopae, or the unusual, large recurved hooks found on the chelipeds of some xanthids and cancrids (e.g., see Martin 1988). The vent crab megalopae have nothing as distinctive as ventral spines or chelipedal hooks that distinguish them from later juvenile crab stages (or from the megalopae of other crab families). However, they are nonetheless recognizable as megalopae by characters shared by all brachyuran megalopae, such as the well developed abdomen, pleopods and uropods. Other "typical" megalopal characters are missing in vent crabs. These include the distinctive long, serrate setae on the dactylus

FIG. 10. — Colour photograph of a relatively large (carapace width estimated as between 7 and 8 mm) live megalopa stage of *Bythograea thermydron* Williams, 1980 collected from the East Pacific Rise (C. Epifanio and A. Dittel collection).

of the fifth pereopod (e.g., see Martin *et al*. 1988: figs 1A, 3E, 4E, F) and the stout serrate spines also commonly found on the dactylus of the fifth pereopod. Had we examined relatively few specimens, it would be reasonable to assume that these had simply broken off on our specimens. However, after having examined a large number of megalopae, we have to conclude that the fifth pereopod in vent crabs is not modified in this regard; Williams (1980) noted this as well.

Overall, the megalopal stage of bythograeid crabs seems quite generalized. There are no salient unique features that distinguish the megalopae as being distinctly bythograeid. Morphological characters linking this stage to megalopae of other crab families, as might be expected if there is much phylogenetic information to be found in these stages (see arguments in Felder *et al*. 1985), also were not found, and thus our study sheds no light on phylogenetic relationships, though perhaps it could be posited that the lack of specialized or unique features in bythograeid megalopae argues for a primitive position relative to other brachyurans. As concerns sensory structures, the larvae possess several structures that might serve a sensory function. The pappose and lightly plumose setae of the carapace, not seen in the adults, may be sensory in nature, though this is of course speculation on our part.

Other interesting aspects of the megalopa larvae include the fact that they are good swimmers, fully the equivalent of other (shallow water) crab megalopae larvae, with recorded speeds of 4 to 10 cm/second (C. Epifanio pers. comm., and Epifanio *et al*. 1999). They are also able to withstand the relatively much lower atmospheric (sea surface) pressure, which is some 250 times less than pressure at the

depths where they are normally found, and they can withstand the relatively high temperatures of surface waters (e.g., see Epifanio *et al*. 1999; Jinks *et al*. 2002). One of us (AD) has maintained and reared the megalopae through several juvenile stages at room temperature and pressure (Epifanio *et al*. 1999), whereas adults are clearly pressure-sensitive and do not survive for long at atmospheric pressure when removed from the deep; adults must be maintained in pressurized chambers when brought to the surface in order to survive. It is possible that the megalopae have a relatively well developed sense of smell that helps them locate suitable vent habitats. Vent crabs (adults) have been reported to feed on tube worms, clams, mussels, and bacterial mats (references in Martin & Haney 2005).

Some of the specimens bore stalked peritrich ciliates, probably vorticellids (Diana Lipscomb pers. comm.), on the dorsal surface of the carapace (Fig. 8C). These have not been reported previously from vent crabs to our knowledge.

The megalopa stage of the vent crab genus *Bythograea* appears to be a large and unspecialized developmental stage. There are no obvious adaptations that would indicate that it is a member of a family of endemic crab species restricted to hydrothermal vent habitats.

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