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Larval Development of Pagurus longicarpus Say Reared in the Laboratory, I. Description of Larval Instars

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LARVAL DEVELOPMENT OF *PAGURUS LONGICARPUS* SAY REARED IN THE LABORATORY, I. DESCRIPTION OF LARVAL INSTARS[1]

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Thompson (1903) described from the plankton four zoeae and a megalopa which he ascribed to *Pagurus longicarpus.* Although his verbal description of the external anatomy is incomplete, his figures are adequate to identify accurately the species with which he was working. His description of the internal anatomy is the most complete study available for any decapod larva. He indicated that some larvae of *P. annulipes* were included in his study material but that he was unable to differentiate the two species.

MacDonald, Pike, and Williamson (1957) and Pike and Williamson (1959, 1960) described the larvae of several British and Mediterannean *Pagurus* species from carefully constructed plankton series. They were able to distinguish three types of larvae in this genus, based on 12 larval characteristics (several of which were composites of two characteristics), suggesting that the genus *Pagurus* may be polyphyletic, but no division of the genus was attempted for lack of adult characteristics supporting the larval data.

Larvae of several additional *Pagurus* species have been described from culture experiments by Coffin (1958, 1960), Hart (1937), Provenzano and Rice (1964) and Shenoy (1967). In addition, *P. bernhardus* has been cultured by Bookhout (1964) and A. Le Roux (personal communication) and shown to agree in all essentials with the description given by MacDonald *et al.* (1957).

This paper deals with the external anatomy of *P. longicarpus* larvae reared in the laboratory. It is clearly demonstrated that Thompson (1903) attributed his larvae to the wrong species and a suggestion is made as to the correct identity of his larvae.

Materials and Methods

Ovigerous *P. longicarpus* were collected from the beach at Gloucester Point, Virginia. Some crabs were maintained at room temperature in finger bowls with filtered water (salinity: 19–22‰). The water was replenished once or twice daily until hatching occurred. This method had two disadvantages: first, there was a danger of hatching occurring without molting the embryonic or prezoeal

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cuticle; second, adult hermit crabs kept in small containers eat many larvae before they can be removed. These problems were overcome in some experiments by removing the eggs from the pleopods of the crabs and culturing the eggs artificially (Costlow and Bookhout, 1960).

Larvae were cultured individually in compartmented plastic boxes with nauplii of *Artemia salina* as food. No bactericide was used and water was changed daily. Living specimens of each instar were preserved in 70% ethanol with 10% glycerol as were exuvia and dead specimens. Live specimens proved most satisfactory for study as they were less likely to be damaged and easier to handle and dissect.

Several larvae in each instar were dissected under 85% lactic acid and mounted in a modified Hoyer's medium for study and figuring. Figures of entire specimens and various appendages were drawn with the aid of an ocular grid and graph paper. Verbal descriptions, prepared from figures and notes taken during study, were subsequently checked against additional specimens. Notes on color were made while observing living larvae immobilized mechanically as suggested by Dean and Hatfield (1963). Larvae handled in this manner survived when returned to the culture dish and showed no obvious deleterious effects.

The following abbreviations are used throughout the description: A 1 = antennule, A 2 = antenna, Mn = mandible, Mx 1 = maxillule, Mx 2 = maxilla, Mxp 1 = first maxilliped, Mxp 2 = second maxilliped, Mxp 3 = third maxilliped, P 1 to 5 = pereiopods 1 to 5, Pl 2 to 5 = pleopods 2 to 5, U = uropods.

Results

Four zoeal stages and a megalopa were obtained. No prezoea was observed except when culture conditions for the eggs were known to be suboptimal. Examination of egg membranes revealed that the embryonic or prezoeal cuticle normally is shed at the time of hatching and remains attached to the egg membrane. It is concluded that the prezoea is not a true planktonic stage and therefore no description is given.

Zoea I (Figure 1)

Rostrum unornamented, curved slightly ventrad, approximately equal to A 1 and A 2. Carapace with small posterolateral spines pointed ventrally. Eyes unstalked. Abdomen with 5 somites plus fused 6th somite-telson. Somites 2 through 5 with 2 pairs of posterodorsal spines and one pair of ventrolateral spines, those of somite 5 longest, reaching fusion of 6th somite-telson. Pleopod buds and uropods absent. Telson formula 7 + 7; process 1, lateral spur; process 2, short ventral hair; processes 3 to 7, long articulated plumose setae, process 4 longest. Fine hairs between processes. Small median notch. Anal spine present.

A 1 (Fig. 1C)—Uniramous, unsegmented, with 4 terminal aesthetascs and a long subterminal plumose seta.

A 2 (Fig. 1D)—Scale with 8 (7–9) plumose setae on inner margin and terminal spur. Endopod about ½ length of scale, fused to peduncle, with 2 terminal plumose setae. Short strong seta with cuneate setules on peduncle near endopod.

Mn (Fig. 1E)—Incisor and molar processes present, palp absent.

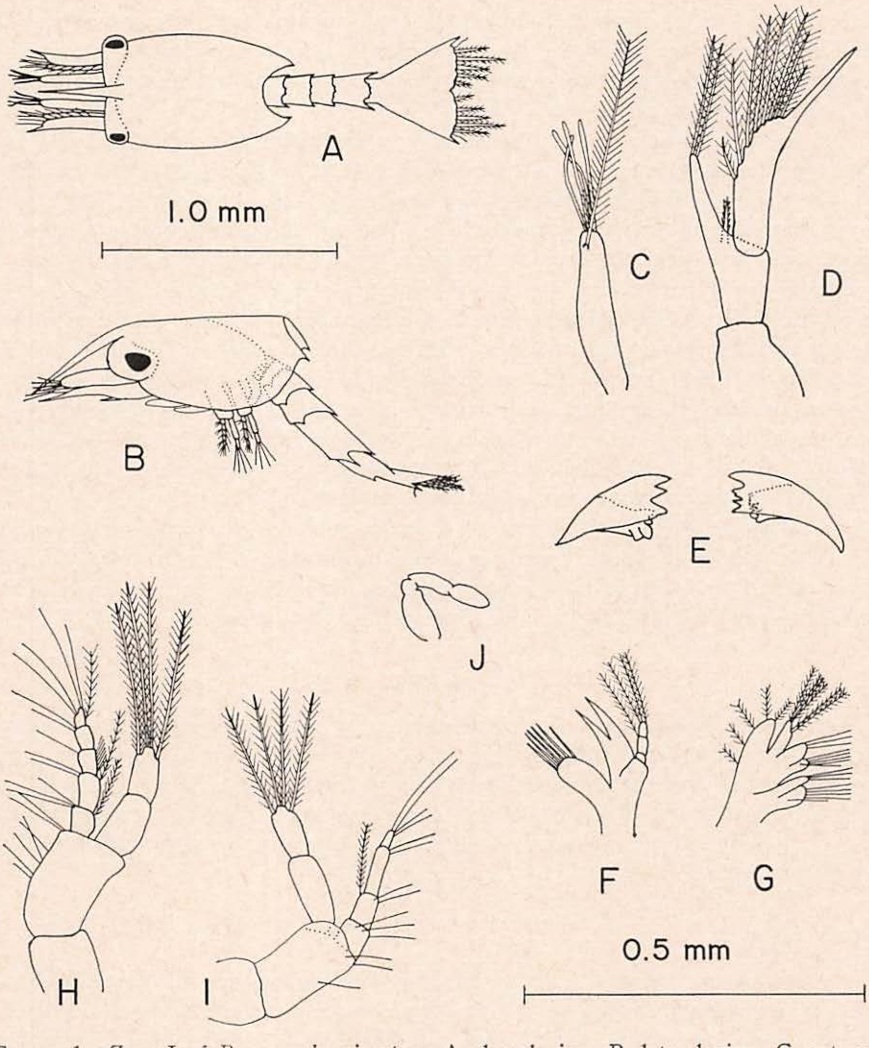

FIGURE 1. Zoea I of *Pagurus longicarpus;* A. dorsal view, B. lateral view, C. antennule, D. antenna, E. mandibles, F. maxillule, G. maxilla, H. 1st maxilliped, I. 2nd maxilliped, J. 3rd maxilliped.

Mx 1 (Fig. 1F)—Coxal endite with 6 setae, basal endite produced into 2 strong spines. Endopod 3-segmented with 3 terminal plumose setae and an additional seta distomedially on second segment.

Mx 2 (Fig. 1G)—Coxal and basal endites bilobed, both with 5 setae on proximal lobe, 3 on distal lobe. Endopod unsegmented with 4 terminal and 2 subterminal setae. Scaphognathite with distal lobe bearing 5 marginal plumose setae.

Mxp 1 (Fig. 1H)—Coxa nude, basis with 7 setae on inner margin. Endopod 5-segmented: long plumose seta on outer margin of segments 1, 2, and 5; fringe of fine hairs on outer margin of segment 3; 3, 2, 1, 2, 4 setae on inner margin of segments 1 to 5. Exopod 2-segmented, with 4 terminal plumose setae.

Mxp 2 (Fig. 1I)—Coxa nude, basis with 3 setae on inner margin. Endopod 4-segmented: long plumose seta on outer margin of segment 2; 3, 2, 2, 4 setae on inner margin of segments 1 to 4. Exopod 2-segmented, with 4 terminal plumose setae.

Mxp 3 (Fig. 1J)—Uniramous unsegmented rudiment, flexed anteriorly and medially between bases of Mxp 2.

P 1 to 5 (Fig. 1B)—Barely distinguishable rudiments initially but noticeably larger by end of stage.

Pigmentation—Red chromatophore midway along rostrum, few if any chromatophores on rest of carapace at hatching, several pairs developing during this stage near posterior margin. Two red chromatophores in each eyestalk region. Red chromatophores on base of A 2, on all inner mouth parts, encircling labrum, and 2 red and yellow chromatophores on basis of Mxp 1, 1 on Mxp 2. Chromatophores sometimes in proximal segment of exopod of Mxp 1 and 2. Chromatophores in intestine in somites 2 and 4; 6th somite-telson with pair of red and 3 pairs of red-yellow chromatophores. In most specimens, a pair of red or yellow chromatophores located at posterolateral corners of telson. Pigmentation variable.

Zoea II (Figure 2)

Rostrum slightly longer than A 1 and A 2. Eyes stalked. Abdomen with 5 somites and fused 6th somite-telson. Pleopod buds and uropods absent, but uropod anlagen visible within telson late in stage. Telson formula 8 + 8; process 8 added medially to process 7; process 4 still articulated and longest. Anal spine present.

A 1 (Fig. 2C)—No change from Zoea I.

A 2 (Fig. 2D)—Slight increase in size; endopod articulated to peduncle.

Mn (Fig. 2E)—No change from Zoea I.

Mx 1 (Fig. 2F)—Coxal endite with 7 setae, basal endite with 4 spines and a small seta, spines articulated. Endopod with 3 terminal plumose setae and 1 plumose seta on inner margin of second segment.

Mx 2 (Fig. 2G)—Coxal and basal endites bilobed. Coxal endite with 7 setae on proximal lobe, 4 on distal lobe. Basal endite with 5 setae on proximal lobe, 4 on distal lobe. Endopod with 3 terminal, 1 subterminal, and 2 (3) medial plumose setae. Scaphognathite with distal lobe bearing 8 plumose setae.

Mxp 1 (Fig. 2H)—Coxa with 1 seta, basis with 10 setae on inner margin. Endopod: long plumose seta on outer margin of segments 1, 2, 3, and 5; 3, 2, 1, 2, 4 setae on inner margin of segments 1 to 5. Exopod with 7 terminal plumose setae.

Mxp 2 (Fig. 2I)—Coxa nude, basis with 3 setae on inner margin. Endopod: long plumose seta on outer margin of segments 2, 3, and 4; 3, 2, 2, 4 setae on inner margin of segments 1 to 4. Exopod with 7 terminal plumose setae.

Mxp 3 (Fig. 2J)—Biramous rudiment. Endopod bud fused to basis; 2 terminal setae. Exopod 2-segmented, with 6 terminal plumose setae, functional for swimming.

P 1 to 5 (Fig. 2B)—Small uniramous buds increasing in length somewhat during stage. Occasionally pseudosegmented at end of stage.

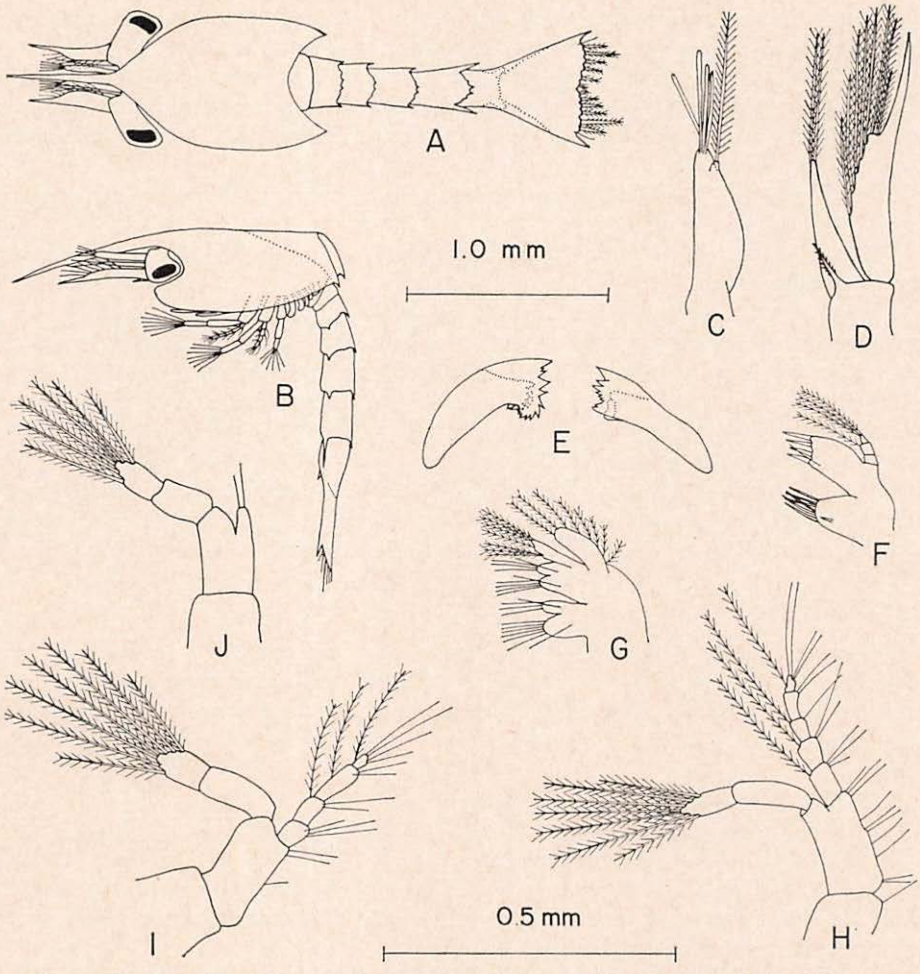

FIGURE 2. Zoea II of *Pagurus longicarpus;* A. dorsal view, B. lateral view, C. antennule, D. antenna, E. mandibles, F. maxillule, G. maxilla, H. 1st maxilliped, I. 2nd maxilliped, J. 3rd maxilliped.

Pigmentation—Generally as in Zoea I but more extensive. Eyestalks with red and yellow chromatophores. Carapace with additional chromatophores on lateral and dorsal regions. Mouth parts pigmented as in Zoea I. Red and yellow chromatophores developing dorsally in abdominal somite 2. Pattern on carapace extremely variable.

Zoea III (*Figure 3*)

Rostrum and carapace unchanged. Abdominal somite 6 free from telson, with smooth posterior margin. Ventrolateral spines on somite 5 projecting posteriorly to about middle of somite 6. Telson formula 8 + 8 as in Zoea II; process 4 fused to telson, greater than $\frac{1}{2}$ maximum telson width.

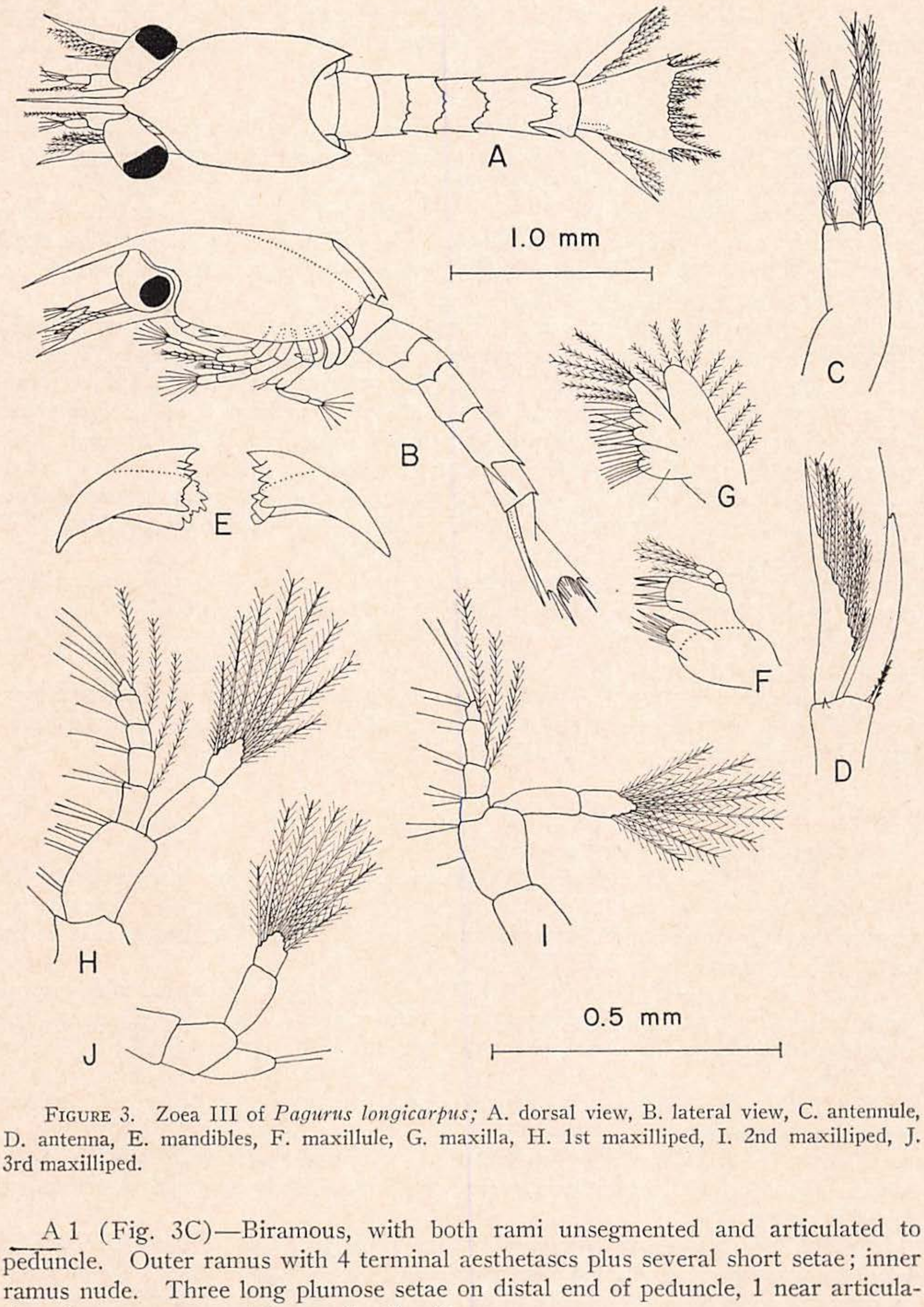

FIGURE 3. Zoea III of *Pagurus longicarpus;* A. dorsal view, B. lateral view, C. antennule, D. antenna, E. mandibles, F. maxillule, G. maxilla, H. 1st maxilliped, I. 2nd maxilliped, J. 3rd maxilliped.

A 1 (Fig. 3C)—Biramous, with both rami unsegmented and articulated to peduncle. Outer ramus with 4 terminal aesthetascs plus several short setae; inner ramus nude. Three long plumose setae on distal end of peduncle, 1 near articulation of outer ramus and 1 on each side of inner ramus.

A 2 (Fig. 3D)—Scale with 9 (8) plumose setae. Endopod equal to scale minus terminal spur, with 1 (2) terminal setae. Ventral seta present as in Zoea I and II plus a short spine added ventral to scale.

Mn (Fig. 3E)—No change from Zoea I.

Mx 1 (Fig. 3F)—Coxal endite with 7 setae, basal endite with 4 spines and a small seta, spines articulated. Endopod with 3 terminal plumose setae and 1 plumose seta on inner margin of second segment.

Mx 2 (Fig. 3G)—Coxal and basal endites bilobed. Coxal endite with 7 setae on proximal lobe, 4 (3) on distal lobe. Basal endite with 6 setae on proximal lobe, 5 on distal lobe. Endopod with 4 terminal and 2 subterminal plumose setae. Distal lobe of scaphognathite with 11 plumose setae.

Mxp 1 (Fig. 3H)—Coxa with 1 seta, basis with 10 setae on inner margin. Endopod: long plumose seta on outer margin of segments 1, 2, 3 and 5; 3, 2, 1, 2, 4 setae on inner margin of segments 1 to 5. Exopod with 8 terminal plumose setae.

Mxp 2 (Fig. 3I)—Coxa nude, basis with 3 setae on inner margin. Endopod: long plumose seta on outer margin of segments 2, 3 and 4; 3, 2, 2, 4 setae on inner margin of segments 1 to 4. Exopod with 8 terminal plumose setae.

Mxp 3 (Fig. 3J) Coxa and basis both nude. Endopod unsegmented, articulated with basis, with 1 terminal and 1 subterminal seta. Exopod with 8 terminal plumose setae.

P 1 to 5 (Fig. 3B)—Increase considerably in size during stage, pseudosegmented at end of stage. P 5 hidden behind P 1 to 4, not readily visible.

U (Fig. 3A, B)—Freely articulated, biramous; exopod $\frac{3}{4}$ telson length with 6 plumose setae on inner margin plus terminal spur; endopod rudimentary.

Pigmentation—Generally as in Zoea II. Chromatophores of abdominal somite 6 spilling over into somite 5 and telson. Small red and yellow chromatophores beginning to develop in pereiopod buds.

Zoea IV (Figure 4)

Carapace, abdominal somites, and telson as in Zoea III.

A 1 (Fig. 4C)—Peduncle with 2 short rami. Outer ramus unsegmented with 4 terminal aesthetascs and 5 (6) aesthetascs on inner margin, plus several fine terminal setae. Inner ramus unsegmented, nude. Three long plumose setae on distal end of peduncle as in Zoea III.

A 2 (Fig. 4D)—Scale with 9 (7–9) plumose setae and terminal spur. Endopod longer than scale, reaching tip of rostrum. Initially unsegmented, but segments evident beneath cuticle just prior to molt; appears folded like an accordion.

Mn (Fig. 4E)—Unsegmented palp rudiment present. Molar and incisor processes unchanged.

Mx 1 (Fig. 4F)—Coxal endite with 8 (7–9) setae, basal endite with 7 (6–8) spines. Endopod with 3 terminal plumose setae plus 1 plumose seta at distal end of second segment.

Mx 2 (Fig. 4G)—Coxal and basal endites bilobed. Coxal endite with 7 (7–8) setae on proximal lobe, 4 (4–5) on distal lobe. Basal endite with 5 (4–6) setae on proximal lobe, 6 (4–6) on distal lobe. Endopod with 4 long terminal plumose setae and 3 (4) plumose setae midway along inner margin. Scaphognathite with

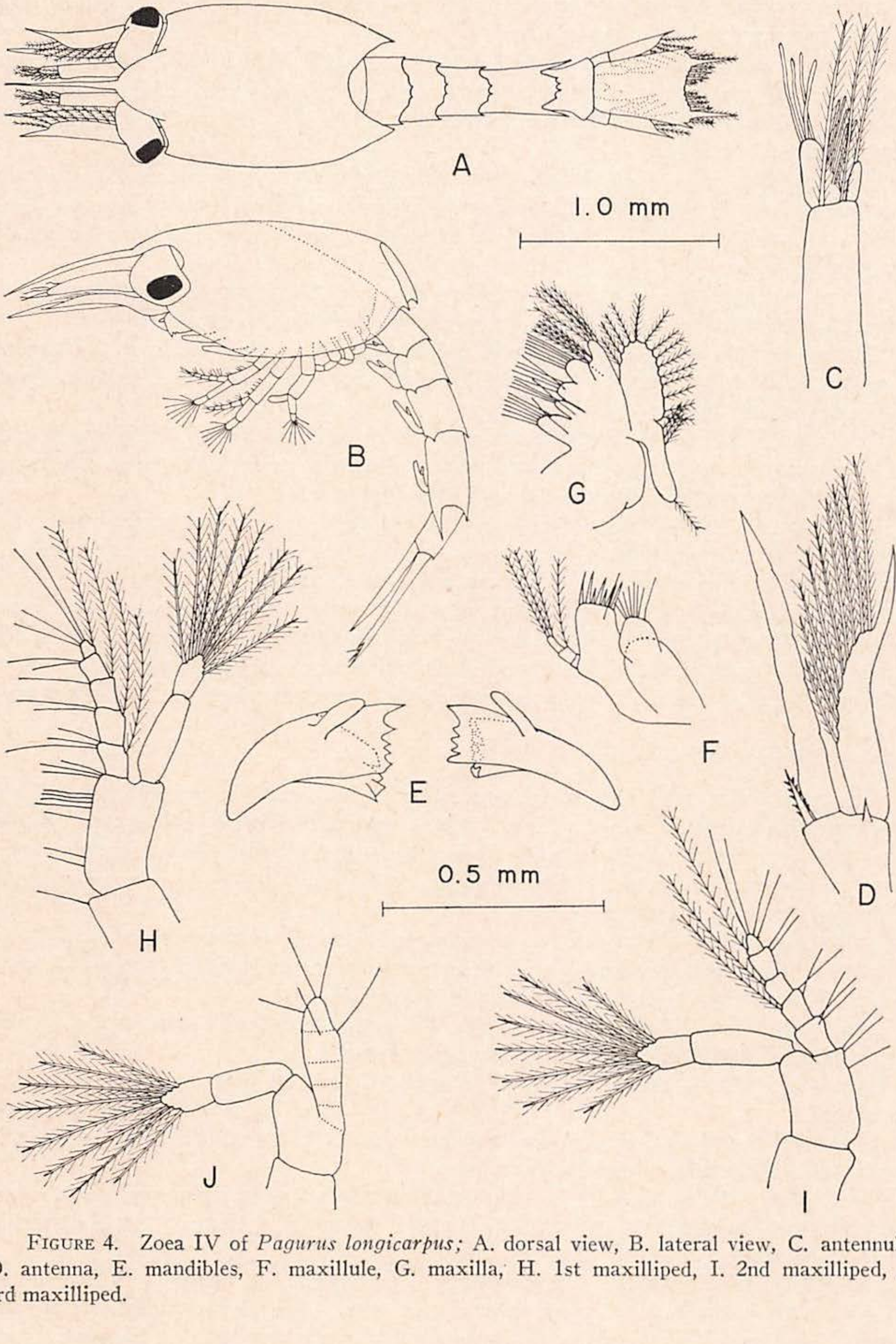

FIGURE 4. Zoea IV of *Pagurus longicarpus;* A. dorsal view, B. lateral view, C. antennule, D. antenna, E. mandibles, F. maxillule, G. maxilla, H. 1st maxilliped, I. 2nd maxilliped, J. 3rd maxilliped.

distal and proximal lobes present, with 18 (11–20) plumose setae. Lobes of equal length; proximal only ½ width of distal.

Mxp 1 (Fig. 4H)—Coxa with 1 seta, basis with 10 (10–12) setae on inner margin. Endopod: long plumose seta on outer margin of segments 1, 2, 3 and 5; 3, 2, 1, 2, 4 setae on inner margin of segments 1 to 5. Exopod with 8 terminal plumose setae.

Mxp 2 (Fig. 4I)—Coxa nude, basis with 3 setae on inner margin. Endopod 5-segmented, unlike previous stages; long plumose seta on outer margin of segments 2, 3 and 5; 3, 2, 0, 2, 4 setae on segments 1 to 5. Exopod with 8 terminal plumose setae.

Mxp 3 (Fig. 4J)—Coxa and basis nude. Endopod short, pseudosegmented, with a few scattered setae distally. Exopod with 8 terminal plumose setae.

P 1 to 5 (Fig. 4B)—Segmented; P 1 cheliform, others styliform. Increase considerably during stage until space beneath carapace filled, but remain flexed against cephalothorax.

Pl 2 to 5 (Fig. 4B)—Pleopod buds paired on somites 2 to 5. Biramous, with endopod minute, nude, inconspicuous. Exopod usually nude, rarely with 5 terminal setae. Buds increase in length by about twice during stage.

U (Fig. 4A, B)—Exopod with 6 plumose setae on inner margin and 1 (2) terminal spurs, approximately equal to telson (exclusive of telson processes). Endopod still rudimentary but longer, with 2 terminal setae.

Pigmentation—As in Zoea III, although more conspicuous on carapace. Abdominal somite 5 and telson increasingly pigmented. Mxp 3 with a red-yellow chromatophore in basis. Pereiopod buds with large chromatophores. As in previous stages, pattern extremely variable even among larvae from a single female.

Megalopa (*Figure 5*)

Carapace (Fig. 5A) with no posterolateral spines, rostrum greatly reduced and broadly rounded as in adult. Eyes stalked, peduncle slightly swollen in middle; eye scales present. Abdomen with 6 discrete segments and telson, slightly asymmetric in many specimens. Telson (Fig. 5A, P) with 4 + 4 terminal plumose setae and a minute lateral spine.

A 1 (Fig. 5C)—Outer ramus 4-segmented with 3 aesthetascs on second segment, 4 on third and proximally on last segment, terminated with 1 long and 3 short setae. Inner ramus 2-segmented with a few short setae.

A 2 (Fig. 5B)—Flagellum with 10 to 14 segments, all with short setae distally. Scale reduced, unidentate, with a few scattered setae.

Mn (Fig. 5D)—Of adult shape. Palp 3-segmented with a few setae on last segment.

Mx 1 (Fig. 5E)—Coxal endite with short setae, basal endite with 3 rows of 5 teeth each. Endopod unsegmented, no palp.

Mx 2 (Fig. 5F)—Coxal and basal endites bilobed with numerous short setae. Endopod unsegmented with 3 terminal and 1 subterminal setae. Scaphognathite with 32–35 setae.

Mxp 1 (Fig. 5G)—Coxal endite small, not completely formed, with 4 setae. Basal endite considerably larger, but also not of adult shape, with many short setae. Endopod slightly reduced, unsegmented, with few setae. Exopod 2-seg-

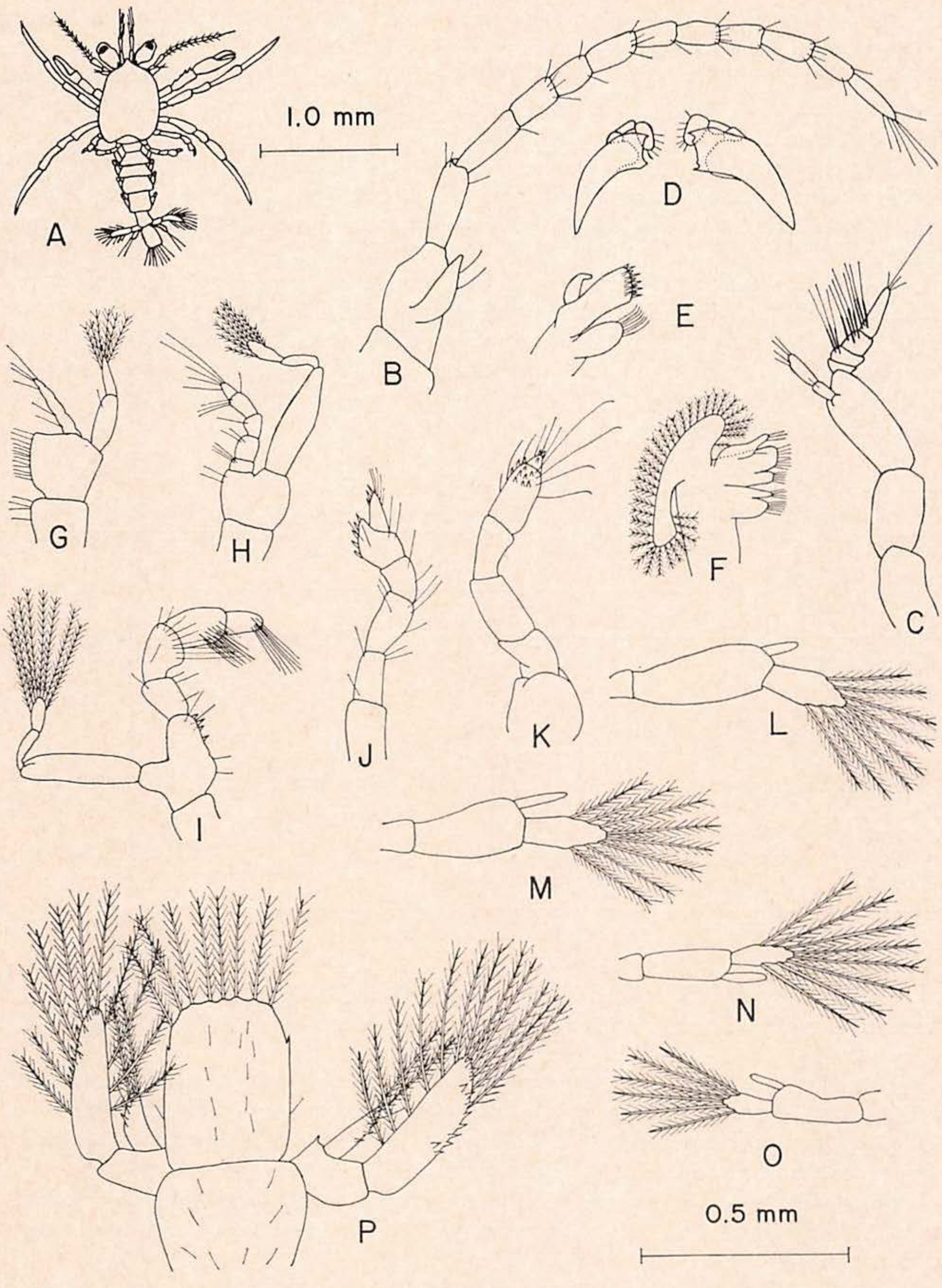

FIGURE 5. Megalopa of *Pagurus longicarpus;* A. dorsal view, B. antenna, C. antennule, D. mandibles, E. maxillule, F. maxilla, G. 1st maxilliped, H. 2nd maxilliped, I. 3rd maxilliped, J. 4th pereiopod, K. 5th pereiopod, L. 2nd pleopod, M. 3rd pleopod, N. 4th pleopod, O. 5th pleopod, P. telson and uropods.

mented with proximal segment still narrow and lacking marginal setae. Distal segment with 6 plumose setae.

Mxp 2 (Fig. 5H)—Coxa nude. Basis with 2 setae on inner margin. Endopod 5-segmented, with fewer setae than adult. Exopod 3-segmented, with 8 terminal plumose setae.

Mxp 3 (Fig. 5I)—Coxa nude. Endopod 5-segmented; basis fused with ischium; dentate ridge with 3 (4) teeth plus accessory tooth and 4 setae; all segments with fewer setae than adult. Exopod 3-segmented, with 8 terminal plumose setae.

P 1 to 5 (Fig. 5A, J, K)—P 1 cheliform, slightly asymmetric, right larger than left, reaching A 2. P 2 and P 3 of adult proportions, functional as ambulatory legs. P 4 (Fig. 5J) subchelate, propodus with a single row of 5 tubercles representing adult rasp, dactylus with 3 tubercles. P 5 (Fig. 5K) with 10 tubercles arranged in several rows and several hooked setae on propodus, 3 tubercles and several hooked setae on dactylus.

TABLE I

Carapace and total length (in mm) of Pagurus longicarpus *and* Pagurus annulipes *larvae*

		Zoea				Megalopa
		I	II	III	IV	
Pagurus longicarpus						
Carapace	$\bar{X}$	1.05	1.23	1.47	1.66	1.13
Length	range	0.99–1.10	1.12–1.40	1.35–1.64	1.44–1.80	0.90–1.26
	N	20	27	35	35	40
Total	$\bar{X}$	1.74	2.40	2.90	3.38	2.39
Length	range	1.67–1.80	2.16–2.61	2.70–3.19	3.06–3.60	2.05–2.70
	N	20	26	35	32	36
*Pagurus annulipes**						
Total Length	range	1.9–2.7	2.7–3.0	3.5–4.0	4.0	2.8–3.3

* after Thompson (1903) as *P. longicarpus.*

Pl 2 to 5 (Fig. 5L, M, N, O)—Pleopods still paired on somites 2 to 5; biramous, endopod small; 8, 8, 8, 5 (6) terminal plumose setae on exopods of Pl 2 to 5, natatory.

U (Fig. 5A, P)—Left larger, with 12 (14) plumose setae and 11 (13) tubercles on exopod, 3 plumose setae and 4 (6) tubercles on endopod. Right with 11 (13) plumose setae and 9 (11) tubercles on exopod, 3 plumose setae and 3 (4) tubercles on endopod. Basis with a small spine near origin of endopod.

Pigmentation—Many more chromatophores present, but pattern essentially same as in zoeae. As next molt approaches, chelipeds become pale yellow or white as in juvenile.

Growth—The larval stages increased relatively uniformly from a total length of 1.74 mm in Zoea I to 3.38 mm in Zoea IV (Table I). With the molt to the megalopa, the total length dropped about 1 mm or 30% to approximately the size of Zoea II. Comparison of carapace lengths revealed the same result. It would be

TABLE II

Summary of anatomical differences between Pagurus longicarpus *and* Pagurus annulipes *larvae*

Stage	Pagurus longicarpus	Pagurus annulipes
Zoea I	A 2 scale with 8 setae	A 2 scale with 10 setae
	A 2 endopod = $\frac{1}{2}$ scale	A 2 endopod $<\frac{1}{2}$ scale
Zoea II	A 2 scale with 8 setae	A 2 scale with 10 setae
	Mx 2 scaphognathite with 8 setae	Mx 2 scaphognathite with 6 setae
Zoea III	A 2 scale with 9 setae	A 2 scale with 10 setae
	Mx 2 scaphognathite with 11 setae	Mx 2 scaphognathite with 10 setae
	Abdominal somite 6 without median dorsal spine	Abdominal somite 6 with median dorsal spine
	Telson process 4 long	Telson process 4 minute
Zoea IV	A 2 scale with 9 setae	A 2 scale with 8 setae*
	Mn palp present	Mn palp absent
	Mx 2 scaphognathite with 18 setae; proximal lobe present	Mx 2 scaphognathite with 11 setae; proximal lobe absent
	Mxp 2 endopod 5-segmented	Mxp 2 endopod 4-segmented
	U with 6 plumose setae	U with 7 plumose setae
	Abdominal somite 6 without median dorsal spine	Abdominal somite 6 with median dorsal spine
	Telson process 4 long	Telson process 4 minute
All Zoeae	Red chromatophores absent ventrolaterally on carapace and on abdominal somites 2 and 5	Red chromatophores present ventrolaterally on carapace and on abdominal somites 2 and 5
	Mx 1 endopod 0, 1, 3 setae	Mx 1 endopod 1, 1, 2 setae Zoea I–III; 1,1,3 setae, Zoea IV
	Mxp 1 and 2 exopod 2-segmented	Mxp 1 and 2 exopod unsegmented
	Mxp 3 exopod 2-segmented (Zoea II–IV)	Mxp 3 exopod unsegmented
	Lateral abdominal spines long	Lateral abdominal spines short
Megalopa		
	Mxp 1,2,3 well developed	Mxp 1,2,3 poorly developed
	P 1 = A 2 $<$ P 2 and P3	P 1 = P 2 and P 3 $>$ A 2
	Pl 2 to 5 with 8,8,8,5 setae	Pl 2 to 5 with 7,7,9,7 setae**

* A 2 scale with 10 setae according to C. Nyblade.
** Pl 2 to 5 with 9(10),9(10),9(10),8 setae according to C. Nyblade.

interesting to follow changes in weight through the larval sequence but this has not been done. The change in length probably reflects the radical change in shape rather than a true change in biomass or volume.

The larva described by Thompson (1903) was considerably larger than *P. longicarpus,* 0.5 mm or more at each instar (Table I). Again there was an increase in total length to Zoea IV and then a reduction to about the length of Zoea II. Thompson used the wide range of lengths within each zoeal stage to justify partially his contention that he was working with two species, but, with the exception of Zoea I, the range of total length which he observed was equal to or smaller than that observed in the present study.

DISCUSSION

The larvae described by Thompson (1903) differ from *P. longicarpus* as described above in many features, some quite conspicuous. Table II summarizes these

TABLE III

Summary of characteristics defining the four groups of Pagurus *larvae recognized with a list of the species in each group (After MacDonald et al., 1957)*

Characteristics	Group			
	A	B	C	D
Zoeal length and telson breadth	elongate narrow	not elongate broad	not elongate broad	not elongate broad
Lateral spines somite 5	long	long	medium	long
Median dorsal spine somite 6	absent	present	absent	absent
Telson process 4, Zoea III and IV	long $>\frac{1}{2}$ telson width fused	reduced $<\frac{1}{2}$ telson width fused	medium $=\frac{1}{2}$ telson width articulated	long $>\frac{1}{2}$ telson width fused
Number setae on endopod of A 2	0	2	2	2
A 2 scale	straight $L \geq 6 \times W$ setae ≤ 8	curved $L < 4 \times W$ 9 setae SI 10 setae SII–IV	curved $L < 4 \times W$ 9 setae SI 10 setae SII–IV	curved $L < 4 \times W$ 8 setae SI–II 9 setae SIII–IV
Mandibular palp, Zoea IV	present	absent	absent	present
Number setae on U endopod	0	2	1	2
Number pleopods, Zoea IV, Megalopa	4	4	4	4
A 2 of Megalopa	long A 2 > P 1	short A 2 < P 1	short A 2 < P 1	medium A 2 = P 1
Yellow chromatophore over stomach	present	absent	present	absent
List of species	*bernhardus*[1] *pubescens*[1] *samuelis*[4] (?) *beringanus*[7]	*prideauxii*[1] *cuanensis*[1] *alatus*[2] *forbesii*[1,2] *marshi*[5] *annulipes*[6]	*anachoretus*[2] *kulkarnii*[3]	*longicarpus*

[1] MacDonald *et al.*, 1957.
[2] Pike and Williamson, 1960.
[3] Shenoy, 1967.
[4] Coffin, 1958, 1960.
[5] Provenzano and Rice, 1964.
[6] Thompson, 1903.
[7] Hart, 1937.

differences in detail with some additional data from Mr. Carl Nyblade, University of Washington, Seattle (personal communication).

Many differences, such as setation, might readily result from differing rates of morphogenesis in cultured versus planktonic specimens. This has been reported previously for *Pisidia longicornis* (LeRoux, 1966) and *Euceramus praelongus* (Roberts, 1968). This type of explanation is less likely for such differences as telson process 4, mandibular palp, and pigmentation. Unfortunately, no specimens of *P. longicarpus* from the field have been obtained for comparison with laboratory-reared specimens. There is little doubt, however, that Thompson was not working with *P. longicarpus*. Carl Nyblade (personal communication) has identified

Thompson's larvae as *P. annulipes* by comparison with cultured larvae of that species.

MacDonald *et al.* (1957) distinguished two groups of *Pagurus* larvae which they designated Group A (Type: *P. bernhardus*) and Group B (Type: *P. prideauxii*). Later, Pike and Williamson (1960) recognized a third group, Group C (Type: *P. anachoretus*) which is similar to Group B but differs by the absence of a median dorsal spine on somite 6, length of telson process 4 (both like Group A), and number of setae on uropod endopod (like *Anapagurus* as described by MacDonald *et al.*, 1957). Detailed comparisons of these groups and a list of the species assigned to each group to date appear in Table III. Until the present study, all described larvae of the genus *Pagurus* have fit into a previously defined group. Larvae of *P. beringanus*, described by Hart (1937), belong to Group A. Larvae of *P. samuelis*, described by Coffin (1958, 1960), appear to belong to Group A but cannot be definitely categorized because his description is not complete. Provenzano and Rice (1964) placed the larvae of *P. marshi* in Group B. Larvae of *P. kulkarnii*, described by Shenoy (1967), probably belong to Group C, accepting Shenoy's conclusion that the "normal" number of instars is 4 and not 3 as he observed. The larvae are comparable in pigmentation of the 5th and 6th abdominal somites and telson, absence of median dorsal spine on somite 6, telson process 4 long, articulated in last zoeal stage observed, and other pertinent characters except size of A 2 in the megalopa.

The larvae of Thompson (1903), herein ascribed to *P. annulipes*, were correctly placed in Group B. *P. longicarpus*, however, does not belong to this group, nor does it belong to either of the other previously defined groups. It differs from Group A by being not elongate, telson broad, having two setae on the endopod of A 2 in Zoea I and II, a curved broad antennal scale, 2 setae on the uropod endopod in Zoea IV, A 2 short and equal to right cheliped in the megalopa, no yellow chromatophore dorsal to the zoeal stomach, from Group B by possessing a long telson process 4 in Zoea III and IV and a mandibular palp in Zoea IV, and from Group C by having 2 setae on the uropod endopod and a rudimentary mandibular palp in Zoea IV. Thus *P. longicarpus* constitutes the type of a fourth group, Group D, of *Pagurus* larvae.

Additional groups of similar larvae will probably be found as further *Pagurus* species are studied. Larvae of *P. pollicaris*, based on a preliminary examination of larvae reared in this laboratory and a description of cultured larvae by another investigator (Carl Nyblade, personal communication), do not belong to any group as defined above. These larvae resemble Group B except for the lateral spines on abdominal somite 5 and the length of telson process 4 which are comparable to Group C and the A 2 scale which is comparable to Group D.

To establish whether this division of the genus based on larval characteristics is of phyletic significance, as suggested by MacDonald *et al.* (1957), will require much further study of larvae and adults with consideration of all characteristics of possible systematic value. Regardless, it has value in identification of plankton specimens.

No attempt will be made to compare larvae of the genus *Pagurus* with larvae or other genera in the family Paguridae or with larvae of the other "hermit crab" families, Diogenidae and Coenobitidae. The subject has recently been reviewed in some detail by Provenzano (1968a, b), although the emphasis was on the latter two families.

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