

STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER REGION OF FLORIDA XXVII.

PHIMOCHIRUS HOLTHUISI (PROVENZANO, 1961)
(ANOMURA: PAGURIDAE): THE COMPLETE LARVAL DEVELOPMENT UNDER LABORATORY CONDITIONS, AND THE SYSTEMATIC RELATIONSHIPS OF ITS LARVAE

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In a recent revision of several pagurid genera, McLaughlin (1981a, b) noted that at least 44 species had been assigned at one time or another to the genus *Pylopagurus* A. Milne Edwards and Bouvier, 1891. In splitting the genus *Pylopagurus* into 10 new genera, McLaughlin restricted only five species to *Pylopagurus sensu stricto*, placing nine other species in her new genus *Phimochirus*. Adults of *Phimochirus* are distinguished from other closely related genera in the "pylopagurid group" primarily by chelipedal and uropodal characters (see McLaughlin, 1981a).

The larval development either within *Phimochirus*, or within *Pylopagurus sensu lato*, is completely unknown, although species in both taxa are not uncommon in the western and eastern Atlantic and eastern Pacific Oceans. Consequently, a comparison of larval characters within and across generic boundaries might provide additional data supporting or negating the recent generic revisions. In this paper we report on the complete larval development of *Phimochirus holthuisi* (Provenzano, 1961), a wide-ranging species found in littoral and continental shelf waters to a depth of 252 m, from North Carolina to Texas, the Caribbean Sea and Colombia to Brazil (McLaughlin, 1981b). We compare possibly important characters exhibited by these larvae with those known in larvae from other related pagurid species.

MATERIALS AND METHODS

A single ovigerous female of *Phimochirus holthuisi* was collected by R/V Sea Diver with an 8 ft otter trawl from 38-22 fathoms (68-40 m) on 8 June 1979 at 27°31.4'N, 80°00.0'W, due east of Ft. Pierce, Florida. The specimen was returned to the laboratory and maintained in nonflowing seawater (35‰) in a 19 cm diameter glass bowl until hatching occurred on 12 June. Only 18 zoeae were obtained and these were cultured individually in compartmented polystyrene trays using methodology previously described by Gore (1973). Food throughout was freshly hatched San Francisco Bay *Artemia* nauplii. The descriptions that follow are based on late-stage zoeae preserved on the day that other zoeae in the series began molting to the next stage. This method ensured having specimens within each zoeal stage for purposes of dissection and illustration.

RESULTS OF THE REARING EXPERIMENT

The larvae of *P. holthuisi* were remarkably healthy and active. Except for one Zoea IV which died in ecdysis the only deaths that occurred within the 18 larvae series were those taken for preservation. Molting to the next stage was more or less uniform, occurring within a one or two-day period for most zoeae, although some stragglers were always present. Duration of the various intermolt phases and relative survivorship are presented in Table 1. These data show that in the laboratory *P. holthuisi* most often passes through 4 zoeal stages and attains glaucothoe in 16 or 17 days. The glaucothoe stage lasted another 7 or 8 days so that *P. holthuisi* is able to complete its planktonic existence under laboratory condi-

Table 1. Duration in days of larval stages of *Phimochirus holthuisi* (Provenzano).

Stage	Minimum	Mean	Mode	Maximum	Total molting to next stage
Zoea I	3	3.8	4	5	16
Zoea II	2	3.3	3	4	14
Zoea III	4	4.0	4	4	12
Zoea IV	4*	5.0	5	6	8 (to glaucothoe) 1 (to stage V)
Zoea V	This stage lasted 5 days before molting to glaucothoe.				
Glaucothoe	7	7.5	7	8	4
Crab 1	6	7.0	7-8	8	3
Crab 2	3	3.5	3-4	4	2

* Died during ecdysis.

tions in a little more than 3 weeks. One individual passed through 5 zoeal stages before attaining glaucothoe in 20 days. This animal, which usually molted from stage to stage one day earlier than the majority of counterparts, died after 5 days as a glaucothoe without further molting.

Four glaucothoes reached first crab stage and two of these survived to crab stage 3 before dying in that stage. The young crabs utilized microgastropod shells provided, and were fed a combination of commercially prepared fish and turtle pellets. Exploratory behavior was observed but none of the 4 surviving individuals attempted to change the shells they occupied. The experiment was terminated 59 days after hatching when the last crab stage 3 died.

DESCRIPTION OF THE LARVAE

First Zoea

Carapace length 1.18 mm; 2 specimens examined.

Carapace (Fig. 1A, B).—Cephalothorax smooth, elongate; rostrum slightly deflexed, blade-like, acute, tapering to a thin point, not extending beyond antennules or antennae; mediodorsal knob posterior to sessile eyes; small paired setae between knob and rostral base, these increasing in number in later stages; ventrolateral carapace margin posterior to eyes produced into rounded pterygostomial lobe.

Abdomen (Fig. 1A, B).—Five somites, 1st naked, 2nd to 5th with paired middorsal setae on posterior margin, and bluntly rounded ventrolateral processes.

Telson (Fig. 1A, B, C, c).—Elongate, fan-shaped, broadening distally; posterior margin slightly convex, armed with 7 + 7 processes, outermost a movable naked spine, 2nd an anomuran hair, 3rd to 7th plumodenticulate spines, of which the 4th is longest, giving process formula of 1 + ii + 3-7 (in formulae for armature of posterior telsonal margin, upper case Roman numerals = fixed spines, lower case Roman numerals = hairs, and Arabic numerals = movable spines or setae); intersetal margins lined with fine spinules and hairs; median notch present. Anal spine, if present, not noticeable in any stages examined.

Antennule (Fig. 1D).—Elongate conical rod extending slightly beyond antennae; 6 unequal terminal aesthetascs, some having pointed tips; 1 long plumose sub-apical seta.

Antenna (Fig. 1E).—Scaphocerite outer margin sinuous, armed distally with short inwardly curving spine; inner margin convex, 10 plumose setae; endopodite rod-like, about 0.6 times scaphocerite length, 2 plumose terminal setae; strong ventral protopodal spine basally, armed with spinules on margins.

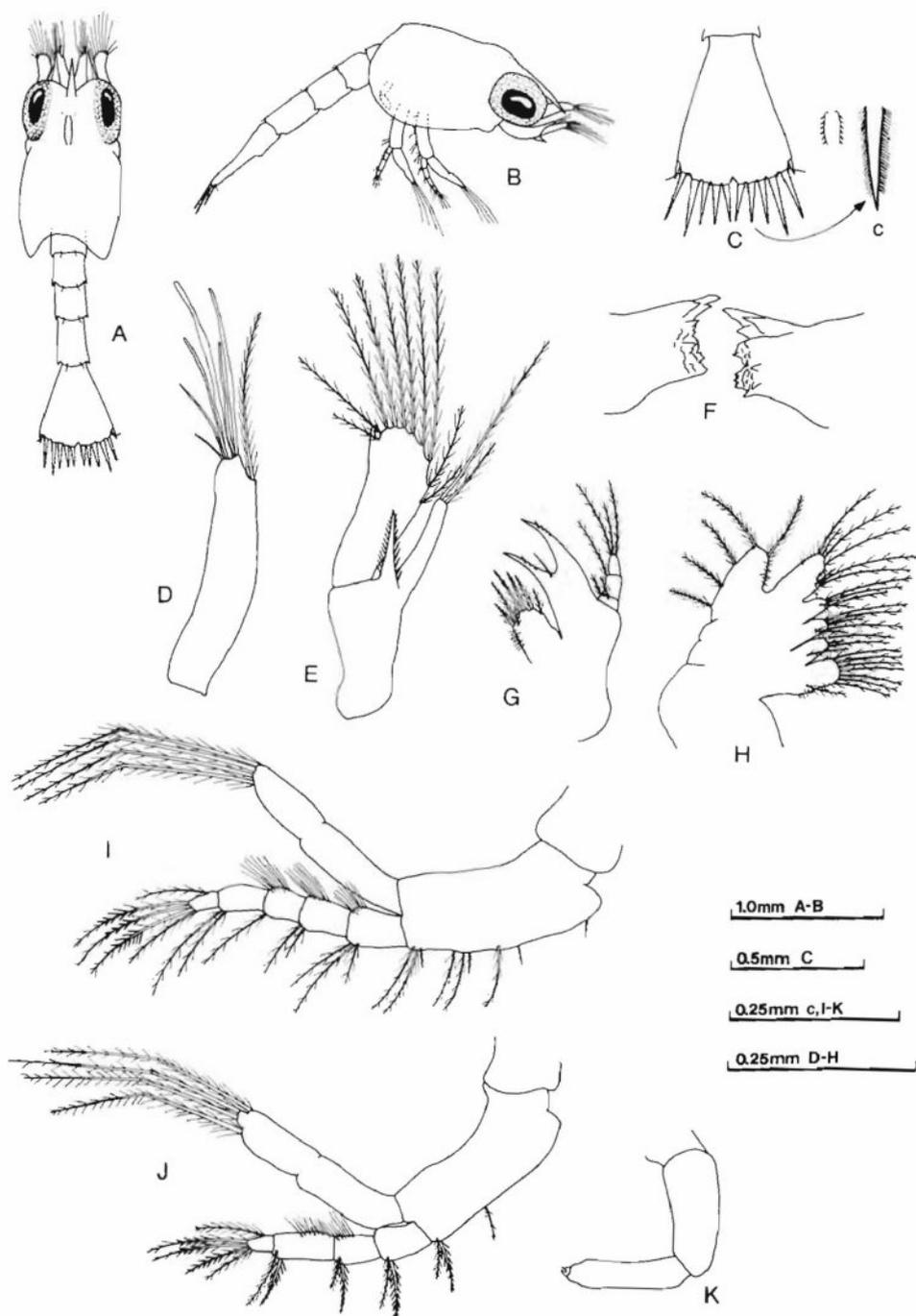


Fig. 1. *Phimochirus holthuisi* (Provenzano): First zoeal stage. (A) Dorsal view; (B) lateral view; (C) telson, dorsal view; (c) detail, sixth telsonal process; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3.

Mandibles (Fig. 1F).—Asymmetrically dentate; incisor process with single strong, prominent tooth plus several shorter teeth; molar process with spinelike denticles and serrate ridges; no palp bud until stage 4.

Maxillule (Fig. 1G).—Endopodite 3-segmented, setal formula progressing distally 2, 1, 3; coxal endite with 5 plumodenticulate plus 2 nondenticulate setae; basal endite with 2 elongate spinelike teeth armed laterally with 2 or 3 small denticles and bearing naked axillary seta; other pubescence as illustrated.

Maxilla (Fig. 1H).—Endopodite bilobed, setae progressing distally 3, 4 placed as illustrated; basal endite bilobed, 5 setae on distal, 4 on proximal lobe; coxal endite bilobed, 8, 4 setae, respectively; scaphognathite bearing 5 plumose setae on margin; other pubescence as illustrated.

Maxilliped 1 (Fig. 1I).—Coxopodite naked; basipodite setal formula progressing distally 1, 2, 3, 3; endopodite 5-segmented, setation distally 3, 2, 1, 2, 4 + I (Roman number denoting dorsal seta), plus additional fine hairs dorsally on proximal 3 articles; setae on distalmost segment 2 thin, plumose, plus 3 stouter, plumose, latter armed midway with 5 or 6 spinules as shown; exopodite incompletely 2-segmented, 4 plumose natatory setae.

Maxilliped 2 (Fig. 1J).—Coxopodite naked; basipodite with 3 setae (2 thin, plumose, 1 stouter armed with 2 rows of spinules); endopodite 4-segmented, first 3 segments each ventrally with 1 thin, plumose, 1 stout, spinulate seta, distalmost as in maxilliped 1 in number and armature; exopodite similar to maxilliped 1; other fine hairs dorsally on articles 2 and 3 as illustrated. Ventral setal form not changing in later zoeal stages.

Maxilliped 3 (Fig. 1K).—Coxopodite and basipodite naked, exopodite rudimentary.

Color.—Zoea transparent overall; red and golden orange chromatophores forming large interior group dorsally on midgut region, extending forward along midline toward rostrum, and backward interiorly to abdominal somite 1; second smaller group ventral to eyes interior to anterolateral surface of cephalothorax; red chromatophores forming ring delineating posterior margin of fifth abdominal somite, extending backward medially onto telson for about $\frac{1}{3}$ its length; corneas of eyes reflecting blue light, with scattered black pigment spots throughout; other appendages transparent.

Second Zoea

Carapace length 1.21 mm; 2 specimens examined.

Carapace (Fig. 2A, B).—Cephalothorax undergoing little change in this and subsequent stages, becoming larger and more elongate but without additional armature; rostrum much flattened, broadening basally; rudimentary pereopods visible beneath carapace posterolaterally; eyes stalked.

Abdomen (Fig. 2A, B).—Similar in form and armature to stage I.

Telson (Fig. 2A, B, C).—Posterior process formula now 8 + 8 with addition of pair of short median spines; median notch obsolescent to absent.

Antennule (Fig. 2D).—Bilobed; setation similar to stage I; 3 short hairlike setae laterally.

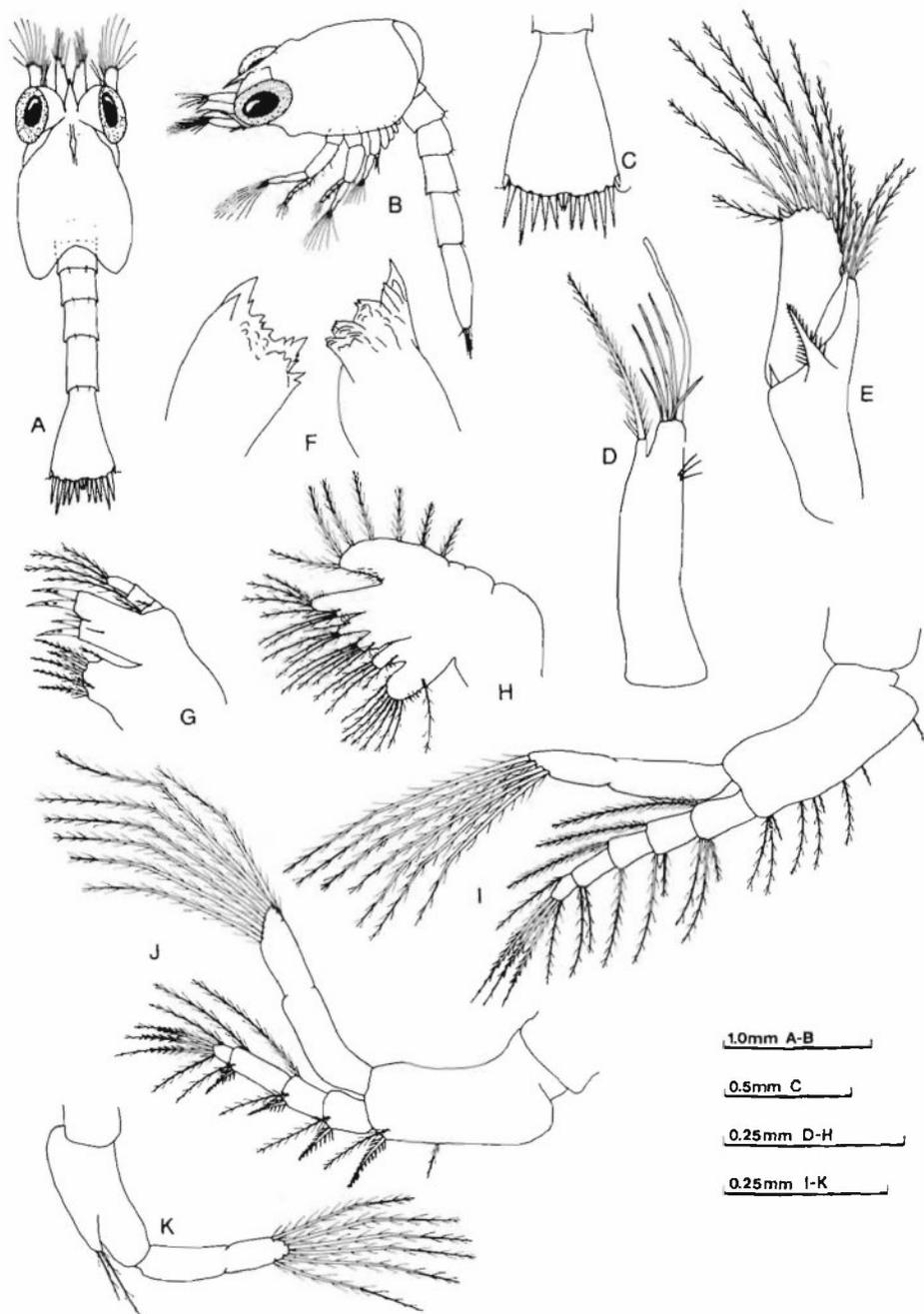


Fig. 2. *Phimochirus holthuisi* (Provenzano): Second zoeal stage. (A) Dorsal view; (B) lateral view; (C) telson, dorsal view; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3.

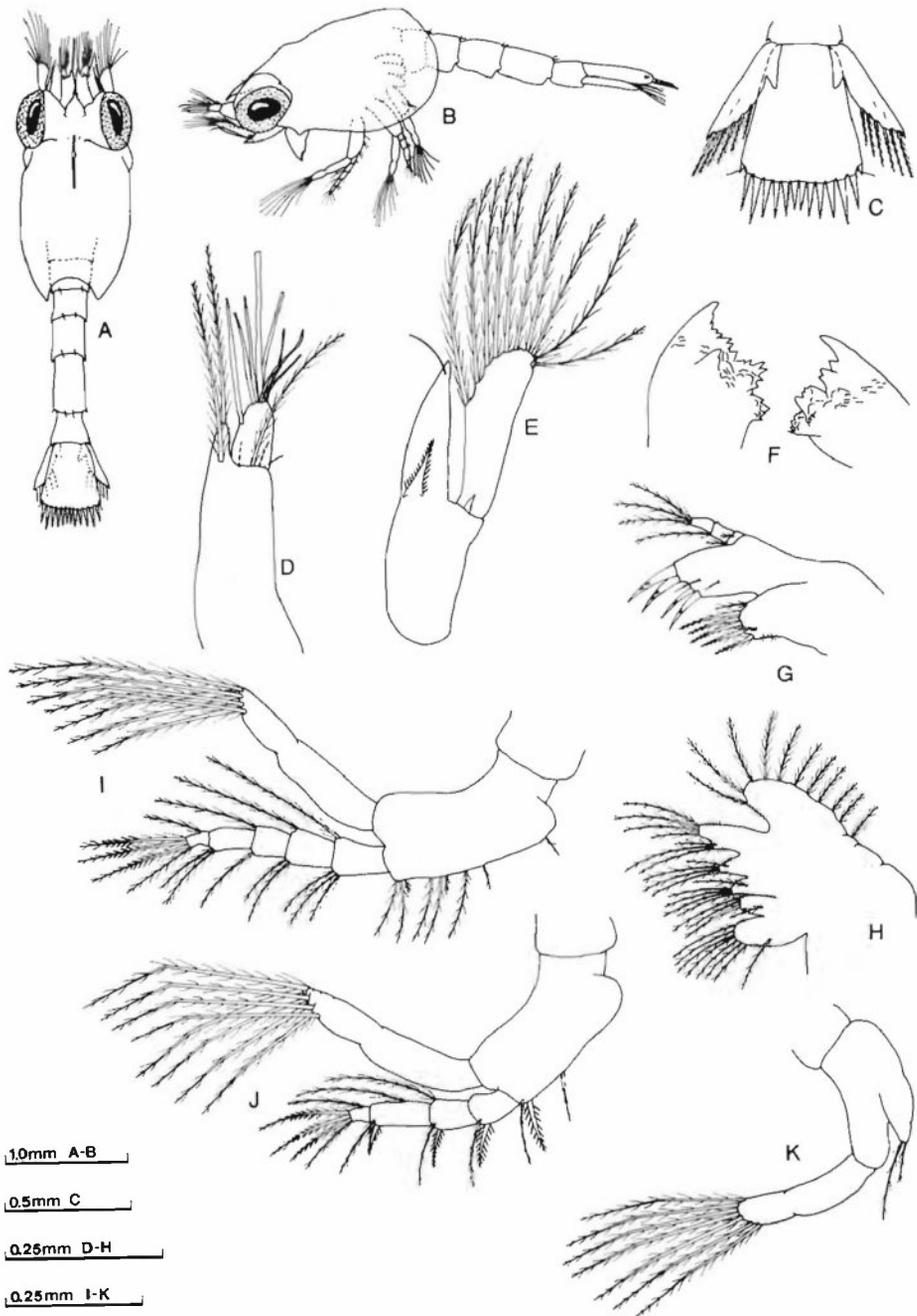


Fig. 3. *Phimochirus holthuisi* (Provenzano): Third zoeal stage. (A) Dorsal view; (B) lateral view; (C) telson, ventral view; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3.

Antenna (Fig. 2E).—Scaphocerite, endopodite, and protopodal spine similar to that in stage I; 2nd, much smaller, sharp spine ventrally on distal border of protopodite; scaphocerite distolateral spine reduced.

Mandibles (Fig. 2F).—As in stage I.

Maxillule (Fig. 2G).—Endopodite and coxal endite unchanged; basal endite now with 4 strong, denticulate, spinelike teeth, plus 2 naked setae.

Maxilla (Fig. 2H).—Endopodal, coxal, and basal endite setation unchanged; scaphognathite now with 7 plumose marginal setae.

Maxilliped 1 (Fig. 2I).—Coxal and basipodal setation unchanged; fine hairs on margins replaced by single long plumose setae, formula now 3 + I, 2 + I, 1 + I, 2, 4 + I; exopodite with 7 natatory setae.

Maxilliped 2 (Fig. 2J).—Coxal and basipodal setation unchanged, fine hairs replaced as above; formula now 2, 2 + I, 2 + I, 4 + I; exopodite with 7 natatory setae.

Maxilliped 3 (Fig. 2K).—Coxopodite and basipodite naked; endopodite short unsegmented bud with 2 terminal setae; exopodite incompletely 2-segmented, 6 natatory setae.

Color.—Color similar to first stage, most intense on midgut and beneath anterolateral and posterolateral regions of cephalothorax; red chromatophore ring on posterior margin of abdominal somite 5 now doubled, each connected medially by red streak; medial red streak on telson flanked by fainter red line of small chromatophores on either side; eye corneas reflecting blue light.

Third Zoea

Carapace length 1.60 mm; 2 specimens examined.

Carapace (Fig. 3A, B).—Rostrum much foreshortened from previous stages, flattened, expanded basally in shape of an ogival arch, ventrally blade-shaped, unarmed; cephalothorax otherwise unchanged from earlier stages except in size.

Abdomen (Fig. 3A).—Sixth somite present, armed with pair of short ventrolateral teeth, no setae.

Telson (Fig. 3A, B, C).—Bilobed, unsegmented uropods present, endopodites rudimentary, naked, exopodites terminating in sharp spine plus 6 plumose setae along inner convex margin, 2 hairs ventrally on each blade; processes on posterior margin remain 8 + 8 (1 + ii + 3 - 8) and in following stage.

Antennule (Fig. 3D).—Segmented; outer ramus with 8 aesthetascs, 7 terminal, 1 subterminal; inner ramus with 2 plumose setae, 1 terminal, 1 subterminal; 3 fine hairlike setae plus single long plumose seta at protopodal-endopodal junction.

Antenna (Fig. 3E).—Scaphocerite setation unchanged, distolateral tooth much reduced; endopodite now quite elongate, about 0.8 times length of scaphocerite, tapering to bluntly rounded end with single subterminal naked seta; protopodal spines as in previous stage.

Mandibles (Fig. 3F).—Enlarged, dentally complex, otherwise similar in general form to 2nd stage.

Maxillule (Fig. 3G).—Similar in form and setation to previous stage.

Maxilla (Fig. 3H).—Scaphognathite now with 11 plumose marginal setae; other setation unchanged on endopodite and endites.

Maxillipeds 1 and 2 (Fig. 3I, J).—Exopodite natatory setae 7, 8, respectively; other setal formulae as in previous stage.

Maxilliped 3 (Fig. 3K).—Endopodal bud more elongate, indistinctly segmented; exopodite with 7 natatory setae.

Color.—Now more intense; large red mass of chromatophores interiorly just posterior to eyes middorsally; 2 elongate red masses interiorly extending posterolaterally from region of midgut, separated by brilliant yellow mass running from mandibular area posteriorly to region of developing pereopods; double ring of red chromatophores on somite 5 connected medially with 1 long, and laterally with 2 shorter red streaks, these extending onto abdominal somite 6 now present and separated from telson; latter transparent; eyes as before.

Fourth Zoea

Carapace length 1.70 mm; 2 specimens examined.

Carapace (Fig. 4A, B).—Cephalothorax unchanged except for minor paired setae in rostral-frontal area; distinctly segmented pereopods continuing to develop, extending from beneath carapace.

Abdomen (Fig. 4A, B).—Unsegmented, bifurcated pleopods present on somites 2–5; ventrolateral spines on somites 2–6 more elongate than in previous stage.

Telson (Fig. 4A, B, C).—Two pairs of setae on medial dorsal surface; uropodal exopodite now segmented, an elongate distolateral spine plus 8 plumose setae on margin; endopodite remaining nonarticulated, with 2 terminal setae.

Antennule (Fig. 4D).—Outer ramus (exopodite bud) about two-thirds length of inner (endopodite bud), aesthetascs progressing distally 2, 1, 2, plus 7 terminally; peduncular junction with 4 hairlike setae plus 2 long plumose setae; endopodite bud shorter than exopodite, single plumose subterminal seta, terminal seta now absent; short hair laterally at base of peduncle.

Antenna (Fig. 4E).—Scaphocerite setation unchanged; endopodite greatly elongate, reaching beyond scaphocerite blade by about one-third its length, single seta; protopodal spines as before.

Mandibles (Fig. 4F, f).—Enlarged, similar to those of stage 3, palp bud present.

Maxillule (Fig. 4G).—Endopodal and coxal endite setae unchanged; basal endite with 5 strong laterally denticulate teeth.

Maxilla (Fig. 4H).—Scaphognathite now with elongate proximal lobe bearing 1 seta, distal lobe with 13 marginal plumose setae; other processes and endites unchanged.

Maxilliped 1 and 2 (Fig. 4I, J).—Exopodites each with 8 natatory setae; other setal formulae unchanged.

Maxilliped 3 (Fig. 4K).—Coxopodite and basipodite naked; exopodite with 8 plumose setae; endopodite elongate, obscurely segmented, bearing 3 setae.

Color.—Red and golden orange chromatophore mass now extending into proximal base of eyestalks, covering entire frontal region, running backward toward midgut;

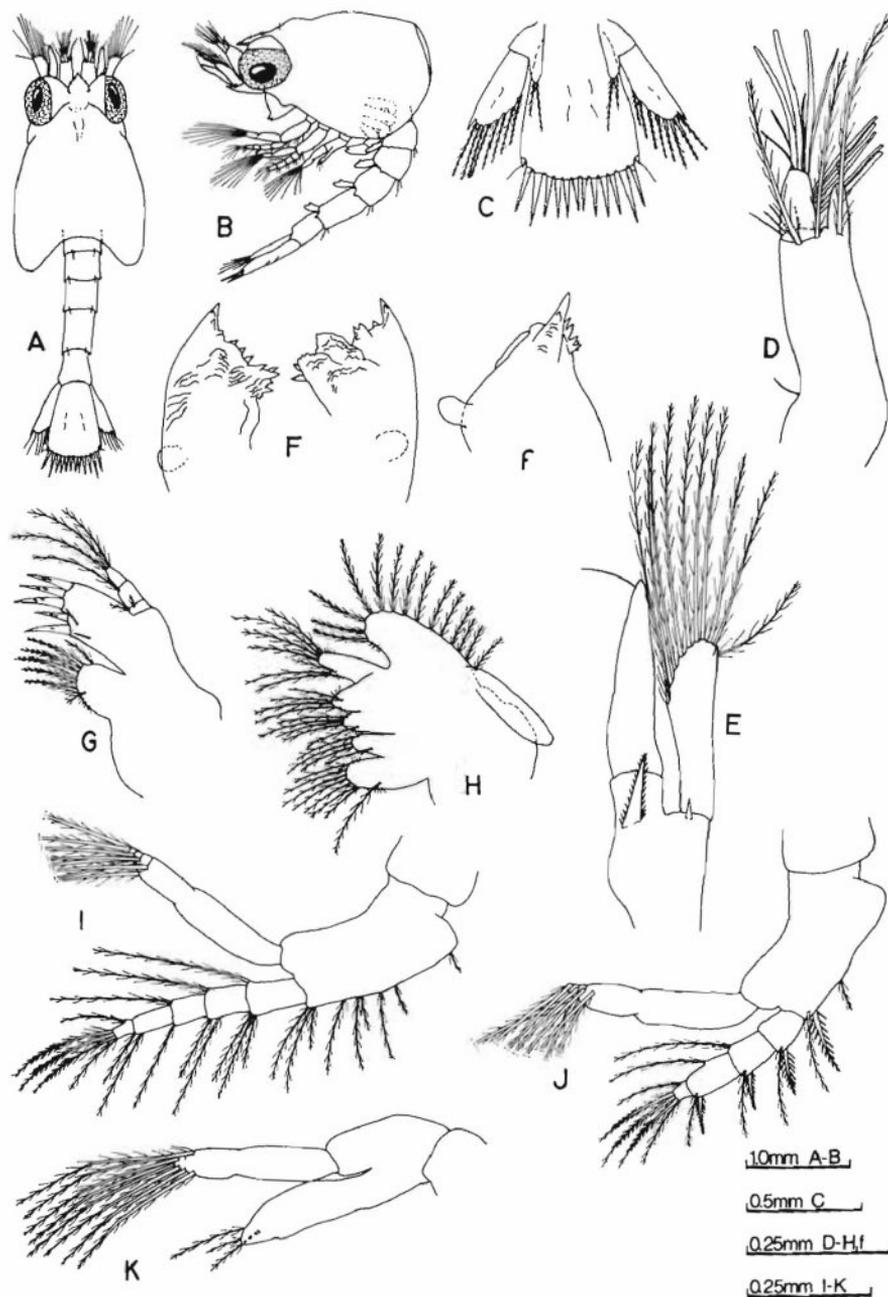


Fig. 4. *Phimochirus holthuisi* (Provenzano): Fourth zoeal stage. (A) Dorsal view; (B) lateral view; (C) telson, ventral view; (D) antennule; (E) antenna; (F) mandibles; (f) mandible, ventral view; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3. Length of maxillipedal 1 and 2 natatory setae not completely illustrated.

anterior ventral region of heart brilliant yellow; scattered red and golden orange specks on mouthparts; mandible golden orange; golden orange and red group of chromatophores beneath posterolateral region interior to cheliped and pereopod buds; posterior margins of somites 5 and 6 ringed with red overlying fainter golden orange, connected mesially by red or orange streak; eyes distinctly blue.

Fifth Zoea

A single 5th zoeal stage was recorded from one individual. However, after molting to glaucothoe, the postlarval animal ate the cast 5th stage exuviae, preventing examination and description of this stage. An examination of the incomplete 4th stage exuviae from this same zoea showed that it differed little in maxillipedal, abdominal, and telsonal characters from other 4th stage zoeae. In the maxillule, the only mouthpart available for examination, there were 4 (instead of the usual 5) large spinelike teeth on the basal endite. Other characters which might be expected to differ would be a different aesthetasc-setal formula on the antennule, and the absence of a mandibular palp (normally present in the 4th stage), but these appendages, regrettably, were lost.

The glaucothoe from the 5th stage zoea showed several notable differences from those obtained from 4th stage zoeae. The antennal flagellar articles were more numerous, slightly expanded distally, and generally similar in form to the crab stage; the antennular aesthetascs were more numerous and better developed; the exopod of maxilliped 3 was 3-segmented instead of 2-segmented; and the branchiostegal region was more rectangularly shaped, and seemed better calcified. It thus appears that a mosaic of 1st crab and glaucothoe characters were exhibited in this specimen, probably as a consequence of longer development through the addition of an extra zoeal stage.

Glaucothoe

Rostral carapace, length 1.2 mm, width 1.2 mm; 2 specimens examined.

Carapace (Fig. 5A, B).—Cephalothorax smooth, only moderately inflated, as wide as long; rostrum short, bluntly rounded, not extending beyond paired ocular acicles; latter with anterior margin produced into small, distinct tooth; branchiostegal lobe convex, produced, bearing 5 marginal setae; cephalic shield subrectangular, clearly delineated, noticeably setose, prominent gastric tubercle replacing zoeal mediodorsal knob; small paired setae adjacent to cephalic shield on each branchial region. Eyestalks long, corneas about 0.4 times eyestalk length.

Abdomen (Fig. 5A, B, D).—Six unarmed somites; ventrolateral borders bluntly rounded, paired setae dorsally and laterally as shown; biramous pleopods on somites 2–5, exopodites well developed, setal formula 8, 8, 7, 6, progressing toward telson, endopodites each with appendix interna of 2 small apical hooks.

Tail Fan (Fig. 5A, B, C, detail).—Telson bearing 3 pairs of dorsomedial setae, 2 more pairs anterolaterally, another pair anterodorsally; posterior margin convex, 7 + 7 processes in formula of $i + 2-7$; uropods biramous, exopodites with 18 lateral setae, 1 fine dorsal hair, plus about 15 dentostegous processes along posterolateral margin (detail); endopodites with 6 plumose lateral setae, single fine hair anteriorly, and 7 dentostegous processes; protopodal setae as shown.

Antennule (Fig. 5E).—Biramous; peduncle 3-segmented, falling short of cornea, bearing numerous naked setae; upper ramus 4-segmented, aesthetascs and setae

progressing distally (0), (6), (4 + 1 long, 3 short setae), (3 + 1 long, 4 short setae terminally); lower ramus 2-segmented, 2, 6 setae.

Antenna (Fig. 5F).—Peduncle 5-segmented; distodorsal margin of second segment bifurcated into 2 strong teeth, 3rd to 5th segments setose; acicle produced apically into 2 acute teeth, 1 large, 1 small, other setae as shown; flagellum with 10 articles of varying length, each bearing sparsely plumose setae.

Mandibles (Fig. 5G).—Much reduced, spatulate, simple; mesial margin with single blunt tooth; palp apparently 3-segmented, weakly chitinized, distalmost article bearing 4 or 5 short, curved, denticulate spinules.

Maxillule (Fig. 5H).—Endopodite naked, incompletely 3- or 4-segmented; coxal endite with 7–9 setae; basal endite with about 9–11 teeth in 2 rows of 5 or 6, 4 or 5, plus 10 long and short setae anterior and adjacent to these; single long seta basally; basal portion of coxal endite developed into rounded, diaphanous flap bearing single thin seta.

Maxilla (Fig. 5I).—Endopodite unsegmented, single subterminal seta; basal endites with 8, 9, coxal endites with 7, 6, processes; scaphognathite well developed, lower lobe rectangular, about 31 long marginal setae, and 3 short plumose setae on blade.

Maxilliped 1 (Fig. 5J).—Exopodite obscurely 2-segmented, 1 and 8 plumose setae; endopodite poorly chitinized, unsegmented, 1 basal seta; basal endite with about 14 setae in 2 long proximal pairs plus 6 or 7 shorter lateral pairs; coxal endite with 4 setae.

Maxilliped 2 (Fig. 5K).—Exopodite distinctly 2-segmented, 8 terminal setae; endopodite 4-segmented, basal 5th article very obscurely defined from protopodite, setae progressing distally 1, 2, 0, 2, 6; protopodal setae not exactly determined.

Maxilliped 3 (Fig. 5L).—Exopodite 2-segmented, 1 lateral, 8 plumose apical setae; endopodite 5-segmented, numerous barbed, plumose and simple setae as illustrated; propodal article bearing 4 distinctly curved denticulate setae; no cresta dentata observed; propodal setation not determined.

Pereopods (Fig. 6A–F, f).—Chelipeds unequal, right larger than left, elongate, well developed, setose; carpus of major chela with large dorsal tooth, smaller tooth laterally; cutting edges of propodus and dactyl irregularly serrate; minor chela carpus with large dorsal tooth; other articles unarmed except for dactyl which possesses row of minute teeth on cutting edge. Pereopods 2 and 3 long, slender, setose, propodi with single distoventral spine, dactyls with 3 and 4 ventral teeth, respectively; pereopod 4 short, not reaching midpoint of merus of pereopod 3, setose, propodus inflated, 6 large rounded teeth along ventral margin, dactyl short, 3 minute teeth before corneous tip; pereopod 5 short, about equal in length to pereopod 4, setose, propodus with about 7 dentostegous processes dorsally, 3 elongate recurved setae, pectinate distally, dactyl extremely small, 2 dorsal dentostegous processes plus 2 acute teeth terminally.

Color.—Postlarval stage beautifully colored; cephalic shield with 4 large red patches interiorly, 2 patches coloring mouthparts as seen through frontal region, 2 patches interlaterally on epibranchial areas; 3 creamy yellow elongate patches extending longitudinally on lateral surface of left and right sides of cephalothorax, these matched by 2 pairs on middorsal and posterodorsal regions of cephalic shield; sternal region and pereopodal coxae lighter red-orange blending into diffuse creamy

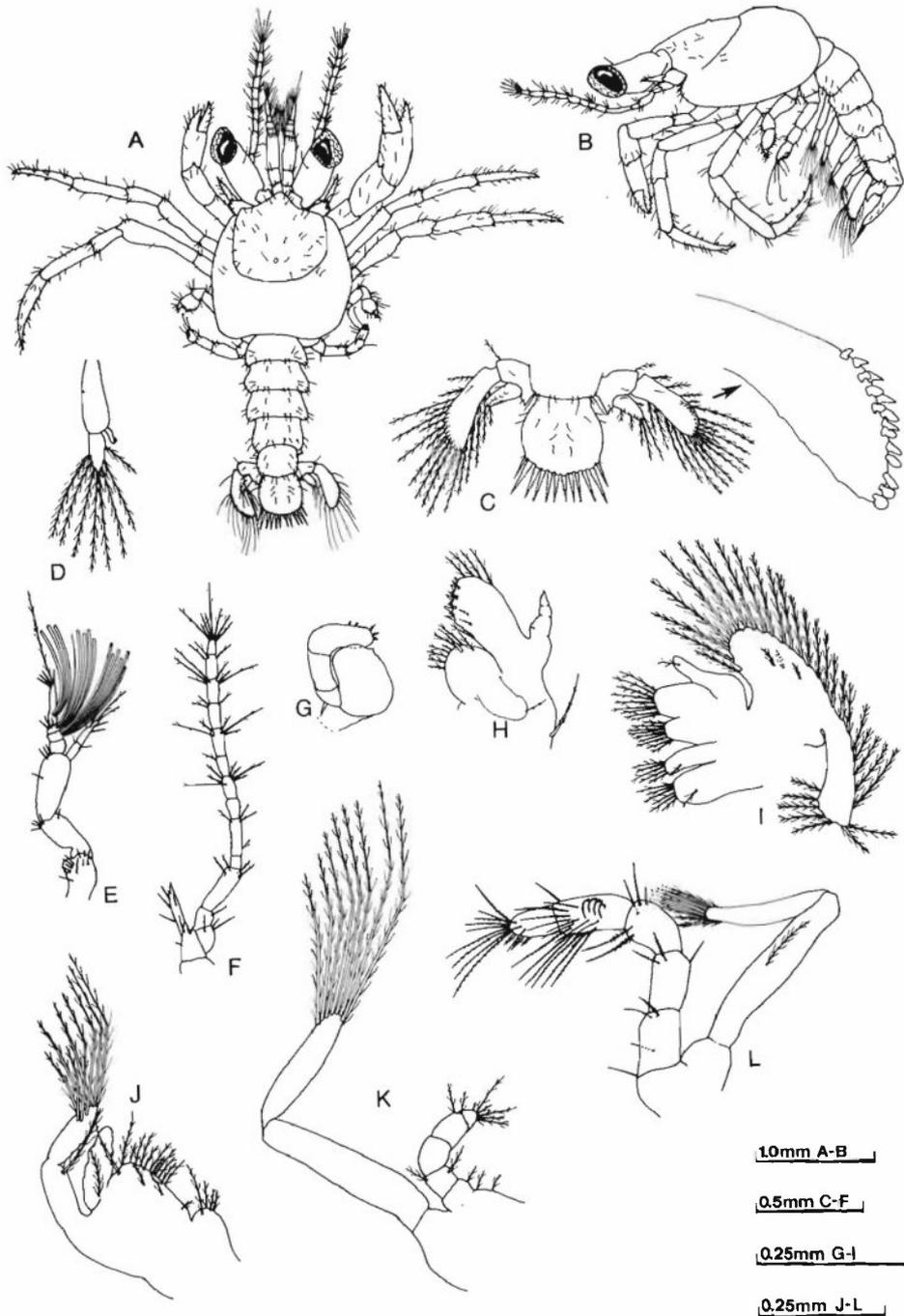


Fig. 5. *Phimochirus holthuisi* (Provenzano): Glaucothoe. (A) Dorsal view; (B) lateral view; (C) tail fan, dorsal view; detail, uropodal exopodite without setae; (D) first pleopod; (E) antennule; (F) antenna; (G) mandible; (H) maxillule; (I) maxilla; (J) maxilliped 1; (K) maxilliped 2; (L) maxilliped 3. Length of natatory setae not completely illustrated.

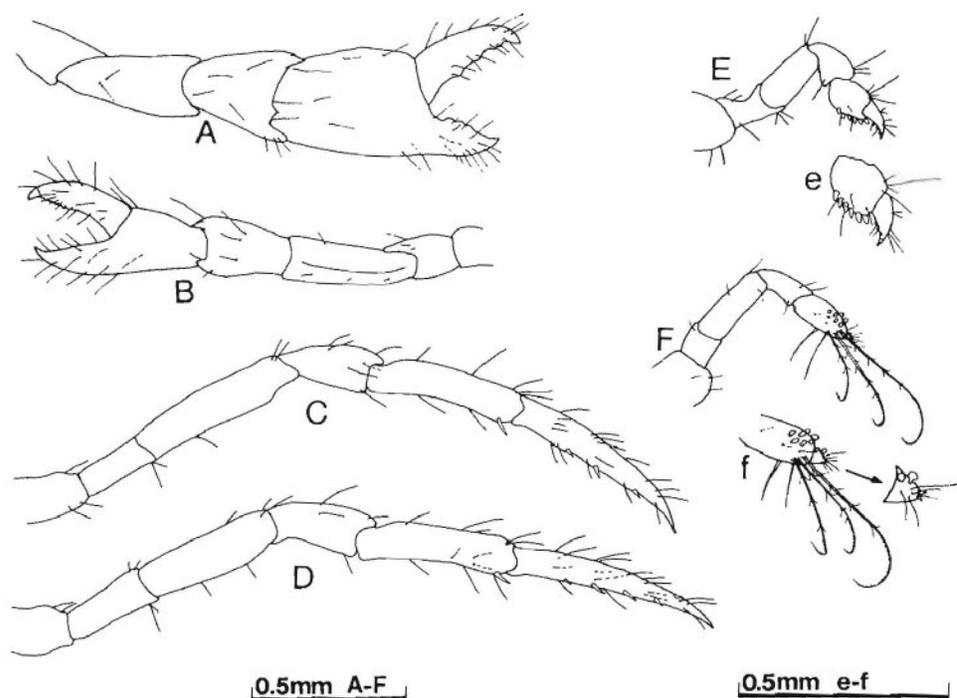


Fig. 6. *Phimochirus holthuisi* (Provenzano): Glaucothoe. (A) Major cheliped; (B) minor cheliped; (C) second pereopod; (D) third pereopod; (E) fourth pereopod; (e) detail, propodus and dactyl; (F) fifth pereopod; (f) detail, propodus and dactyl.

color over entire ventral surface of cephalothorax; eyestalks with diffused cream color at base extending along mesial margins, overlain by row of minute red chromatophores, posterior margins outlined by bright red streak extending from ophthalmic base to cornea; under higher magnification each eyestalk having numerous creamy yellow spiderlike chromatophores both interiorly and laterally, appearing like light gold filigree extending to corneas; latter reflecting blue light. Antennal flagella transparent except last 2 articles which are orange. Chelipeds transparent with large creamy yellow patches on distal half of carpus and manus; these each overlain by large, red spiderlike chromatophores, single at the meral-carpal junction, paired at the carpal-propodal junction and at base of movable finger; walking legs transparent; pereopod 4 coxa and basis creamy yellow overlain by red chromatophore, ischium without chromatophore, merus with large single red spot; pereopod 5 ischium and merus each with single red chromatophore. Abdomen transparent overall, diffused creamy patches at bases of pleopods, uropods, and paired dorsomedially on telson; large paired bright red chromatophores overlying those on telson, and connecting posterodorsal and anterodorsal margins of somites 5 and 6, respectively.

DISCUSSION

The zoeal stages of *Phimochirus holthuisi* can be separated from other known larvae in the Paguridae, Coenobitidae, Diogenidae, and Parapaguridae in the plankton by using collectively a series of morphological characters. Those not

requiring dissection are: 1) the acute, narrow, bladelike rostrum that never overreaches the antennule or antenna, and which becomes progressively dorsoventrally flattened as development proceeds; 2) the presence of a short but distinct dorsomedian carina on the carapace; 3) the absence of posterolateral spines on the carapace; 4) the presence of a strong distolateral spine on the antennal scaphocerite; 5) the lack of a hooked spine on the anteroventral margin of maxilliped 1; 6) the presence of paired setae instead of spines on the dorsomedial margins of the abdominal somites; 7) the nonarticulation and sparse setation of the uropodal endopods in stages III and IV, and the acute distolateral spine on the uropodal exopods; 8) the slight but progressive change of shape in the telson from elongately spatulate to more squarely spatulate in later zoeal stages; 9) the retention of articulation of all telsonal processes in every zoeal stage; 10) the posterior marginal formula of $1 + ii + 3-7$, and $1 + ii + 3-8$ in the zoeae, without further addition of medial spines or fusion of any processes; 11) the appearance of paired dorsal setules on the telson in stage IV; and 12) the occurrence of biramous pleopod buds on abdominal somites 2-5 in the last zoeal stage.

Other distinguishing characters require dissection to observe and include: 1) the presence of a mandibular palp in stage IV; 2) the 3-segmented maxillary endopodite bearing a setal formula of $2 + 1 + 3$ in every stage; 3) the bilobed maxillary endopodite with a constant setal formula of $3 + 4$; 4) the appearance of a naked apical lobe on the maxillary scaphognathite in stage IV; 5) the presence of only 2 setae on the antennal endopodite in stages I and II plus the ultimate reduction of that article to an elongate, spinelike rod bearing a single thin hair; and 6) the appearance in stage II and thereafter of a small, distinct accessory protopodal spine on the antenna. Although some of these characters are also seen in other paguridean larvae, except for *Phimochirus* no known larvae in any family exhibits all of these characters collectively.

The glaucothoe of *Phimochirus holthuisi* is also distinctive, and may be separated from other paguridean postlarvae by using the following combination of easily observed characters: 1) the presence of ocular acicles; 2) a single long seta on the dorsomesial area of each eyestalk; 3) the bluntly rounded, slightly produced rostrum; 4) a prominent dorsomedian gastric tubercle (a remnant of that seen in the zoeae); 5) the dissimilar size of the chelipeds, the right larger than the left; 6) the presence of movable spines (and not fixed teeth) on the ventral margins of the propodus in the first and second walking legs; 7) 11 articulations, and the terminal setal tuft, on the antennal flagella; 8) the absence of a crista dentata on maxilliped 3; 9) a strong protopodal spine, plus numerous setae on the articulated endopods of the uropods; 10) the occurrence of 12 spines plus 2 fine hairs on the posterior margin, and paired setae on the dorsal surface, of the telson; and 11) paired biramous pleopods on abdominal somites 2-5.

Comparative characters differing from those seen in other glaucothoes, but requiring dissection to observe, include: 1) the unidentate margin of the mandible and the reduced setation on the 3-segmented palp of that appendage; 2) the naked endopodite, diaphanous flap on the coxal endite base, and single basal seta on the protopodite of the maxillule; and 3) the single seta on the unsegmented maxillary endopodite, and the scattered setules on the proximal portion of the scaphognathite. In addition, careful comparison of setal formulae and position of setae on the mouthparts will reveal additional differences useful in separating *Phimochirus* postlarvae from other paguridean glaucothoes in the plankton.

Finally, the position and color of chromatophores in both zoeal and glaucothoeal stages may be of aid in identifying living, or recently preserved, planktonic material. Unfortunately, color notes are often incomplete, or totally lacking in many

Table 2. Comparison and zoeal characters in four families of Paguridea.

COENOBITIDAE*	
Stages	4, 5, or 6
Rostrum	Narrow, daggerlike, tapering, margins smooth.
Carapace	Smoothly rounded, but with short dorsomedian carina. No posterolateral or pterygostomian spines.
Abdomen	
Lateral spines	Paired, somite 5 only.
Dorsomedial spines	Singly, somites 2-5 (<i>Coenobita</i>); absent in <i>Birgus</i> except paired on somite 5; small single spine somite 6, stages III-V (or VI).
Telson	
Process morphology	Usually setaelike.
Stage III	T4 enlarged, fused. T2 may disappear in <i>Coenobita</i> , stage V. Single 9th median process added stage III, no other processes thereafter.
Antenna	
Endopod setae	2 terminal, 1 subterminal stages I + II; single terminal seta thereafter.
Scaphocerite	Distolateral spine present. Outer marginal setae absent.
Mandibular palp bud	No data available.
Maxillule	
Endopod segments	3
Endopod setae	1 + 1 + 3 stage I; 0 + 1 + 3 (<i>Coenobita</i>), 0 + 0 + 3 (<i>Birgus</i>) remaining zoeal stages.
Maxilla	
Endopod segments	3 fused; bilobed.
Endopod setae	Probably 2 + 3 all stages <i>Coenobita</i> , <i>Birgus</i> stages I + II; 3 + 4 in <i>Birgus</i> later stages.
Scaphognathite	Smooth apical lobe penultimate (<i>Birgus</i>) and ultimate (<i>Coenobita</i>) stages.
Pleopods	Present somites 2-5 in penultimate (<i>Birgus</i>) and ultimate (<i>Coenobita</i>) stages.
Uropods	Both rami articulated in penultimate zoeal stage.
Endopod	Numerous setae present. Not greatly reduced or modified in late zoeae or glaucothoe.
DIOGENIDAE†	
Stages	2-5, up to 7 (<i>Dardanus</i>) or 8 (<i>Calcinus</i>).
Rostrum	Usually broad, daggerlike to rounded apically, margins smooth.
Carapace	Usually smoothly rounded; dorsal carina (some <i>Paguristes</i> , <i>Calcinus</i> , <i>Clibanarius</i> , <i>Trizopagurus</i>); ridged, grooved (<i>Petrochirus</i>); scalelike spines (<i>Dardanus</i>); tubercles (<i>Trizopagurus</i>). No posterolateral spines; submarginal posterior spines (<i>Calcinus</i>); pterygostomian spines (<i>Paguristes</i>).
Abdomen	
Lateral spines	Usually paired somite 5 (except <i>Clibanarius</i> , <i>Petrochirus</i>).
Dorsomedial spines	Usually none; paired somite 5 (<i>Diogenes</i>); singly somite 5 (<i>Calcinus</i>); trispinose somite 5 (<i>Trizopagurus</i>); singly somites 2-5 some <i>Paguristes</i> .

Table 2. Continued

DIOGENIDAE†	
Telson	
Process morphology	Usually setaelike (spinelike in <i>Paguristes</i>).
Stage III	T4 enlarged, fused (<i>Calcinus</i> , <i>Dardanus</i> , <i>Petrochirus</i>). T4 unfused (<i>Paguristes</i>). T4 reduced, disappears (<i>Diogenes</i> , <i>Clibanarius</i>). T1 reduced, disappears (<i>Petrochirus</i>). 9th pair of processes added (except <i>Diogenes</i>).
Antenna	
Endopod setae	Usually 3 terminal, stages I + II (2, <i>Diogenes</i> , <i>Calcinus</i> ; 1, some <i>Paguristes</i>); outermost seta reduced, becoming subterminal usually a single seta stage III and later.
Scaphocerite	Distolateral spine usually present; if absent, outer marginal setae may be present (<i>Clibanarius</i> , <i>Petrochirus</i>).
Mandibular palp bud	Usually present stage IV, or ultimate zoeal stage.
Maxillule	
Endopod segments	0-3
Endopod setae	Usually 1 + 2, 1 + 3, 1 + 1 + 3, or varying combination.
Maxilla	
Endopod segments	2 fused; bilobed.
Endopod setae	Usually 2 + 2 (<i>Calcinus</i> , <i>Clibanarius</i> , <i>Dardanus</i> , <i>Diogenes</i> , <i>Petrochirus</i>); 3 + 2 + 3 (<i>Paguristes</i>).
Scaphognathite	Smooth apical lobe usually added last zoeal stage, may bear 1 or few setae.
Pleopods	Present somites 2-5 in ultimate zoeal stage (somites 2-4 in <i>Diogenes</i>).
Uropods	Both rami articulate with protopod stage IV, V, or last zoeal stage (except some <i>Diogenes</i> , <i>Paguristes</i>).
Endopod	Usually more than 2 setae (except some <i>Diogenes</i> , <i>Paguristes</i>). Not greatly reduced or modified in late zoeae or glaucothoe (except some <i>Diogenes</i> , <i>Paguristes</i>).
PARAPAGURIDAE‡	
Stages	4-6?
Rostrum	Elongate, broad at base, narrow distally with parallel margins, smooth, may be ventrally turned at tip.
Carapace	Dorsal carina present; grooves and ridges or prominent denticles may also be present; a dorsal spine may occur (Larva N.3 of Pike and Williamson, 1960 [<i>Sympagurus</i> "= <i>Parapagurus</i>]). Posterolateral spines absent; pterygostomian spines may be present; directed laterally.
Abdomen	
Lateral spines	May be paired somite 5; absent in some species.
Dorsomedial spines	Spines or setae may be present or absent on somites 2-5.
Telson	
Process morphology	Usually setaelike.
Stage III	T4 may be enlarged, fused, unchanged and articulated, or reduced in later stages. T1, T1-3 may be reduced or lost in later stages of some species. Additional processes (up to 13) may be added in later stages.
Antenna	
Endopod setae	3 terminal (stage I), 2 terminal (stage II), 1 terminal (stage III and thereafter).

Table 2. Continued

PARAPAGURIDAE†	
Scaphocerite	Distolateral spine present, often reduced or lost in later stages.
Mandibular palp bud	Present in penultimate stage in at least 1 species.
Maxillule	
Endopod segments	3
Endopod setae	0 + 1 + 3 setae as far as is known.
Maxilla	
Endopod segments	3? fused segments; bilobed.
Endopod setae	2 + 3 or 2 + 4.
Scaphognathite	Smooth apical lobe present last zoeal stage.
Pleopods	Present on somites 2-5 in last 2 zoeal stages some species.
Uropods	Endopod may or may not articulate with protopod last zoeal stage.
Endopod	Numerous setae present. Shorter than exopod in penultimate and ultimate zoeal stages.
PAGURIDAE‡	
Stages	4 (rarely 3).
Rostrum	Smooth, narrow, tapering, occasionally spindle-shaped, or short.
Carapace	Smoothly rounded (most <i>Pagurus</i>); short or long dorsal carina or prominent dorsal spine may be present (some <i>Pagurus</i> , <i>Labidochirus</i> , <i>Phimochirus</i> , <i>Acanthopagurus</i>); strong dorsolateral ridge (some <i>Pagurus</i> , <i>Labidochirus</i> , <i>Pylopaguropsis</i>); inflated, globose (<i>Munidopagurus</i>). Posterolateral spines usually present (except some <i>Pagurus</i> , and <i>Munidopagurus</i> , <i>Lithopagurus</i> , <i>Parapagurodes</i> , <i>Phimochirus</i>); spines dorsolateral (<i>Pylopaguropsis</i>).
Abdomen	
Lateral spines	Usually paired somite 5; small or absent (<i>Anapagurus</i> , ? <i>Spiropagurus</i> , <i>Lithopagurus</i> , at least 1 <i>Pagurus</i>); occasionally on somites 2-5 (some <i>Pagurus</i> , and <i>Labidochirus</i>).
Dorsomedial spines	Usually paired or multidentate somites 2-5 (except 1 <i>Pagurus</i>); vestigial or absent (<i>Lithopagurus</i> , <i>Spiropagurus</i> , <i>Phimochirus</i>).
Telson	
Process morphology	Usually spinelike (setaelike some <i>Pagurus</i>).
Stage III	T4 broad, long, fused in many genera and species. T4 unchanged, articulated in some <i>Pagurus</i> , <i>Labidochirus</i> , <i>Phimochirus</i> . T4 reduced in some <i>Pagurus</i> . No processes added in zoea III or later (except <i>Lithopagurus</i> and related forms).
Antenna	
Endopod setae	2 terminal setae Stages I + II; naked (some <i>Pagurus</i> , <i>Labidochirus</i>); 2 small teeth (<i>Munidopagurus</i>); as bifid spine (some <i>Pagurus</i>); or naked lobe (<i>Lithopagurus</i>); with 2 spinules (<i>Acanthopagurus</i>).
Scaphocerite	Distolateral spine usually present; doubled or multidentate (<i>Pylopaguropsis</i> , <i>Lithopagurus</i>).
Mandibular palp bud	Usually absent most genera; present some species of <i>Pagurus</i> , and <i>Phimochirus</i> , last zoea.

Table 2. Continued.

PAGURIDAE§	
Maxillule	
Endopod segments	Usually 3; 0 or 2 in some species.
Endopod setae	Generally 0 + 1 + 3, 1 + 1 + 3 or 2 + 1 + 3, but other variations occur.
Maxilla	
Endopod segments	2 or 3 fused segments based on setal formulae; appearing more or less bilobed.
Endopod setae	2 + 3, 3 + 3, 3 + 4 or combinations thereof, apparently not restricted within genera or species.
Scaphognathite	Smooth apical lobe usually present last zoeal stage (sparsely setose some <i>Pagurus</i>); lobe absent some <i>Pagurus</i> , <i>Pylopaguropsis</i> .
Pleopods	Present somites 2-5 in ultimate zoeal stage; somites 2-4 (some <i>Anapagurus</i> , <i>Spiropagurus</i>); somites 2, 3 (other <i>Anapagurus</i>).
Uropods	
Endopod	Endopod never articulates with protopod in last zoeal stage. Usually 2 setae or less; 3 in <i>Pylopaguropsis</i> . Uropods symmetrical in zoeal stages; left greater than right in glaucothoe; endopod shorter than exopod, essentially nonfunctional in zoeae; reduced to short rod in glaucothoe.

* Data from Provenzano, 1962, and Reese and Kinzie, 1968.

† Data from authors listed in Lang and Young, 1977; also Le Roux, 1966; Nayak, 1981; Nayak and Kakati, 1977; Provenzano, 1978; Shenoy and Sankolli, 1977; Tirmizi and Siddiqui, 1979.

‡ Data from Williamson and Von Levetzow, 1967.

§ Data from authors listed in Nyblade and McLaughlin, 1975; also Fitch and Lindgren, 1979; Hebling and Brossi-Garcia, 1981; Hong, 1969; Ivanov, 1979; Lee and Hong, 1970; McLaughlin and Haig, 1973; Menon, 1937; Saint Laurent, 1969; Tirmizi and Siddiqui, 1980.

descriptions of paguridean larvae, preventing these attributes from being compared in any detail. The interested reader is directed to the extensive literature (especially papers cited herein by MacDonald *et al.*, Pike and Williamson, and Provenzano) for further information.

Relationships of *Phimochirus* Larvae with Other Paguridean Zoeae

In a series of earlier papers, MacDonald *et al.* (1957), Pike and Williamson (1960), and Sclezo and Boschi (1969) developed a synopsis of characters categorizing zoeae in the families Diogenidae and Paguridae. Provenzano (1962) and Reese and Kinzie (1968) provided data on larvae of *Coenobita* and *Birgus*, respectively, allowing the family Coenobitidae to be compared with pagurids and diogenids. Provenzano (1967, 1968a, 1971a) also compared the larvae of *Trizopagurus* and *Petrochirus* (Diogenidae), and *Pylopaguropsis* (Paguridae) with known larvae of other paguridean genera. St. Laurent-Dechancé (1964) and Williamson and Von Levetzow (1967) added data obtained on larvae attributed to *Parapagurus* (Paraguridae), and the latter authors provided an emended categorization for larvae of this family. More recent studies include Nyblade and McLaughlin's (1975) discussion of the relationships of *Labidochirus* to other pagurid larvae, and Lang and Young's (1977) summary of larval relationships within the Diogenidae. Table 2 summarizes these data and allows comparison of larval characters between *Phimochirus* and those occurring in larvae of related families.

Larvae of *Phimochirus holthuisi* cannot be assigned completely to any familial group because they share characters with each. Inasmuch as *Phimochirus* (and previously as *Pylopagurus*, *sensu lato*) is a member of the family Paguridae, it

comes somewhat as a surprise that the larvae of *P. holthuisi* completely disagree in several general characters delineating pagurid larvae, while sharing four or five characters either wholly or in part with larval members of the Diogenidae, Coenobitidae, and Parapaguridae. The most interesting of these are the lack of spines on the posterolateral carapace margins, the absence of abdominal spines, and the retention of setaelike processes, without fusion or addition of other processes, on the telson. Although these characters indicate that *Phimochirus* is clearly intermediate between pagurid-type larvae on the one hand, and diogenid-coenobitid-parapagurid-type larvae on the other, the preponderant relationship is still clearly pagurid (Table 2).

This situation is complicated, of course, by the fact that some characters are considered to be typically paguridean and thus are shared among the larvae of several genera in different families. Moreover, our knowledge is still insufficient to be able to determine just which characters will remain totally exclusive, because exceptions to one or the other classification often appear in the larvae of different species within the same genus. MacDonald *et al.* (1957) exemplified this problem when they attempted to formulate several groupings of larvae within the Paguridae, only to have later authors (e.g., Roberts, 1970) revise their categories or create new ones to which they assigned their differing pagurid larvae.

The question also involves determining which characters are primitive or plesiomorphic, and which are derived or apomorphic. For example, if the following suite of characters are correctly considered to be plesiomorphic, then the possession of four (instead of three or fewer) zoeal stages, plus the retention of a distolateral spine on the antennal scaphocerite, a three-segmented maxillulary endopodite and its concomitant setation, and the relatively slow development of the third maxilliped would all indicate that *Phimochirus* larvae are less advanced than some pagurid, and many diogenid larvae.

On the other hand, some presumably apomorphic characters seen to a great extent in the Diogenidae, also occur in *Phimochirus holthuisi*. These include the lack of posterolateral spines on the carapace, and no dorsal abdominal spines, the presence of abdominal dorsal setae, the reduction of the antennal endopod to a spinelike process in later zoeal stages, and reduced formulae and retention of articulation in the telsonal setae. A major difference between *Phimochirus* larvae and most diogenid larvae is in the nonarticulation of the uropodal endopods with the protopod in the last zoeal stage of *P. holthuisi*, and the presence of only 2 setae (instead of many) on the endopodal buds.

A comparison with genera in other families shows additional similarities. Thus, the generally decreased spination seen in many diogenid and coenobitid larvae implies that these zoeae may also be more advanced than those of most pagurids, although to be sure some diogenid genera retain presumably less advanced features; for example, a setose antennal endopod in early stages, absence of an apical scaphognathite lobe in the last stage, and more than four zoeal stages. The Coenobitidae, being terrestrial forms as adults, might be thought the most advanced, but their larvae nevertheless retain allegedly primitive features including additional zoeal stages, fused fourth telsonal spines, and three-segmented maxillulary endopods. The Parapaguridae, a notably aberrant group, also possess larvae that exhibit a varying array of both supposedly primitive, and advanced, characters, which often are not shared between species in the same genus. Possibly primitive characters include a multisetose telson with fused spines (e.g., 1 + ii + 3-10, 1 + ii + 3 + IV + 5-13 in later zoeal stages), setose antennal endopods, articulation of uropodal endopods in the ultimate zoeal stage, a three-segmented maxillulary endopod, and more than four zoeal stages in development. Derived characters

Table 3. Comparison of glaucothoeal characters in four families of Paguridea.

	COENOBITIDAE	DIOGENIDAE	PAGURIDAE	PARAPAGURIDAE
Ocular scales	Absent	Usually absent (except some <i>Diogenes</i> and <i>Clibanarius</i>).	Present or absent (variable in some <i>Pagurus</i> species).	No data available on any glaucothoe in the family.
Chelipeds	Symmetrical	Usually symmetrical (left larger than right in <i>Diogenes</i> ; right larger than left in <i>Petrochirus</i>).	Right usually larger than left (except in some <i>Pagurus</i>).	
Telson formula	<i>Birgus</i> : 6-9 setae <i>Coenobita</i> : 9 setae	Variable, not consistent within a genus. <i>Diogenes</i> : 3 or 4 setae, posterolateral spines may be present. <i>Trizopagurus</i> : 8 setae. <i>Clibanarius</i> : 8 or 9 setae. <i>Calcinus</i> : 9-15 setae. <i>Paguristes</i> : 10-13 setae. <i>Petrochirus</i> : 11-13 setae. <i>Dardanus</i> : 12-17 setae, posterolateral spines may be present.	Usually 8 setae. Some <i>Pagurus</i> with 6 or 10; posterolateral spines may be present; <i>Labidochirus</i> with 8 or 9 setae plus 2 or 3 fused posterolateral teeth; <i>Phimochirus</i> with 12 processes.	

Data from sources listed in Table 2.

exhibited in concert with those just noted are the lack of posterolateral carapacial spination, dorsal setae (but no dorsal spines) on the abdominal somites, the reduction or loss of the distolateral scaphocerite spine in later zoeae, and the articulation or possible loss of the first telson process. As noted by Williamson and Von Levetzow (1967) the larvae of the Parapaguridae show links to both diogenid and pagurid larvae. When compared with larvae of *Phimochirus* these links seem to be more of degree than of kind, although the zoeal stages of *Parapagurus* and *Phimochirus* are certainly sufficiently distinct from one another in general morphology. The transitional nature of these resemblances, however, remains intriguing, and a phylogenetic basis for such cannot at present be ruled out.

While *Phimochirus* may not be expected to fit within any of the proposed groupings for *Pagurus* larvae summarized by Roberts (1970), it is interesting to see the general resemblance of many *P. holthuisi* zoeal characters with those listed in groups B and C. Chief differences are in the relatively short lateral spines on abdominal somite 5, the presence of 10 (not 9) setae on the scaphocerite in stage I, 3 setae on the uropodal endopod (instead of 2), and the presence of a mandibular palp (absent) in stage IV. With the recent division of *Pylopagurus* by McLaughlin

(1981a, b) we may expect to see similar groupings in the related taxa as their larvae become known.

In summary, the zoeal stages of *Phimochirus holthuisi* are definitely pagurid in larval characters, but appear to be slightly more advanced than most zoeae in the Paguridae, in possessing several features often seen in diogenid and parapagurid zoeae, and to a lesser extent in coenobitid larvae. However, with larvae from only one species of *Phimochirus* presently known, the importance of these features as transitional links between Paguridae, Diogenidae, and Parapaguridae cannot be assessed.

Relationships of *Phimochirus* Glaucothoes with Other Paguridea

As seen in Table 3, the glaucothoe of *Phimochirus holthuisi* exhibits primarily pagurid characters in possessing ocular scales, slightly disparate chelipeds, and numerous setae on the endopods of the uropods. Although some diogenid glaucothoes also have ocular scales (*Diogenes*, *Clibanarius*), the presence of less than 12 processes on the posterior telson margin (3 or 4 in *Diogenes*, 8 or 9 in *Clibanarius*) is sufficient at present to separate the postlarvae of these genera from *Phimochirus*. In fact, based on a survey of the available literature, most glaucothoeal stages appear to possess many of the features which will characterize the adult stages of the various species, so that both identification, and eventually perhaps general phylogenetic relationships, may be easier to determine intragenerically.

Within the Paguridae, however, the situation remains unclear, although as a generality it can be said that *Phimochirus* seems to show closest relationships with many (but not all) *Pagurus*. Thus, a comparison of *Phimochirus holthuisi* with *Pagurus similis* glaucothoe (one of 2 species of *Pagurus* in which posterolateral carapace spines are lacking in the zoeae) shows that a general resemblance exists in the glaucothoeal antennule, antenna, mandible, maxillule, and the apparent absence of a crista dentata on maxilliped 3. However, because so few glaucothoes have been described for other pagurid genera little more can be said. Nyblade and McLaughlin (1975) provided a concise summary of both larval and postlarval relationships among the known Paguridae, and our knowledge has advanced but little since then.

Polyphyly in the Paguridae?

Pike and Williamson (1960) hypothesized that the genus *Pagurus* might be polyphyletic, because of the range of characters found in the zoeae of the various genera, and the derivation of four groups of features separating *Pagurus prideauxi-bernhardus*, *Anapagurus*, and *Pagurus anachoretus*. However, more recent evidence obtained from larval pagurids in the unusual genus *Lithopagurus*, and from *Pylopaguropsis* and *Munidopagurus* (Provenzano, 1968b, 1971a, b), and now from *Phimochirus* as well, suggests instead that the family Paguridae may be polyphyletic. Dechancé (1961) had also alluded to this in her study on *Catapaguroides* (= *Cestopagurus*) larvae. Further evidence appeared in studies by Saint Laurent-Dechancé (1966) on adult pagurids that produced three major generic groups, and laid the foundation for the ultimate resurrection of the Parapaguridae from Paguridae (Saint-Laurent, 1972). Provenzano's studies showed that *Lithopagurus*, *Munidopagurus*, and *Pylopaguropsis* larvae differed in many respects from typical pagurid zoeae, but that the three genera shared some important characters, including a widely spatulate telson with a multiprocess formula in all zoeal stages, as well as exhibiting relationships in scaphocerite and carapacial features. However,

no clear derivation from either a pagurid or diogenid line was apparent. A similar situation occurs in *Phimochirus* larvae, which show the following resemblances to other paguridean zoeae: 1) a *Clibanarius*-type carapacial and abdominal armature; 2) a telson shaped like that of some *Anapagurus* or perhaps *Parapagurodes*, but having a *Diogenes* or *Labidochirus* type of setal formula (at least in the early stages); 3) a typically *Pagurus*-like antenna; 4) an antennule reminiscent of *Calcinus* or some species of *Pagurus*; 5) a mandibular palp ontogeny assignable to any of several genera in either of the four paguridean families being considered; and 6) a maxillipedal morphology similar to that of several pagurid and diogenid genera.

Although these characters may be merely a consequence of convergence, they also may alternatively reflect a phylogenetic trend, suggesting that *Phimochirus* was perhaps derived from an ancestral form possessing pagurid- and diogenid-like characters. Pike and Williamson (1960) attributed many of the similarities they observed in larvae of different genera within the Paguridae to convergence, but at the time of their study they had data from far fewer genera and species than are presently available. With increased attention being paid toward usage of mouthpart morphology in deriving relationships (e.g., Van Dover *et al.*, 1982) phylogenetic lineages may soon be clarified. However, if the larvae of *Phimochirus holthuisi* seem to offer evidence for polyphyly within the Paguridae, it still remains to be seen whether this can be supported using larvae from the eight other species in the genus. Perhaps more interesting would be the relationships revealed by the larvae from *Pylopagurus sensu stricto*, when they become known.

Finally, it should be noted again that phylogenetic evidence obtained from larval stages does not always agree with assessments based on adult morphology. For example, a recent re-evaluation of some larval and many adult characters by Dr. Patsy A. McLaughlin (MS, in preparation) provides evidence against polyphyly in hermit crabs. The latter study emphasizes yet again the dichotomy between using larval versus adult characters in attempting to erect phylogenetic schemes.

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The following catalogue numbers have been assigned for the adult female and larvae: USNM 191039 (National Museum of Natural History, Washington, D. C.); BM(NH) 1982:250 (British Museum (Natural History), London); IRCZM 89:5360 (Indian River Coastal Zone Museum, Ft. Pierce, Fl.; includes spent female).