Studies on Thalassinid Crustacea (Decapoda, Macrura Reptantia) with a Description of a New *Jaxea* from New Zealand and an Account of its Larval Development

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CONTENTS

Abstract

A SHORT review of the New Zealand Thalassinidea, and of known species in the family Laomediidae is given, with a generic key to adults of the laomediid genera *Jaxea, Laomedia* and *Naushonia.* A key is given for the only species of the genus *Jaxea* known in the adult form, *viz. J. nocturna* and a second species (*J. novaezealandiae* n.sp.) here described from New Zealand waters.

Adults of *J. novaezealandiae* were obtained from mud bottoms between 2 and 12 fathoms, from Hawke Bay on the east coast of the North Island to Port Underwood on the south side of Cook Strait. They are abundant in suitable areas of Wellington Harbour and taken there in association with *Squilla armata* and *Echinocardium cordatum.* In the life history of *J. novaezealandiae* six essential "trachelifer" larval stages and a non-obligatory seventh contrast with the usual three, but rarely four or five, stages in most Reptantia.

Keys are given to the larvae of five species of *Jaxea* (including three species known only from larvae), to all six essential larval stages of *J. novaezealandiae,* and to the first post-larval stages of *J. novaezealandiae, J. nocturna, Naushonia crangonoides* and *N. portoricensis.*

PART I

An Outline of the New Zealand Thalassinidea with Keys to the Genera of the Family Laomediidae and to Recent Adults of the Genus *Jaxea* Nardo, 1847.

1. The New Zealand Thalassinidea

IN this account the laomediids and their thalassinid allies will be regarded as belonging to the supersection Macrura Reptantia and their relationship to the Anomura will not be considered.

Order DECAPODA
Supersection MACRURA REPTANTIA
Section THALASSINIDEA

The seven families now regarded as belonging to the section (previously called tribe) Thalassinidea are the Callianassidae, Callianideidae, Upogebiidae, Axiidae, Axianassidae, Laomediidae and Thalassinidae. These are discussed in some detail and a key for their separation is given by Gurney (1938: 339–343). All are apparently burrowing forms characterised by:— a reasonably well calcified, compressed carapace; a symmetrical, extended, often feebly calcified abdomen terminating in a well developed tail fan; the first pair of legs chelate or subchelate, second chelate, subchelate or simple, and third legs always non-chelate.

The family Callianassidae is represented in New Zealand by at least two species. *Callianassa* (*Trypaea*) *filholi* A. Milne Edwards (see Chilton, 1907; de Man, 1928: 101) is a widespread burrower of intertidal sandy beaches and can be locally abundant; its first larval stage has been described by Lebour (1955) and by Wear (1965). The rarely collected *Ctenocheles maorianus* Powell, 1949, is known from both shallow water and the continental shelf, where it is often recognised merely from detached examples of its highly characteristic comb-like chelae (see also Glaessner, 1960: 13).

The minor family Calliandeidae presumably is represented in our waters since *Callianidea typa* H. Milne Edwards has been listed from New Zealand by de Man (1928: 30).

The Upogebiidae is represented by the subtidal and shallow water species *Upogebia* (*Upogebia*) *hirtifrons* (White) and *U.* (*U.*) *danai* (Miers)—see Chilton, 1907; de Man, 1928: 39–43.

The Axiidae is represented by at least three species on the New Zealand continental shelf and probably others as yet unrecognised. *Axius* (*Axius*) *novaezealandiae* Borradaile, 1916, has seldom been taken; *Calocaris* (*Calocaris*) *macandreae* Bell, "Indian form" has been recorded (Kirk, 1879; de Man, 1925: 8), and an undescribed *Axiopsis* (*Axiopsis*) n.sp. is quite common (see Griffin and Yaldwyn, 1965: 43).

The Axianassidae, Laomediidae and Thalassinidae complete the list of families included in this section. A single species of the family Laomediidae is described here, while the other two families have not yet been recorded from the New Zealand area. The family name "Axianassidae" used by Wear (1965: 13) for two species of axiid larvae from Wellington Harbour is a *lapsus* for Axiidae. One of these two larval species was provisionally placed in *Iconaxiopsis*, a subgenus of *Axius*.

2. The Family Laomediidae Borradaile, 1903

The laomediids are rather rare, burrowing decapods, macrurous in form, regarded by some authors as true Anomura in their systematic relationships. The family is at present represented by three genera and six described species.

Laomedia de Haan is known from one species, *L. astacina* de Haan, 1849, from Japan and Korea (see de Man, 1928; Sakai, 1962). The authors know a large undescribed adult laomediid from eastern Australian shallow waters which also appears to belong to the genus *Laomedia*.

Jaxea Nardo is known from one named species, *J. nocturna* Nardo, 1847, from the Mediterranean and North Atlantic (see Selbie, 1914; Bouvier, 1940), and from four, apparently specifically distinct, but unnamed species known only by their larvae—in New Zealand waters (Gurney, 1924), off Samoa (Gurney, 1938), off New South Wales (Dakin and Colefax, 1940) and from the Adriatic Sea (Kurian, 1956). In Part II of this paper we wish to report the finding of the adults and all the larval stages of the New Zealand species which we propose to name *Jaxea novaezealandiae* n.sp.

The remaining genus, *Naushonia* Kingsley, is known from four species: *N. crangonoides* Kingsley, 1897, from off Massachusetts (Atlantic Coast of U.S.A.); *N. portoricensis* (Rathbun, 1901) from Puerto Rico, West Indies; *N. perrieri* (Nobili, 1904) from the Red Sea, and *N. macginitiei* (Glassell, 1938) from Southern California (see Chace, 1939). Larval stages referred to *Naushonia* have been described from off New South Wales (Dakin and Colefax, 1940) and, with less certainty in generic placing, from off Samoa and from the Great Barrier Reef (Gurney, 1938).

The family Laomediidae, as now constituted, consists of those Thalassinidea having:— a *linea thalassinica* (a transverse, hinged groove along each side of the carapace) present; 1st pereiopods subequal, and chelate or subchelate; 2nd pereiopods subchelate or simple, never chelate; no appendix interna on pleopods; uropod with transverse suture on both endopod and exopod; podobranchs on at least 2nd and 3rd maxillipeds and 1st and 2nd pereiopods, and epipods on 1st to 4th pereiopods.

A KEY TO THE GENERA OF THE LAOMEDIIDAE

1	(4)	First pereiopods chelate, 5th pereiopods subchelate; antennal scale (scaphocerite) rudimentary or absent (LAOMEDIINAE)	
2	(3)	First pereiopods with stout and heavy chelae (hand length less than 2½ times hand width and less than carapace length), 2nd pereiopod subchelate or simple*; peduncles of both antennule and antenna short (penultimate segment of antennal peduncle subequal with ultimate)†	*Laomedia* de Haan, 1849
3	(2)	First pereiopods with relatively heavy but elongated chelae (hand length three or more times hand width and subequal with or greater than carapace length); 2nd pereiopod subchelate; peduncles of both antennule and antenna elongated and relatively slender (penultimate segment of antennal peduncle at least four times ultimate)†	*Jaxea* Nardo, 1847
4	(1)	First pereiopods subchelate, 2nd and 5th pereiopods simple; antennal scale well developed (NAUSHONIINAE)	*Naushonia* Kingsley, 1897

Genus *Jaxea* Nardo, 1847

Laomediids with a firm, white exoskeleton covered with a densely crowded fur of very short setae. The *linea thalassinica* of the carapace is distinct and well

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* The 2nd pereiopod of *Laomedia astacina* is described as "simple" (see Borradaile, 1903: 540, under generic name only) or implied to be so (Sakai, 1962: 30 and fig. 19. Note that Sakai calls this limb "fifth pereiopodite", apparently regarding the 1st maxilliped as equivalent to his "first pereiopodite"), but the 2nd pereiopod of an undescribed *Laomedia* from eastern Australian waters must be termed "subchelate". In this species the dactyl closes against part of the prodopus and can be regarded as subchelate, just as in the 2nd pereiopod of *Jaxea novaezealandiae*.

† The 1st maxilliped of *Laomedia astacina* is described as having "no lash to the exopodite nor podobranch", while that of *Jaxea nocturna* is described as having "a lash to the exopodite and a podobranch" (see Borradaile, 1903: 540–41, under generic names only). These features do not appear to be good generic differences as Sakai (1962: 31 and fig. 11) clearly figures a flagellum on the exopod of the 1st maxilliped (= his "first pereiopodite") of *L. astacina* and lists, but does not figure, a rudimentary podobranch on this appendage. The eastern Australian *Laomedia, Jaxea nocturna* (see Selbie, 1914: 99 and Pl. XV, fig. 6) and *J. novaezealandiae* all have a flagellum on the exopod of the 1st maxilliped, with a podobranch recorded, though not figured, in *J. nocturna* only (Selbie, 1914). Caroli (1924) denies the presence of this podobranch in *J. nocturna*, and from personal examination neither *Jaxea novaezealandiae*, nor the undescribed *Laomedia*, have any trace of a podobranch on this appendage.

developed. The eye is reduced and hidden under the rostrum in dorsal view and the pigmentation of the cornea is reduced. The peduncles of both the antennules and antennae are greatly elongated and relatively slender. The scaphocerite is rudimentary but distinct. First maxilliped with flagellum on exopod but no podobranch. First pereiopods subequal, with enlarged and elongate chelae, 2nd and 5th pereiopods subchelate. A single arthrobranch on 1st maxilliped and two on 2nd and 3rd maxillipeds and on 1st to 4th pereiopods. Podobranch present or absent on 3rd pereiopod. Male 1st pleopods absent, female 1st pleopods reduced and uniramous, 2nd to 5th pleopods biramous and similar in both sexes.

The type of the genus is *Jaxea nocturna* Nardo, 1847 (of which *Calliaxis adriatica* Heller, 1863, is a synonym) known from the British Isles and Irish Sea (Selbie, 1914), the Mediterranean coast of Spain (Zariquiey, 1946), the Adriatic (numerous authors), and apparently more abundant in the eastern Mediterranean, including the coasts of Israel and Egypt, than in the western Mediterranean (Holthuis and Gottlieb, 1958).

A fossil from the Miocene of the Vienna Basin has been described as *Jaxea kuemeli* Bachmayer, 1954 (corrected from *kümeli*). It can be distinguished at once from the two named recent species in this genus by the position of the cervical groove in the adult stage. In the fossil form this groove is situated distinctly posterior to the midpoint of the carapace, exclusive of the rostrum.

A KEY TO ADULTS OF KNOWN RECENT SPECIES OF *Jaxea*

Hand between 1 and 1½ times length of carapace and rostrum; fingers more than 1½ times length of palm. Anterolateral margin of carapace with several small teeth below origin of *linea thalassinica* and sometimes several minute "thorns" above. Third maxilliped with ischium armed medially with a crest of about 14 to 16 strong teeth	*J. nocturna*
Hand subequal in length to carapace and rostrum; fingers a little longer than palm. Anterolateral margin of carapace with single small tooth immediately above origin of *linea thalassinica* and sometimes several minute "thorns" below. Third maxilliped with ischium armed medially with a crest of about 12 to 14 (usually 13) strong teeth	*J. novaezealandiae*

PART II

A New *Jaxea* from New Zealand (Decapoda, Laomediidae) with an Account of its Larval Development.

1. Description of *Jaxea novaezealandiae* n.sp. with Notes on Distribution and Habits

Adults of the New Zealand *Jaxea* have been elusive. The first significant record was of a large ovigerous female taken alive in a deep dredge haul from soft muddy ground at 11 fathoms in Wellington Harbour (New Zealand Oceanographic Institute, NZOI Stn. A355, 23 July 1957). This survived in an aquarium for several days, but died without any of the eggs hatching. The second record was also obtained by the New Zealand Oceanographic Institute when an associated pair was taken alive in an orange peel grab from about 8 fathoms in Port Underwood, Marlborough, on the south-western side of Cook Strait (NZOI Stn. C228, 15 September 1959). These also survived for several days but did not attempt to burrow or to take food while under observation in an aquarium.

During 1964–65, R.G.W. was able to obtain live adult specimens at night using a small otter trawl in about 2 to 10 fathoms in Evans Bay, Wellington Harbour. Specimens were taken in July, August and November, 1964, and during 1965.

They were trawled from a bottom of soft putrid mud, apparently living in association with the stomatopod *Squilla armata* (H. Milne Edwards) and an abundant spatangoid urchin, *Echinocardium cordatum* (Pennant). Specimens of *Jaxea* taken by this method were kept alive for up to 11 days in the Victoria University Marine Laboratory at Island Bay, Wellington. None appeared to take food or to burrow successfully during these periods.

Adult *Jaxea* are now known in New Zealand waters from Hawke Bay on the east coast of the North Island in the north, to the Marlborough coast of Cook Strait in the south. All records have been from protected inshore waters in depths ranging from about 2 to 12 fathoms on muddy or sandy bottoms.

Fragments of unknown reptants taken from fish stomach contents in the Wellington Harbour and Cook Strait areas during the period 1954–59 can now be identified as the New Zealand *Jaxea*. These records, coupled with the abundance of trachelifer larvae of *Jaxea* in the Wellington plankton (Wear, 1965), give an indication of the true status of this species in the Wellington area where substrate conditions appear to suit the apparently restricted habitat preference of *J. novaezealandiae*.

Larvae attributed to the New Zealand *Jaxea* were first taken from the Bay of Islands, northern New Zealand, by the British Antarctic "*Terra Nova*" Expedition in 1910 (Gurney, 1924). Larvae have also been examined (R.G.W.) from the Hauraki Gulf and Auckland Harbour, Wellington Harbour, off Kaikoura and off Banks Peninsula (east coast of the South Island). From this it would appear that the species may be widespread in the New Zealand area on suitable ground and at suitable depths.

ADULT MATERIAL EXAMINED

Hawke Bay: NZOI Stn. B2, off Mohaka, 39° 08′ S., 177° 13′ 30″ E., 25/8/1956, cone dredge on muddy with fine sand bottom at 18 metres (1 damaged specimen, 5.5mm).

Wellington Harbour: From dogfish stomach, off Petone Beach, 16/11/1954 (female carapace length 11mm). Victoria University Zoology Department Collections VUZ 32, off Petone Beach, 41° 14′ 30″ S., 174° 52′ 6″ E., 16/1/1956, dredge on mud bottom at 8 fathoms (associated pair, male 8mm, female 7.5mm); VUZ 68, between Somes Island and Days Bay, 41° 16′ 12″ S., 174° 52′ 51″ E., 16/5/1956, Petersen grab on mud bottom at 11 fathoms (associated pair, ? male 6mm, female 6mm). NZOI Stn. A 355, between Somes Island and Kaiwharawhara, 41° 15.6′ S., 174° 50′ E., 23/7/1957, Knudsen sampler dredge on mud bottom at 11½ fathoms (ovigerous female 18mm). From dogfish stomach (*Mustelus lenticulatus*) 6/7/1964, taken in otter trawl from 3 fathoms off Petone Beach (3 males 13mm, 13mm and 16mm). Shelly Bay, Evans Bay (R. G. Wear study area) numerous specimens taken by otter trawl from mud bottom in 2 to 10 fathoms, 1964–65, including the following: male 9mm, 6/7/1964; male 11mm (figured specimen) 11/7/1964; male 15mm (holotype), male 13mm, female 13mm, 3/8/1964; 2 males 9mm and 13mm, female 15mm, 26/8/1964; 1 male 10mm, 6/11/1964; 3 males 11mm, 11mm and 13mm, 1/6/1965.

Cook Strait: NZOI Stn. C 228, Port Underwood, Marlborough, 41° 19′ S., 174° 10′ E., 15/9/1959, orange peel grab on sandy mud at about 8 fathoms (associated pair, male 11mm, female 15mm).

TYPE MATERIAL

The holotype is the male from Shelly Bay, 3/8/1964, with carapace length of 15mm; the paratype upon which figs. 1 and 2 are mainly based is the male from the same area, 11/7/1964, with carapace length 11mm, though the figure of the

mandible and certain other details are based on other specimens from Shelly Bay. All other material listed above, with the exception of the NZOI Stn. B 2 specimen is paratypic.

The holotype (Z. Cr. 1667), the figured paratype (Z. Cr. 1669) and the majority of the paratypes (8 specimens, Z. Cr. 1668, 1670–73) are in the Dominion Museum, Wellington; other paratypes are in the Victoria University of Wellington, Zoology Department (6 specimens), the New Zealand Oceanographic Institute, Wellington (3 specimens, 29, 30, 31), the Australian Museum, Sydney (2 specimens, P. 15164), and the Rijksmuseum van Natuurlijke Historie, Leiden (2 specimens, Crust. D. 22652–53). All measurements in the material examined list are of carapace length only (from posterior corner of orbit to level of dorsal midpoint of hind margin of carapace) and thus exclude the rostrum.

ILLUSTRATIONS

All drawings in this paper have been done by R.G.W.

Description of *Jaxea novaezealandiae* n.sp. (figs. 1 and 2)

A degenerate-eyed, relatively large, white, burrowing shrimp with elongated and enlarged chelipeds.

The carapace is laterally compressed and considerably shorter than the abdomen. The body and appendages are covered with a short and dense " pile " of fine, fur-like setae, which gives the shrimp a soft, grey indistinct appearance. Fine, rust-like mineral grains, presumably from the substratum in which the animal burrows, are almost invariably enmeshed with the setal fur in the material examined and

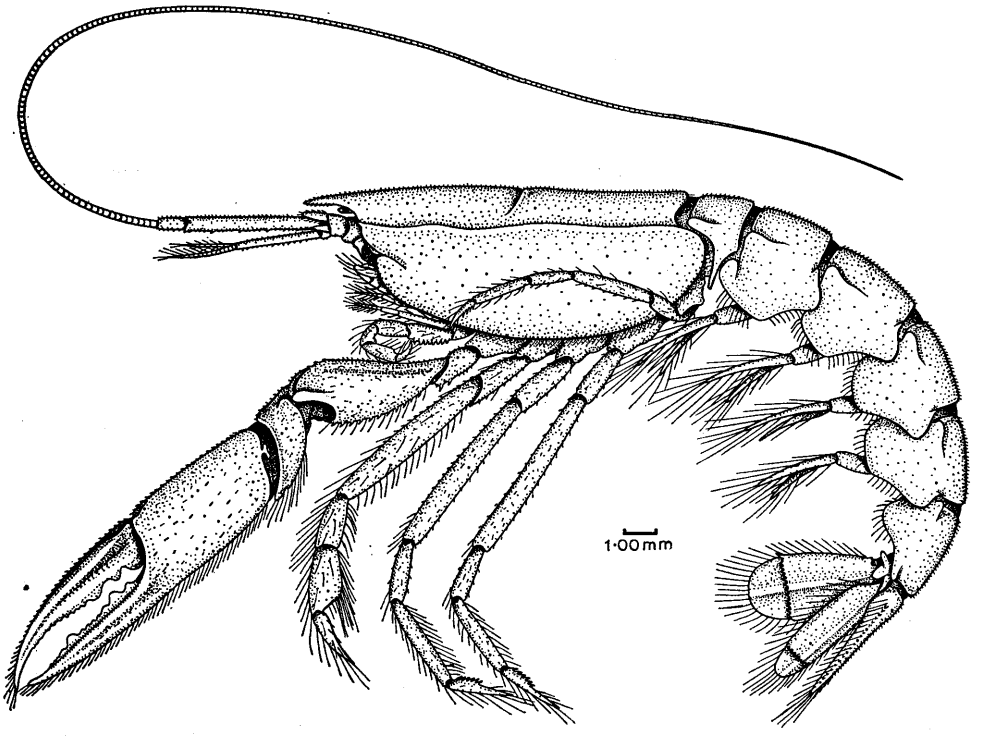

FIG. 1.—*Jaxea novaezealandiae* n.sp., adult male, carapace length (excluding rostrum) 11mm, lateral view.

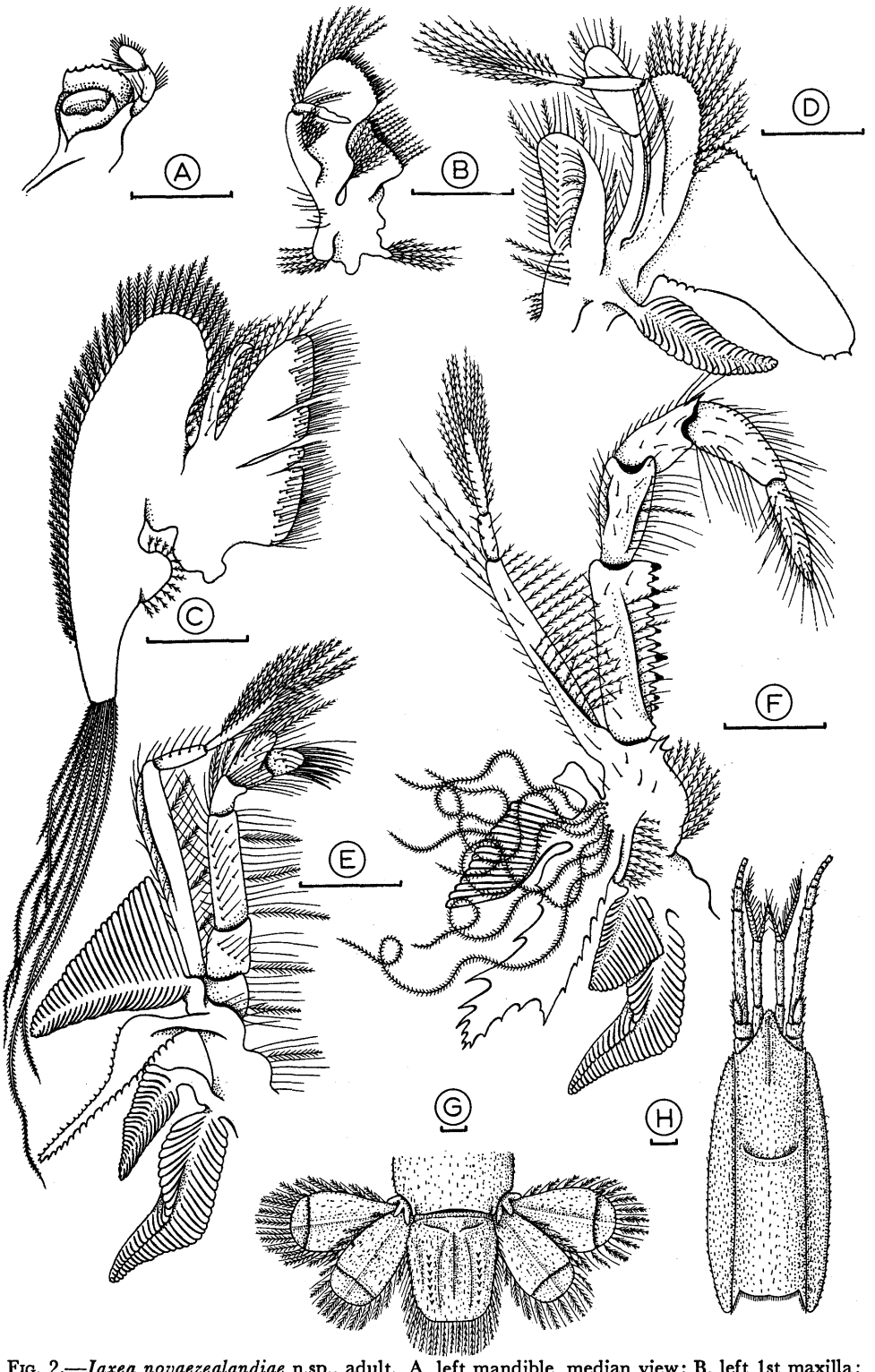

FIG. 2.—*Jaxea novaezealandiae* n.sp., adult. A, left mandible, median view; B, left 1st maxilla; C, left 2nd maxilla; D, left 1st maxilliped; E, left 2nd maxilliped; F, left 3rd maxilliped; G, 6th abdominal segment, uropods and telson, dorsal view; H, carapace and cephalic appendages, dorsal view. (All scale lines equal 1.00mm).

may superficially give the appearance of a pigmented exoskeleton. The cuticle is, however, firm, white, smooth and almost chalky rather than shiny. There is a very distinct *linea thalassinica* laterally on each side of carapace forming a hinged line upon which each pterygostomiobranchial portion of carapace can move. A distinct cervical groove is situated dorsally a little anterior to midpoint of carapace, exclusive of rostrum, but does not extend ventrally across *linea*. Anterodorsal surface of carapace smooth and produced anteriorly as a depressed, flattened, triangular rostrum, armed on each side of rounded tip with about 4 to 5, small, irregularly-placed teeth. Upper surface of rostrum with shallow, longitudinal depression extending a short distance onto carapace in midline. Anterolateral margin of carapace with a single small tooth immediately above origin of *linea thalassinica* and sometimes several minute " thorns " below. There is a short ?branchiostegal groove, directed posteroventrally, below level of antenna; remainder of anterolateral and ventrolateral border smooth and unarmed.

Abdomen of uniform depth throughout; pleuron of 1st segment triangular and overlapping anteriorly the convex posterolateral margin of carapace at level of *linea*. Pleura of other segments broadly rounded with weakly concave posterolateral margins, each overlapping posteriorly the next segment; ventral margins of 3rd to 6th pleura with minute serrations. Telson quadrate with distal edge weakly calcified and almost transparent; there is an indistinct, median, longitudinal groove dorsally flanked on each side by a row of about 6 to 7 small spines on a low, broad, longitudinal crest. Lateral margins are weakly and rather indistinctly serrated and posterior margin bears a row of long setae.

Eyes reduced and not extending laterally from beneath rostrum, not visible in dorsal view; cornea with black pigment in central portion only.

Antennules arise close together under rostrum, which extends to about midpoint of 2nd segment of peduncle. Second segment about half 1st and a little less than one-third of 3rd peduncle segment. Antennular flagellum a little longer than elongated 3rd segment. Exopod of about 23 segments longer and stouter than endopod of about 14 segments. Peduncle of antenna 5-segmented; proximal three and distal one short, 4th or penultimate segment greatly elongated, somewhat flattened, about 4 times length ultimate segment and about 5 times its own width in dorsal view. Scaphocerite greatly reduced and extending anteriorly from dorsodistal margin of 2nd peduncle segment; rounded in profile with about 1 to 3 irregular teeth anterolaterally. Antennal flagellum simple and about equal in length to carapace and abdomen excluding telson.

Mandible consists of molar process with curved serrated ridges and 3-segmented palp. First maxilla with two endites armed with stout bristles and setae medially, and a 2-segmented endopod with distal segment shorter and more slender than proximal. Second maxilla with two endites each partially and unevenly divided into two, simple endopod and large scaphognathite with proximal lobe unusually long, tapering, truncate and bearing long whip of setae. All maxillipeds have large and prominent exopods, consisting of two parts, peduncle and flagellum, articulated at a distinct angle to one another; flagellum with single proximal segment at least half length of multi-segmented portion. First maxilliped with 2 incompletely separated endites; 2-segmented endopod with distal segment enlarged and rounded, and large triangular epipod. Second maxilliped with penultimate segment expanded as a rounded lateral lobe and with well developed podobranch and slender serrated epipod. Third maxilliped small and pediform, endopod of 5 segments with ischium bearing a prominent medial crest of about 12 to 14 sharp teeth; complex epipod consisting of small anterior lobe and bunch of long setae (setobranch), a podobranch and a posteriorly directed, serrate-margined mastigobranch. Two arthrobranchs are present on 2nd and 3rd maxillipeds, but only one on 1st.

Chelipeds greatly developed, subequal in length and shape, and about equal in length to carapace and 1st to 3rd or 1st to 4th abdominal segments. Free finger slightly longer than fixed, both straight proximally and slightly curved together and acute distally (in large specimens finger tips tend to become blunt and rounded); free finger with two longitudinal angles rather than carinae along both inner and outer faces, fixed finger with one such longitudinal angle (indistinctly but evenly tuberculated or beaded) along both inner and outer faces. Both free and fixed fingers toothed; free with 3 broad, irregularly spaced teeth in proximal half and with distal half finely toothed; fixed with 1 to 4 broad teeth proximally, followed by one much larger, truncate tooth placed so as to interlock when closed between the two more distal of the broad proximal teeth of free finger; remainder of cutting margin of fixed finger with irregular series of differently sized teeth and often one enlarged tooth in distal third. Hand subequal in length to carapace including rostrum; hand length 3 to 4 times hand width; palm parallel-sided, rather than swollen, without ridges or tubercles, a little shorter than fingers. Carpus short, broad and unarmed. Merus long, a little shorter than fingers, enlarged distally so that distal width is nearly half length; unarmed dorsally but with row of 12 or more, sharp, slender teeth on narrow ventral margin. Ischium short and armed with row of 6 or more similar teeth ventrally as well as some sharp tubercles medially. Basis with single slender ventral tooth.

Second to 5th pereiopods short, compressed and, except for dactyls, rather similar in structure. Second pereiopod, unlike others, with fringe of setae along most of dorsal and ventral edges; dactyl flattened and blade-like, acute distally but otherwise unarmed, subequal to carpus and a little shorter than propodus; dactyl articulated to propodus so as to close with ventral edge against part of straight distal margin of latter and thus qualify as "subchelate"; propodus and other segments of this appendage unarmed, except for setal fringe; merus slender, width about 6 times length and length about 3 times that of propodus. Third and 4th pereiopods similar; both limbs with dactyl slender, triangular in section, curved distinctly laterally (out of plane of appendage), acute distally and armed ventrally with a curved, proximal, comb-like row of about 6 or more slender teeth; dactyl about ⅔ carpus; carpus a little shorter than propodus and a little less than half merus (a little more than half merus in 4th); all segments, except dactyl unarmed. Fifth pereiopod distinctly shorter than others; dactyl slender, acute, flattened but articulated in plane of propodus so as to close with part of its flat ventrally-oriented face against distal margin of propodus, both ventrolateral portion of distal margin of propodus and proximal portion of lateral edge of dactyl each armed with short row of slender teeth which meet and match when dactyl is closed against propodus in a "subchelate" manner; remainder of propodus and other segments unarmed; dactyl a little shorter than carpus, dactyl equal to half propodus, and propodus subequal to merus.

First pleopods absent in male; reduced, uniramous, slender and setose in female. Second to 5th pleopods in both sexes similar, well developed, biramous, with exopod and endopod in each subequal, lanceolate and setose. No appendix interna or appendix masculina present. Uropods with exopod subequal in length to telson and endopod a little longer; both endopod and exopod with transverse suture at about ¾ length of ramus and with row of short spines overlapping suture; one spine at outer edge of exopod suture row enlarged and extending posterolaterally; a few inconspicuous spines on lateral edge of both rami proximal to suture; each ramus with low, longitudinal ridge in midline.

Both male and female with 2 (occasionally 3) strong, anteriorly curved spines medially on coxa of 4th pereiopod; opening of vas deferens in male on raised tubercle medially on coxa of 5th pereiopod; oviduct opening in female medially on coxa of 3rd pereiopod. Eggs very small and numerous in the NZOI Stn. A 355 female. Both male and female have a broad, simple, rectangular plate on thoracic

sternite between 4th pereiopods. This plate is oriented slightly posteriorly, concave in transverse section, with a longitudinal median groove which is deeper and more pronounced in the female.

Branchial Formula

	Maxillipeds			Pereiopods				
	1st	2nd	3rd	1st	2nd	3rd	4th	5th
Pleurobranchiae	–	–	–	–	–	–	–	–
Arthrobranchiae	1	2	2	2	2	2	2	–
Podobranchiae	–	1	1	1	1	1	–	–
Epipodites	1	1	1	1	1	1	1	–
Exopodites	1	1	1	–	–	–	–	–

This formula differs from that given by Selbie (1914) for *J. nocturna* in the presence of an arthrobranch but no podobranch on the 1st maxilliped, and two arthrobranchs instead of one on the 2nd maxilliped. Caroli (1924) critically re-examined the branchial formula of *J. nocturna* and gave a revised version which differs from that given above for *J. novaezealandiae* only in that there is no podobranch on the 3rd pereiopod. Thus both Selbie and Caroli record 17 gills in the European *J. nocturna* but differ in their rank and distribution. Our formula records 18 gills and agrees in complete detail with that given for the genus *Jaxea* (presumably based on *J. nocturna*) by Gurney (1942: 150). As reported below, a recent personal examination of *J. nocturna* gives 18 gills as formulated here for the New Zealand species.

The branchial formula given here for *J. novaezealandiae* also agrees in detail with the 18 gills recorded by Sakai (1962) for *Laomedia astacina* from Japan (disregarding the enigmatic "rudimentary" podobranch on the 1st maxilliped), and agrees with the formula we have for our undescribed eastern Australian *Laomedia.* In addition *Naushonia crangonoides* and *N. portoricensis* both have 18 gills (Chace, 1939: 528) and Thompson's formula for the former agrees with ours in distribution and rank; Chace's formula for the latter differs only in the status of gills on the 1st maxilliped and 4th pereiopod.

It would appear therefore that all known adult members of the family have 18 (or possibly 17) gills but there is no complete agreement on the distribution of these gills at either end of the series.

Systematic Position

Jaxea novaezealandiae is remarkably similar in general facies to the European *J. nocturna,* though it differs in many minor morphological features and in some body and appendage proportions. These differences are indicated in the key to the two species and can be studied in detail by comparing this description with the description and figures of Selbie (1914) for *J. nocturna.* The branchial formula and the ischial armature of the 3rd maxilliped in the latter are still inadequately described.

We have been able to examine a specimen of *J. nocturna* through the kindness of Dr L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden. This is a male, carapace length 10mm, from Ria de Arosa, Coruna, N.W. Spain (1.5km W. to N. of lighthouse on Rua Isle, depth 24 metres, bottom grey-greenish clay, 28/6/1964, R.M.N.H. Stn. 1.672), now in the Australian Museum. The carapace and rostrum are 12mm in length, while the hand is only 14mm long. The slender, straight, elongated fingers are a little more than $1\frac{1}{2}$ times the length of the palm. The anterolateral margin of the carapace has four minute "thorns" above origin of *linea thalassinica,* several minute "thorns" below origin and two small, but distinct, teeth immediately below the ?branchiostegal groove. Contrary to Selbie's

description (1914: 98), the ischium of the 3rd maxilliped has a medial crest of 14 strong teeth on the right member, and one of 16 teeth on the left member. The merus of the 3rd maxilliped has two distolateral teeth and the carpus has a strong tooth distally on the lower edge. The new data recorded here have been used in the key to adults of recent species of *Jaxea* given above. On examination, the branchial formula was found to be exactly as set out for *J. novaezealandiae,* i.e., there are 18 gills, including an arthrobranch, but no podobranch, on the 1st maxilliped and a podobranch on the 3rd pereiopod. We wish to thank Dr Holthuis for sending this specimen and for answering so readily other questions on the nomenclature and morphology of laomediids.

The adults of Kurian's Adriatic form and of the species known only from larvae taken off New South Wales and Samoa can be expected to be closely allied and very similar to the conservative generic structural " type " now known from two antipodean parts of the world. The absence of *Jaxea* from the greater part of the Atlantic, its concentration in Mediterranean waters with an extension in European Atlantic coastal waters to the British Isles, its representation by several species in the Indo-West Pacific, coupled with its presence in the Vienna Basin in the Miocene, all point to a Tethyan origin and distribution for this genus of burrowing laomediids.

Notes on Burrowing

Direct evidence for burrowing is slender, though we believe that the animal's general facies, including its lack of pigmentation and reduced cornea, indicate burrow living. Otter trawling on the Evans Bay study area has produced specimens only at night; trawl shots apparently identical as to depth, length of rope, speed, etc., during daylight produced no *Jaxea* on any occasion. *Squilla armata* is taken in the same manner in the same hauls and also only at night; it is similarly believed to be a burrowing form, but on stronger evidence as we have numerous burrowing records for intertidal and immediately subtidal species of Stomatopoda. Presumably both *J. novaezealandiae* and *S. armata* are trawled at the mouths of their burrows or wandering outside them at night, while in the day both species are below the surface within the burrow systems.

Bottom photographs taken at New Zealand Oceanographic Institute Stn. A 335 in Wellington Harbour show irregular relief and obscure current markings on the surface of the mud, but unfortunately no burrows, holes or signs of animal life are visible in the prints examined. A deep Knudsen dredge haul at this station produced a large ovigerous female *J. novaezealandiae* with dead shells of the bivalves *Nemocardium pulchellum* (Gray) (abundant, shells often in pairs) and *Neilo australis* (Quoy and Gaimard) (uncommon), but no *Echinocardium.* The dredge haul at VUZ 32, the Petersen grab haul at VUZ 68 and the orange peel grab haul at NZOI Stn. C 228, all produced associated pairs of *Jaxea,* which may or may not have been sharing the same burrow system.

Laomedia astacina appears to be the only laomediid for which we have direct evidence of burrowing. Sakai (1962: 30) records for his Japanese specimens that they " are hollowers in the muddy sand of tidal zone, their openings of holes circling around with piled sand ". It is interesting to note that *L. astacina* also has a mineral-grain coating like that described above for the New Zealand *Jaxea.* Sakai (p. 30) records that his animals were " as usual, covered with reddish-brown grain-like particles all over the surface and its hairs, but taking their coverings off from the surface, all the texture turns to white ".

Notes on Behaviour in Laboratory

Specimens of *Jaxea novaezealandiae* taken in Evans Bay on 1/6/1965, were kept alive under observation by R.G.W. for eleven days in a 400 gallon aquarium at

the Victoria University Marine Laboratory at Island Bay, Wellington. The following brief observations on attempted burrowing, locomotion and perception were made during this period and are presented here as a contribution to the biology of this little known animal.

Neither during this period, nor during previous attempts (1957–59) to keep *J. novaezealandiae* alive, could specimens be induced to take food. All foods normally taken by local Decapoda of similar size, such as fragments of fat-free meat, fish or bivalve were ignored. Though these shrimp tore organic matter to pieces with their chelae, they were not observed to eat anything in captivity. The gradual death of the animal, was possibly due partly to starvation and partly to failure to adjust to substratum differences and consequent inability to burrow. Specimens failed to move in any but minor ways for five or more days till final collapse in the 1957–59 observations. Collapse appeared to indicate shock due to lack of thigmotactic stimulation.

(i) *Attempted Burrowing*: Fine silica sand was placed in the Island Bay Laboratory aquarium. This did not permit normal burrowing, but at night *Jaxea* attempted to burrow actively in different situations against the glass walls or under a small stone overhang. Little activity was observed in daylight. In attempting to burrow, the chelipeds were kept in front of the animal and alternately pushed quite deeply into the sand and withdrawn. The loosened sand was then moved with the 2nd pereiopods. These limbs were the most active pair in burrowing and their broad and flattened propodi appeared to be of great use. The 2nd pereiopods moved more or less in unison; they were pushed into the loose sand under the animal and then moved swiftly to the left or to the right with a load of sand which was hurled out to the side. This digging rate was about one complete movement every second.

The 3rd pereiopods were occasionally used to assist the 2nd, but their main use in burrowing was either to loosen sand as described above for the chelipeds, or more frequently to move in a "breaststroke" swimming manner, in unison, and sweep sand backwards from the surface and throw it out behind the shrimp. The 4th pereiopods were similarly used in a swimming manner, or as stabilisers, when anterior limbs were working. The 5th pereiopods were usually inactive and held mainly against the side of the animal, but occasionally took part in sand moving by swimming action or in stabilising and supporting the shrimp.

(ii) *Locomotion*: Crawling either forwards or backwards is the usual form of locomotion in *J. novaezealandiae*. This was assisted at times by movement of the pleopods. Swimming also took place in the aquarium, either forwards or backwards, using the pleopods with the chelipeds extended to the front. When the specimen was disturbed, its abdomen and telson were violently flexed and the animal withdrew wildly and rapidly backwards. When severely agitated *Jaxea* ceased to move and shammed death.

(iii) *Perception*: Sight appeared to be very poor or virtually non-existent, but the sense of touch was immediately observable. *Jaxea* did not react to any surrounding movement within the aquarium, or to any object, till the antennae had made contact; only then did the animal move chelipeds, walking legs or body to avoid or investigate the confronting action or situation. Sight was obviously sufficient to detect day from night, as during daylight hours activity was at a minimum.

2. Larval Development and First Post-Larval Stage of *Jaxea novaezealandiae* with Keys to Larvae known of the Genus *Jaxea* and to First Stage Post-Larvae of the Family Laomediidae

Larvae of the genus *Jaxea* are striking, long-necked, *Lucifer*-like zoeae to which the name of "Trachelifer" was given by Brook (1889). New Zealand trachelifer larvae, first taken in the Bay of Islands, were assigned by Gurney (1924) to *Jaxea* on the basis of their resemblance to larvae of *J. nocturna* from the northern hemisphere. Trachelifer larvae have been observed in the Wellington Harbour plankton for a long time, but the first published record from the Wellington area is that of Wear (1965) who showed that these larvae were among the most abundant and conspicuous larval decapods in the summer plankton.

The abundance of larval material has allowed me (R.G.W.) to trace the entire larval history of *J. novaezealandiae* up to and including the first post-larval stage. The first larval stage has not yet been hatched from ovigerous adults, so the identification of this larval series is based entirely on morphological similarities between the first post-larval stage and the adult *Jaxea,* and on our recognition of only one series of laomediid larvae and only one adult laomediid in the New Zealand region.

Some larval stages of this species taken from the Bay of Islands have already been described by Gurney (1924) and compared with the larvae of *J. nocturna.* Six essential larval stages have now been recognised in the planktonic life history of *J. novaezealandiae.* Five of these (stages 1, 2, 4, 5 and 6) have been described by Gurney (1924) and additional details only are given in this paper.

A further essential stage in this larval series (stage 3) not found by Gurney, and a seventh larval stage (designated here as stage 6*a*) of uncertain significance, which occurs only rarely, are each described in detail.

The laboratory method used to obtain successive larval stages has been outlined in a previous paper (Wear, 1964). Total length of larvae and of the first post-larval stage is here measured from the tip of the rostrum to the most posterior margin of the telson, and excludes all telson processes and setae. In descriptions of the larval stages, measurements of total length are followed by additional total length measurements italicised and in parentheses. These latter measurements were made from the tip of the rostrum to the posterior tips of the lateral telson cornua to conform with the earlier measurements of Gurney (1924), and those of Caroli (1924) on the larvae of *J. nocturna.* However, the difference between our measurements and those italicised is in fact the length of the lateral cornu on each side of the telson, which are modified posterior setae. This distance varies considerably with the form of the telson in successive larval stages, and therefore gives an inaccurate assessment of length increase per moult.

Nomenclature of larval limbs and limb segments is based on Borradaile (1926) and Hale (1927) with the suffix "ite" in limb terms deleted.

KEY TO THE LARVAL STAGES OF *Jaxea novaezealandiae*

1 (4) Total length less than 6.0mm; 1st antenna with one-segmented peduncle, no setae along inner margin; 2nd antenna having endopod with three terminal plumose setae; 1st pereiopod without natatory exopod; abdomen of five segments and a telson; uropods absent; telson with posterolateral cornu as a single spine; thalassinid hair (reduced 2nd telson seta) present; setae articulating with telson fringed with fine hairs and small spines.

2 (3) Total length 4.0mm; protopod of 2nd antenna with one ventral spine, exopod (squama) with 10 marginal setae; 1st and

2nd maxillipeds having exopods with four natatory setae; 3rd maxilliped as uniramous rod, without natatory exopod; telson as two slender rami, deeply cleft in posterior midline, 7 + 7 posterior setae including thalassinid hair .... Stage 1 (fig. 3A, B, H)

3 (2) Total length 4.9mm to 5.3mm; protopod of 2nd antenna with two ventral spines, exopod with 11 marginal setae; 1st and 2nd maxillipeds having exopods with six natatory setae; 3rd maxilliped biramous with exopod having six terminal natatory setae; telson triangular with shallow cleft in posterior midline, 10 + 10 posterior setae (occasionally 10 + 11 or 11 + 11) .... Stage 2 (fig. 3I)

4 (1) Total length greater than 6.0mm; 1st antenna with two-segmented peduncle fringed with plumose setae along inner margin; 2nd antenna having endopod without terminal plumose setae, but with a small subterminal hair; 1st pereiopod with a natatory exopod; abdomen of six segments and a telson; uropods present; telson with posterolateral cornu bifurcate; thalassinid hair absent; setae articulating with telson fringed with small spines, but usually without fine hairs.

5 (8) Total length less than 11.0mm; 2nd antenna with endopod not exceeding length of exopod; 1st pereiopod not chelate; pleopod buds absent or only just visible; 3rd visible telson seta (not articulating with telson) shorter than lateral process (1st seta).

6 (7) Total length less than 8.0mm (7.4mm to 7.7mm); 2nd antenna with endopod about $\frac{3}{4}$ length of exopod; 2nd pereiopod having rod-like exopod without setae; uropod with endopod and exopod not separate from protopod, exopod without lateral tooth; telson usually with 11 + 11, 11 + 12 or 12 + 12 posterior setae (original 2nd seta or thalassinid hair absent); telson without lateral distal spines .... Stage 3 (fig. 3C, D, E, J)

7 (6) Total length greater than 8.0mm (9.3mm to 10.0mm); 2nd antenna with endopod and exopod subequal in length; 2nd pereiopod having segmented exopod with four or six natatory setae; uropod with endopod and exopod separate from protopod, exopod with a prominent lateral tooth; telson usually with 13 + 13 or 13 + 14 posterior setae; telson with 4, 5, 6 or 7 lateral distal spines on each side .... Stage 4 (fig. 3K)

8 (5) Total length greater than 11.0mm; 2nd antenna with endopod longer than exopod; 1st pereiopod with rudimentary chela; pleopod buds present, distinct and well developed; 3rd visible telson seta equal to or extending beyond 1st seta.

9	(10)	Total length less than 13.0mm (11.6mm to 12.5mm); 2nd antenna with endopod shorter than total length of 1st antenna; pleopod buds short, much less than half the length of abdominal somites; 3rd telson seta and lateral process (1st seta) about equal in length	**Stage 5 (fig. 3L, M)**
10	(9)	Total length greater than 13.0mm (13.8mm to 15.2mm); 2nd antenna with endopod equal to total length of 1st antenna; pleopod buds about half the length of abdominal somites; 3rd telson seta extending well beyond lateral process	**Stage 6 (fig. 3N)**

Description of Larval Stages

STAGE ONE (fig. 3A, B, H), total length 4.0mm (*4.25mm*)

The first larval stage (fig. 3A) is described by Gurney (1924: 150–151, fig. 60). The protopod of the 2nd antenna has only one ventral spine. The second spine which Gurney attributes to all larval stages does not appear until stage two. The telson (fig. 3H) is deeply cleft, and comprises two narrow and tapering rami each bearing plumose setae posteriorly. The posterior border of the telson is fringed with fine hairs medially and between each of the inner five pairs of long plumose setae.

The first (outer) seta is smooth and does not articulate with the telson. Gurney (1924) records the second telson seta present as a fine, smooth hair, springing from the base of the third seta—a condition normal among anomuran and thalassinid larvae. This is commonly known as the "thalassinid hair". In the Wellington larvae this seta is conspicuous and fringed with fine hairs along its entire length (fig. 3B). This reduced seta was not seen in the larvae of the Sydney species (Dakin and Colefax, 1940: 180–181, fig. 269a) though specifically looked for by those authors, but is present in the Samoan species (Gurney, 1938), and in *J. nocturna* (Gurney, 1942, fig. 101b) though missed by Caroli (1924) and by Tattersall (1938).

In *J. novaezealandiae* the third, fourth and shorter seventh telson setae are each fringed with fine hairs and minute spines along their entire length, but the fourth seta may have two or three large basal spines (fig. 3B). The fifth seta has a row of about ten large, basal spines along both inner and outer margins, but is without fine hairs in this region. Minute spines and fine hairs decreasing in size distally, occur for the remainder of its length. The sixth seta is similar, but large spines without supplementary hairs fringe its outer margin for approximately half its length (fig. 3B).

The armature of these posterior telson setae is of specific significance and must therefore be placed on record. With the lateral cornu of the telson considered as a modified first seta (Gurney, 1924) the telson formula is 7 + 7 setae as is normal in stage one larvae of Anomura and Thalassinidea.

Chromatophore Pattern

Chromatophores of the stage one larva have been illustrated in a previous publication (Wear, 1965; text-fig. 5D). All chromatophores are orange, small, numerous and very diffuse. Concentrations of pigment are found below the eyes, above the mandibles and maxillae, in the basipods and exopods of the 1st and 2nd maxillipeds, in the last four abdominal segments and in the telson. In later larval stages chromatophores appear above the 3rd maxillipeds and the pereiopods.

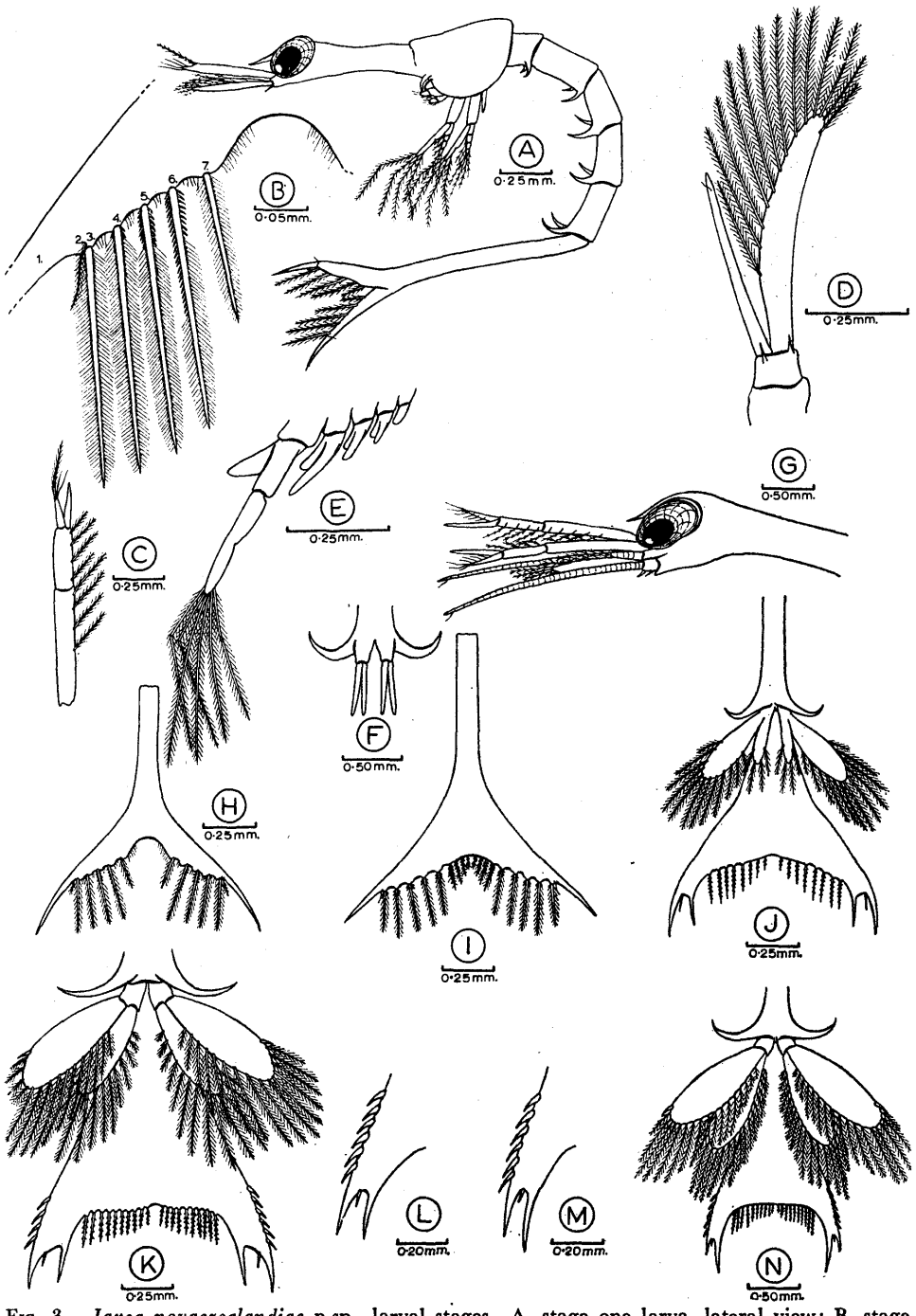

FIG. 3.—*Jaxea novaezealandiae* n.sp., larval stages. A, stage one larva, lateral view; B, stage one larva, posterior telson processes (one to seven) of right side, ventral view; C, stage three larva, left 1st antenna, dorsal view; D, stage three larva, left 2nd antenna, ventral view; E, stage three larva, left pereiopods, lateral view; F, stage six *a* larva, pleopods of 2nd abdominal segment; G, stage six *a* larva, cephalic appendages, lateral view; H, stage one larva, telson, ventral view; I, stage two larva, telson, ventral view; J, stage three larva, uropods and telson, ventral view; K, stage four larva, uropods and telson, ventral view; L, stage five larva, left lateral telson cornu, dorsal view; M, stage five larva, left lateral telson cornu, dorsal view to show extension of third telson seta beyond first seta; N, stage six larva, uropods and telson, ventral view.

STAGE TWO (fig. 3I), total length 4.9mm to 5.3mm (*5.15mm to 5.55mm*)

The second larval stage has also been described by Gurney. The protopod of the 2nd antenna now has a second spine ventrally. The 1st and 2nd maxillipeds have natatory exopods each with six long plumose setae, and the exopod of the 3rd maxilliped bears four such setae. The telson (fig. 3I) is rather more triangular than in stage one and usually bears 10 + 10, 10 + 11 or occasionally 11 + 11 posterior setae. These setae, with the exception of the lateral cornu and the thalassinid hair, usually possess a few marginal basal spines.

STAGE THREE (fig. 3C, D, E, J), total length 7.4mm to 7.7mm (*7.6mm to 7.9mm*)

The third larval stage was not present in Gurney's material and has therefore not been described.

The peduncle of the 1st antenna is two-segmented, with eight plumose setae along its inner margin (fig. 3C). The unarmed inner ramus exceeds the length of the outer ramus.

The 2nd antenna possesses a two-segmented protopod, with two ventral spines arising from the anterior margin of the distal segment (fig. 3D). The endopod is three-quarters the length of the exopod (squama) and is without terminal plumose setae, but has a small, ventral subterminal hair. The exopod has 13 or 14 marginal plumose setae (fig. 3D).

The 3rd maxilliped has a natatory exopod with six terminal setae as in stage two, but the endopod is somewhat longer and more robust.

The 1st pereiopod comprises a long rod-like endopod and a natatory, two-segmented exopod with six terminal plumose setae (fig. 3E). The 2nd, 3rd and 4th pereiopods are biramous. The exopod of the 2nd pereiopod is a slender unsegmented rod without setae, and those of the 3rd and 4th pereiopods are undeveloped buds (fig. 3E).

The telson is now separate from the 6th abdominal segment which has ventral procurved hooks similar to those of the first five segments (fig. 3J). There is no sign of pleopods. Uropods are present but the endopod and exopod have not separated from the protopod. The exopod has about 12 marginal setae but no lateral tooth, and the much smaller endopod has about four marginal setae (fig. 3J). The telson is broadly triangular, with the concave posterior margin having 11 or 12 pairs of setae including those of the slender posterolateral cornua. The third visible pair of setae (probably the original 4th setae) is now smooth, has lost articulation with the telson and migrated towards the cornua giving the posterolateral angles a more or less bifurcate appearance. Within this bifurcation of the lateral process (1st seta) and the third visible pair of setae, the second seta is reduced to a small spine. This spine is probably the third seta of stage two, as the thalassinid hair is now absent. The inner eight (or nine) pairs of setae which articulate with the telson, each have a few marginal basal spines.

It is in the third and subsequent larval stages of *J. novaezealandiae* in which the telson bifurcates at the posterolateral angles, that specific distinction from the later stage larvae of *J. nocturna,* the Sydney species and Kurian's Adriatic species becomes really apparent. In these latter three species the posterolateral cornu of the telson remains as a single process.

STAGE FOUR (fig. 3K), total length 9.3mm to 10.0mm (*9.45mm to 10.15mm*)

The stage four larvae of *Jaxea novaezealandiae* agree in essential detail with the larva Gurney describes as stage three. However the following additional points have been noted.

The endopod of the 2nd antenna does not exceed the length of the exopod as in Gurney's larva, but the two rami are subequal. The 2nd pereiopod has a natatory exopod with four or six terminal plumose setae. Pleopod buds are not usually visible, but in occasional larvae tiny pleopod rudiments may be seen on segments two to five. The telson is more usually of the form shown in fig. 3K rather than that drawn by Gurney (1924: 152, fig. 61g). The "serrations" present on the lateral distal third of the telson are in fact stout spines, each having a definite articulation with the telson (fig. 3K). These spines vary in number between four and seven, but larvae are rarely found with an equal number of these spines on each side of the telson. Telson spines of this type are rare among thalassinid larvae, and certainly unique in the Laomediidae.

STAGE FIVE (fig. 3L, M), total length 11.6mm to 12.5mm (*11.75mm to 12.65mm*)

This stage agrees with Gurney's stage four. The third (unarmed) telson setae only rarely extend beyond the tips of the outermost pair (fig. 3M). However, this trend become more obvious in the sixth larval stage (fig. 3N).

STAGE SIX (fig. 3N), total length 13.8mm to 15.2mm (*14.1mm to 15.5mm*)

This stage agrees with Gurney's stage five. The third telson setae now extend well beyond the outermost pair. This sixth stage is abundant in the plankton, and is probably the final trachelifer stage in the life history, as the first post-larval stage was obtained from these in the laboratory. There are also six stages in *J. nocturna* (Caroli, 1924) and in the Sydney species (Dakin and Colefax, 1940). Although post-larvae were not obtained by Dakin and Colefax, their sixth larval stage (15mm in total length) is at a similar stage of development to *J. novaezealandiae* stage six, and it is not expected that further trachelifer stages would follow in the Sydney species.

STAGE SIX *A* (fig. 3F, G), total length 15.5mm to 17.0mm (*15.9mm to 17.4mm*)

Stage six *a* was not seen by Gurney. This larva differs from stage six in the following characters.

The endopod of the 2nd antenna extends beyond the 1st antenna, and the segments of the endopod are visible beneath the cuticle (fig. 3G). The pereiopods have increased in size and are visibly segmented beneath the cuticle. The abdominal pleopods are now long biramous rods without setae (fig. 3F) and are longer than half the length of the abdominal segments. The telson is similar to that of stage six, but the third telson setae are more strongly developed than the first setae which are now relatively reduced and subterminal.

The status of this six *a* trachelifer stage is uncertain, but it is not regarded as an essential stage in the larval life history of *J. novaezealandiae*. Stage six *a* was obtained by moult in the laboratory but is extremely rare in the plankton, and it seems probable that the majority of larvae bypass this stage and moult directly from stage six to the first post-larval stage. Stage six larvae showed no sign of a further trachelifer stage beneath the cuticle. However, larvae at a stage of development intermediate between stages five and six were found rarely in the plankton. These showed a further trachelifer moult beneath the cuticle, and although the casts of larvae from which the original stage six *a* larvae were obtained in the laboratory were unfortunately destroyed, it is likely that stage six *a* follows this intermediate stage between five and six. This alternative route to the first post-larval stage appears to be taken only rarely.

Discussion of Larval Stages

Dakin and Colefax (1940) have recognised at least three distinct Indo-Pacific species of *Jaxea, viz.,* a New Zealand species (*Jaxea novaezealandiae*) of which the adult and larval stages are now fully described, a "Sydney" species from New South Wales of which only the trachelifer larval stages are known, and *Jaxea* sp. from Samoa, which is known only from its first larval stage. Two species are known from the northern hemisphere. These are *J. nocturna* from the Mediterranean and North Atlantic with both the adult and larvae described and a distinct species from the Adriatic Sea known only from a single sixth stage larva.

The larvae of all five "species" appear to be distinct though closely interrelated. Characters by which these larvae may be separated in the first zoeal stage are given in the key below. The separation of stage one larvae of the five species attributed to the genus *Jaxea* is difficult, as published descriptions show the first stage larvae to be closely similar. However, specific differences become more apparent in later larval stages. For example, in the unnamed Australian species and the New Zealand species, *J. novaezealandiae,* stage one larvae are almost identical, but the later stage larvae of these two species are quite distinct, especially in the form and armature of the telson.

The significance of observations on the presence or absence of the reduced second telson seta (thalassinid hair) is not clear. Though not recorded by Dakin and Colefax (1940) for the Sydney larvae, it is known to occur in *J. novaezealandiae,* the Samoan species (Gurney, 1938) and in *J. nocturna* (Gurney, 1942). The armature of the telson in stage six of the Adriatic species (Kurian, 1956) suggests that it may also occur in the early larval stages of that species.

In *J. novaezealandiae* it is, however, important to discuss the derivation of the posterior telson process which loses its articulation with the telson in stage three, and enlarges greatly in subsequent larval stages forming the inner ramus of the bifurcated posterior telson cornu. This seta can be seen beneath the cuticle of second stage larvae about to moult, and appears to be the fourth seta. In stage three larvae the third seta is reduced to a small stout spine within the bifurcated cornu. The thalassinid hair of stage two is apparently lost in the third and subsequent larval stages. Enlargement of the fourth seta occurs in the Euphausiacea, Penaeidea, later stage Thalassinidea (*Upogebia, Callianassa* etc., see fig. 4) and Anomura, but is most pronounced in the Brachyura in which it forms the greater part of the fork of the telson (Gurney, 1942). This character has therefore been paralleled in *Jaxea novaezealandiae.*

However, among the Laomediidae of which later stage larvae are known (with the exception of *J. novaezealandiae*) no such enlargement of the fourth seta is immediately obvious (fig. 4 I-N), as the lateral cornua of the telson are of one process as in the Brachyura. The lateral cornua of the laomediid telson are considered by many authors to be modified first setae (Caroli, 1924; Gurney, 1942; Kurian, 1956; Dakin and Colefax, 1940), and the two or three small spines usually found on the posterolateral margins in late stage laomediid larvae (fig. 4 H-N) are thought to be accessory developments. These spines are admittedly accessory developments in *J. novaezealandiae* (fig. 4H), and also in *J. nocturna* (fig. 4K) where they are medial to the lateral cornu. However, in other laomediid larvae (fig. 4I, J, L-N) these posterolateral spines may be the first, second and third telson setae in a more advanced stage of reduction than that shown by the Callianassidae and Axiidae in which the fourth seta enlarges, and the first, second and third setae are reduced to conspicuous lateral sub-terminal telson spines in later larval stages (fig. 4 A-G).

In the Laomediidae, therefore, the uniramous telson cornua of the third and subsequent larval stages may in fact be the true fourth setae, in which case the persistence of comparatively well-developed telson setae lateral to the fourth in *Jaxea novaezealandiae* (fig. 4H) is a rather more primitive condition.

In possessing at least six and occasionally a seventh stage (six *a*) in the larval life history, *Jaxea novaezealandiae* passes through a much longer series of ecdyses than do the majority of the Reptantia where the usual number of larval stages is three, rarely four or five. Gurney (1924) comments on this fact, but was unable to establish whether or not the entire series was passed through by a single larva. From laboratory rearing this now appears likely, at least for the first six stages.

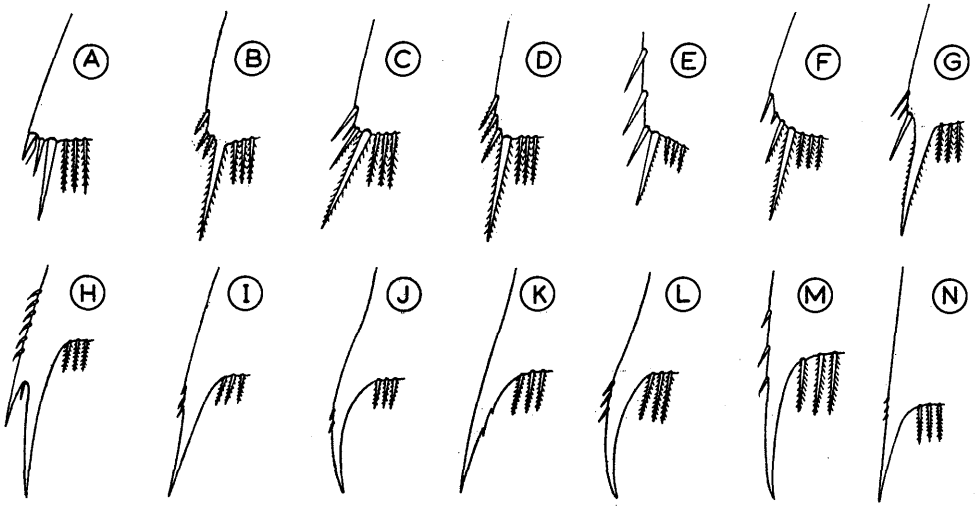

FIG 4.—Posterolateral telson setae of thalassinid larvae (fourth seta is largest in all examples). A to G, Families Upogebiidae, Axiidae, Callianassidae and unidentified thalassinid. H to N, Family Laomediidae.

A, *Upogebia* sp., stage three (from Gurney, 1938: 331, fig. 32b); B, *Upogebia danai,* stage four (from Gurney, 1924: 166, fig. 66b); C, Axiid sp., stage three (from Gurney, 1924: 147, fig. 58d); D, *Callianassa* sp., stage four (from Gurney, 1924: 162, fig. 65e); E, Thalassinid sp. (from Gurney, 1938. 316, fig. 16b); F, *Callianassa* (*Trypaea*) *australiensis,* stage six (from Dakin and Colefax, 1940: 183, fig. 271h); G, *Callianassa ?* sp. (from Gurney, 1938: 325, fig. 25e); H, *Jaxea novaezealandiae,* stage six; I, *Jaxea* sp., stage six (from Dakin and Colefax, 1940: 181, fig. 269f); J, *Jaxea* sp., stage six (from Kurian, 1956: 74, fig. 146); K, *Jaxea nocturna,* stage six (from Caroli, 1924: 181, fig. 20); L, *Naushonia* sp., stage three (from Dakin and Colefax, 1940: 176, fig. 264b); M, *Naushonia* ? sp., stage four (from Gurney, 1938: 336, fig. 37b); N, *Naushonia portoricensis* ?, stage five (from Gurney and Lebour, 1939: 612, fig. 7).

KEY TO FIRST STAGE LARVAE OF THE GENUS *Jaxea*

Stage one larvae of four species are known, but a fifth species from the Adriatic Sea is known only from a stage six larva (Kurian, 1956). I have therefore deduced key stage one characters of this species from Kurian's description (see footnote p. 21) in order that the five known larval species may be separated in the first zoeal stage. A complete series of larval stages has been described for the Australian species (Dakin and Colefax, 1940), for *Jaxea nocturna* Nardo (Claus, 1884; Brook, 1889; Cano, 1891; Bouvier, 1914; Caroli, 1924; Tattersall, 1938; Gurney, 1942; Kurian, 1956) and for *J. novaezealandiae,* but the Samoan species is known only from a stage one larva (Gurney, 1938).

1	(8)	Total length greater than 3.0mm.	
2	(5)	Lateral pleural process of 1st abdominal somite absent or present as a small blunt structure.	
3	(4)	Rostrum present, small, not extending beyond anterior margin of eye; basis of 2nd antenna with two ventral spines; 3rd maxilliped a long uniramous rod; lateral pleural process of 1st abdominal somite absent; 7th telson seta (5th long seta) having outer margin with fine hairs along its proximal half, and small spines along its distal half	*Jaxea nocturna* Nardo (Caroli, 1924, etc.)
4	(3)	Rostrum absent; basis of 2nd antenna with one ventral spine; 3rd maxilliped a bud-like rudiment; lateral pleural process of 1st abdominal somite present, but small and blunt; 7th telson seta having outer margin without fine hairs, but with small spines along entire length	*Jaxea* sp.—Samoa (Gurney, 1938: 333–334, fig. 35)
5	(2)	Lateral pleural process of 1st abdominal somite well developed, sharp and procurved.	
6	(7)	Rostrum short, extending to anterior margin of eye or just beyond; thalassinid hair absent; all 5 inner pairs of posterior telson setae having spines along both inner and outer margins of basal third, but with fine hairs distally; posterior border of telson with fine hairs medially, and between 2nd and 3rd long plumose setae only	*Jaxea* sp.—Sydney Harbour, Australia (Dakin and Colefax, 1940: 179–182, figs. 268, 269)
7	(6)	Rostrum longer, extending beyond eye by about half length of eye; thalassinid hair present, conspicuous and plumose; 6th, 5th and occasionally 4th telson setae having large basal spines along inner and outer margins extending along outer proximal half of 6th seta; no hairs occurring together with large spines; otherwise minute spines and fine hairs decreasing in size distally along entire inner and outer margins of 7th, 6th, 5th, 4th and 3rd telson setae; posterior border of telson with fine hairs medially and between all five pairs of long plumose setae	*Jaxea novaezealandiae* (fig. 3A, B, H)
8	(1)	Total length probably less than 3.0mm*	*Jaxea* sp.—Adriatic Sea (Kurian, 1956: 75, figs. 144–146)

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* This character is based on a single stage six larva with a total length of 5.7mm, which is less than half the length of *J. nocturna* stage six—the otherwise smallest stage six *Jaxea* larva. Other first stage larval characters likely to be found in Kurian's Adriatic species are listed below:

(a) Rostrum short, with a double curve, not reaching the anterior margin of eye.

(b) 3rd maxilliped well developed—long uniramous rod as in *J. novaezealandiae.*

(c) Lateral pleural process of 1st abdominal somite small and blunt.

(d) Thalassinid hair present.

The First Post-Larval Stage

The first post-larval stage of *Jaxea novaezealandiae* (fig. 5), total length 7.50mm, was obtained by moult from larval stages six (three times) and six *a* (once) in the laboratory. Post-larvae were not found in the plankton and it therefore seems likely that metamorphosis takes place on the sea floor. This has been suggested by Tattersall (1938) for *J. nocturna*. The unusual metamorphosis of *J. nocturna* involving a considerable reduction in size from that of the final trachelifer larval stage has been described by both Tattersall and by Caroli (1924). In *J. nocturna*, 12mm to 15mm trachelifer larvae moult to a first post-larval stage measuring only 6.5mm in total length. In *J. novaezealandiae*, stage six or six *a* larvae measuring between 14mm and 17mm in length moult to a 7.5mm post-larva (fig. 5). These specimens are rather opaque, with small red chromatophores scattered over the carapace, around the basal segments of the cephalic appendages, the joints of the pereiopods, abdominal segments and the telson. There was no evidence of a definite pattern in the arrangement of the chromatophores.

First stage post-larvae survived in finger bowls in the laboratory for up to three weeks, but did not feed.

As the first post-larval stage of *J. novaezealandiae* is closely similar to that of *J. nocturna* fully described by Tattersall (1938) and Caroli (1924), we do not therefore propose to describe this New Zealand form in great detail. Differences between the adult and post-larva of *J. novazealandiae* are similar to those noted by Tattersall for *J. nocturna*. The more important differences are listed below.

1. The post-larva of *J. novaezealandiae* carries a more conspicuous armature of hairs and small spines than does the adult. The five or six ventral pleural teeth found on the post-larval abdominal segments, and the small spines on the carpus and prodopus of the post-larval chelipeds, do not persist through as teeth to the adult condition (there are minute serrations on the 3rd to 6th adult pleura). The stronger ventral spines and dorsal distal spines on the merus of the chelipeds, and the lateral serrations on the rostrum are all retained by the adult. However, adult structures such as the sub-orbital carapace spines, and teeth on the dactyli of the 3rd, 4th and 5th pereiopods, and on the dorsal surface of the telson are not developed in the first post-larval stage.
2. The post-larval rostrum is relatively larger than that of the adult, and the "neck" is quite well defined in both dorsal (fig. 5B) and lateral (fig. 5A) views. All traces of cervical elongation of the carapace are lost in the adult. The *linea thalassinica* is incomplete and weakly developed in the post-larva but relatively strong in the adult (fig. 1).
3. The eyes are very much larger than in the adult. In the post-larva the eyes protrude beyond the margin of the carapace (fig. 5B) but in the adult the eyes are very tiny and completely concealed beneath the rostrum (fig. 1). This great reduction in the size of the eyes and the adult's virtually blind condition is presumably related to the supposed deep-burrowing habit of *J. novaezealandiae*.
4. The antennal scale (scaphocerite) of the post-larva is relatively larger than that of the adult. Also the basal segment of the post-larval antennal endopod is considerably shorter than in the adult where it is greatly elongated.
5. The chelipeds of the adult are more robust and sculptured than those of the post-larva. The propodus of the 2nd pereiopod is not flattened as in the adult (fig. 1).

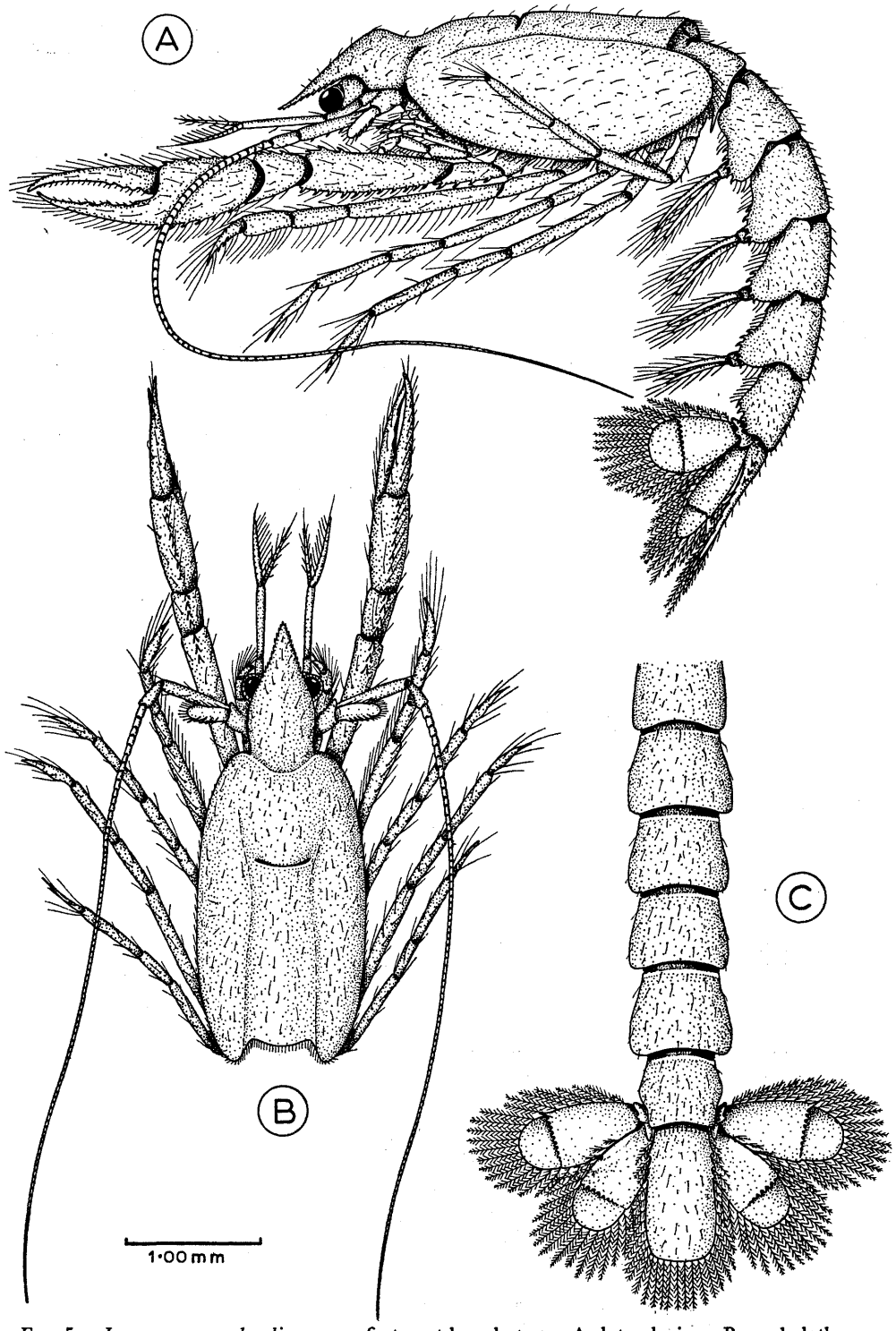

FIG. 5.—*Jaxea novaezealandiae* n.sp., first post-larval stage. A, lateral view; B, cephalothorax with appendages, dorsal view; C, abdominal segments, uropods and telson, dorsal view.

6. The post-larval tail-fan lacks the ridges and sculpturing characterising that of the adult (fig. 2G). The telson is twice as long as broad in the post-larva (fig. 5C) but only slightly longer than broad in the adult. Transverse sutures are incomplete medially on the post-larval uropods (fig. 5C).

The differences discussed above are not great, and indicate the nature and extent of changes undergone during successive ecdyses from the first post-larval stage to the adult condition. The essential morphological features of the post-larva are so similar to those of the adult that there can be no doubt concerning their belonging to the same species, especially when larval evidence for this deduction is considered in support.

There are now four laomediid crustacean species from which the first post-larval stage is known. These are *Jaxea novaezealandiae; J. nocturna* described by Caroli (1924), Tattersall (1938) and figured by Gurney (1942); *Naushonia crangonoides* described by Thompson (1903); and "*Naushonia portoricensis?*" described by Gurney and Lebour (1939). Gurney and Lebour obtained the first *and* second post-larval stages of their "*N. portoricensis?*". Post-larvae of *Jaxea nocturna* and of *J. novaezealandiae* are more readily separated than are their respective larval stages. The main differences between the first post-larval stages of these two species of *Jaxea* and the characters by which *Jaxea* post-larvae may be distinguished from post-larvae of the genus *Naushonia* are given in the key below.

KEY TO KNOWN FIRST STAGE POST-LARVAE OF THE FAMILY LAOMEDIIDAE

1	(4)	Ischium of 3rd maxilliped with from 9 to 14 strong blunt medial spines; 1st pereiopods chelate; pereiopods one to four without vestigial exopods; 1st abdominal pleuron extended ventrally as a long slender process; telson with three or more lateral teeth	genus *Jaxea* Nardo
2	(3)	Total length 6.5mm; "neck" not well defined, shape of carapace similar to that of adult; *linea thalassinica* well defined; suborbital carapace spines present; anterolateral margin of carapace with several small spines; 3rd pereiopod without podobranch; basal segment of uropodal exopod serrated; telson rather rectangular with lateral margins toothed, terminating posterolaterally in a strong tubercle	*Jaxea nocturna* Nardo (Caroli, 1924; Tattersall, 1938; Gurney, 1942)
3	(2)	Total length 7.5mm; "neck" well defined, shape of carapace dissimilar to that of adult; *linea thalassinica* poorly defined, especially anteriorly; suborbital carapace spines absent; anterolateral margin of carapace without spines; 3rd pereiopod with podobranch; basal segment of uropodal exopod not serrated but with biplumose hairs; telson rounded posteriorly with lateral margins having only three or four proximal teeth, no posterolateral tubercle	*Jaxea novaezealandiae*
+	(1)	Ischium of 3rd maxilliped serrated or smooth, but without large spines; 1st pereiopods subchelate; pereiopods one to four with	

		vestigial exopods each with apical setae; 1st abdominal pleuron not extended ventrally; telson with one lateral tooth	genus *Naushonia* Kingsley
5	(6)	Rostrum with two lateral teeth and with a small apical process; *linea thalassinica* very faint; eye with a small anterior tubercle; 3rd maxilliped with ischium smooth; 1st maxilliped without arthrobranch; 1st pereiopod slender, not reaching beyond level of eye, propodus with one large inner tooth, dactyl broad	*Naushonia portoricensis?* (Rathbun) (Gurney and Lebour, 1939)
6	(5)	Rostrum with many lateral serrations but without apical process; *linea thalassinica* strongly developed; eye without anterior tubercle; 3rd maxilliped with ischium serrated distally; 1st maxilliped with arthrobranch; 1st pereiopod robust, extending well beyond level of eye, propodus with two large inner teeth, dactyl slender and falcate	*Naushonia crangonoides* Kingsley (Thompson, 1903)

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