THE PELAGIC LARVAE OF *CHORISQUILLA TUBERCULATA* (BORRADAILE, 1907) (STOMATOPODA)

BY

A. MICHEL *) and R. B. MANNING **)

INTRODUCTION

The larval stages of most stomatopods are unknown. Recent studies on the family Squillidae with the recognition of additional genera and families (Manning, 1962, 1968, 1969; Serène, 1962) have helped clarify the systematic position of adults. It now appears necessary to extend our knowledge of the larvae. Earlier studies (Brooks, 1892; Giesbrecht, 1910; Komai, 1924; Komai & Tung, 1929; Gurney, 1937, 1946; Manning, 1962; Manning & Provenzano, 1963) suggest that the larval development of stomatopods occurs in three distinct phases, one embryological, one propelagic, and one pelagic, ended by the stomatopodic molt at which time some adult characters begin to appear in the postlarvae. The present report concerns only the pelagic larvae and the first postlarvae of *Chorisquilla tuberculata*, one of the rarest of the Indo-West Pacific stomatopods.

METHODS

Larvae and postlarvae were sorted from micronectonic collections taken by an Isaacs-Kidd ten foot Midwater Trawl or were found in the stomach contents of the yellowfin tuna, *Thunnus albacares* (Bonnaterre), caught along the New Caledonian barrier reef. Two broad areas were sampled, one located between the parallels 24°S and 05°N and the meridians 160°E and 180°E, and the other in the coastal area west of the Marquesas Islands.

The late larval stages were reared on board N.O. "Coriolis" in glass jars of 100 cc capacity with sea water filtered through glass wool. Late larvae were held with the aim of obtaining metamorphosis to the postlarva in experiments designed to produce identifiable postlarvae from known late larvae. This method has been employed with success by Alikunhi & Aiyar (1942), Alikunhi (1944a-b, 1950, 1952, 1959, 1967) and by Manning (1962) to identify larvae with adults.

With sufficient material it is possible to reconstruct the larval series from the last larval stage. The exact number of molts occurring from hatching to meta-

*) Oceanographer, Centre O.R.S.T.O.M., Noumea, New Caledonia.

**) Chairman, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C., U.S.A.

morphosis cannot be determined using planktonic material alone because of the absence of propelagic stages. For this reason the larval stages have been identified here by stage numbers n-1, n-2, n-3, etc..., with the postlarvae as stage n.

Drawings were made from preserved specimens using a stereoscopic microscope with a camera lucida.

The descriptions are based on several specimens of each stage. Measurements were made with an ocular micrometer. Total length (TL) was measured from the base of the rostrum to the median posterior margin of the telson for the larvae and from the tip of the rostrum to the apex of the submedian spines for the postlarvae. Carapace length (CL) was measured from the base of the rostrum or of the rostral plate to the median posterior margin of the carapace.

125 larvae and 51 postlarvae were examined.

RESULTS

One of the late larval stages reared in the aquarium underwent metamorphosis to the postlarva at night 24 hours after the specimen was caught. The adult characters exhibited by the postlarva were adequate to identify it with *Chorisquilla tuberculata* (Borradaile, 1907).

Among the larvae, 8 stages were recognized. On the basis of planktonic material, it is difficult to determine whether the observed stages represent consecutive molts or whether intermediate molts also occur. In the series reported here the development of the characters compared to the length suggest that only one molt is involved in each stage.

DESCRIPTION

Larval stages. — All the larvae show a larval carapace with long spines, a second maxilliped modified into a raptorial claw and an abdomen with 5 pairs of functional pleopods. Morphological changes in each stage are primarily concerned with the appearance and modification of different appendages; changes during development are summarized in table I and the table II [1]).

Larval carapace (fig. 1A, B; fig. 3A, C). — The carapace is easily recognizable by its globular form and its long spines. The rostrum bears 2 or 3 spinules on its ventral margin until stage n-5 at which time they disappear; the anterolateral and posterolateral spines are long and pointed, and at the base of the last pair there is a ventrally-directed spinule. The median dorsal spine is also long and remains until the late stages. The ventral surfaces of the lateral margins are finely denticulated. The carapace extends to the last thoracic somite.

Eyes. — Stalked at all stages. The cornea in the postlarva has the characteristic bilobed appearance.

---

[1]) For the n-8 stage only the raptorial claw has been illustrated; the unique specimen was not dissected.

TABLE I

Summary of the characters of the larval stages of *Chorisquilla tuberculata*

Stages	CL range	TL mean	A_2 groups of hairs	Ischimeral articulation of raptorial claw	Thoracic appendages 1	3	4	5	6-7-8	Epipods	Gills	Uropods	6th abdominal segment
n - 8	2.0	4.0	—	terminal	dactylus absent	bud	bud	bud	—	1	—	—	—
n - 7	2.6-3.7	5.0	—	sub-terminal	,,	slightly longer and curved	slightly longer	slightly longer	—	2	—	bud bilobed	—
n - 6	4.2	5.8	3-4	,,	,,	longer, curved apex constricted	longer, curved	longer, curved	bud	5	bud	bud basal process with 1 spine	separate from telson
n - 5	4.5-4.7	6.9	4-5	,,	dactylus bud	dactylus formed	apex constricted	apex rounded	two-segmented bud	,,	present	basal process with 2 spines exopod : 1 spine	,,
n - 4	5.0-5.6	9.0	5-6	,,	,,	,,	dactylus formed	apex constricted	endopod present, exopod one segment	,,	,,	exopod: 2 spines	,,
n - 3	6.0-6.6	10.5	7-8	,,	,,	,,	,,	dactylus formed	exopod elongate	,,	,,	exopod: 3 spines	,,
n - 2	7.2-8.0	12.4	8-9	,,	sub-chelate	,,	,,	,,	exopod two-segmented	,,	,,	exopod: 4 spines	,,
n - 1	7.8-9.6	16.0	8-11	,,	,,	,,	,,	,,	,,	,,	,,	exopod: 6 spines	,,
n	3.5-4.2	19.0	8-11	,,	,,	,,	,,	,,	,,	,,	,,	exopod: 9 spines	,,

TABLE II

Changes in anterior appendages and mouth parts during development

Stages	Antennule	Antennal endopod	Antennal scale	Mandible	First maxilla	Second maxil
n — 8	2 flagella: inner 2 seg., outer 1 seg.	bud	present 11 or 12 setae	present	endopod as lobe with one seta	1 seg. with s
n — 7	„	„	16 setae	„	„	„
n — 6	3 flagella; middle bud, outer 2 seg.	1 seg.	numerous setae	„	„	„
n — 5	inner 3 seg. middle 1 seg.	3 seg.	„	„	„	2 seg.
n — 4	—	„	„	palp appears	endopod present with two setae	„
n — 3	inner 4 seg. outer 3 seg.	„	„	palp present 1 seg.	„	„
n — 2	—	„	„	„	„	„
n — 1	inner 6 seg. middle 2 seg. outer 5 seg.	„	„	„	„	„
Postlarva	flagella completely segmented	flagellum completely segmented	„	palp three-segmented	„	„

Antennules (fig. 2Q, R; fig. 4G). — In stage n-8 the antennule has a three-segmented stalk with 2 flagella, the internal two-segmented, the external with 1 segment bearing 4 setae. In stage n-6 the external flagellum is separated into 2 parts, the smaller carrying 3 groups of setae. The number of groups of setae increases to 8-11 in the last stage.

Antennae (fig. 2S, T; fig. 4E). — In stage n-8 the antenna has the bud of 1 flagellum and the antennal scale has 11 or 12 setae. The flagellum increases in length with growth.

Mandible and maxillae (fig. 5C, D, E). — The mouth parts are present in stage n-8. A mandibular palp appears as a bud in stage n-4. In stage n-8 the proximal endite of the first maxilla has 7 teeth and the distal endite 1 strong tooth flanked by 1 seta proximally and 2 distally; the proximal seta disappears in stage n-5. In stage n-1 the number of teeth on the proximal endite is 14. The second maxilla appears with 1 setose segment in n-8 and is two-segmented in stage n-5. Development of the anterior appendages is summarized in Table II.

Maxillipeds. — The first maxilliped (fig. 2U, V; fig. 3D, E) is clearly segmented in n-8, but the dactylus is not differentiated; it becomes visible in stage n-5 and is subchelate in stage n-2. The epipod is present from stage n-7 onward.

The second maxilliped (fig. 1C, D; fig. 4A) is a functional claw in stage n-8; in later stages only the location of the ischiomeral articulation changes: it is terminal in n-8, but it becomes subterminal in n-6 and the merus projects posteriorly beyond the articulation with the ischium in stage n-1. The dactylus has a proximal tubercule on its inferior margin and the propodus has a strong fixed proximal

spine. The tip of the dactylus enters a ridge of the propodus. The epipod is present in all stages.

The 3rd, 4th and 5th maxillipeds (fig. 2F to J; fig. 4I) each exhibit a progressive development which is characteristic of the stages. They appear as small buds in n-8, as short, finger-like projections in n-7, and they are recurved in n-6. In n-5 the third ends in a claw, the fourth is pointed and the fifth is rounded.

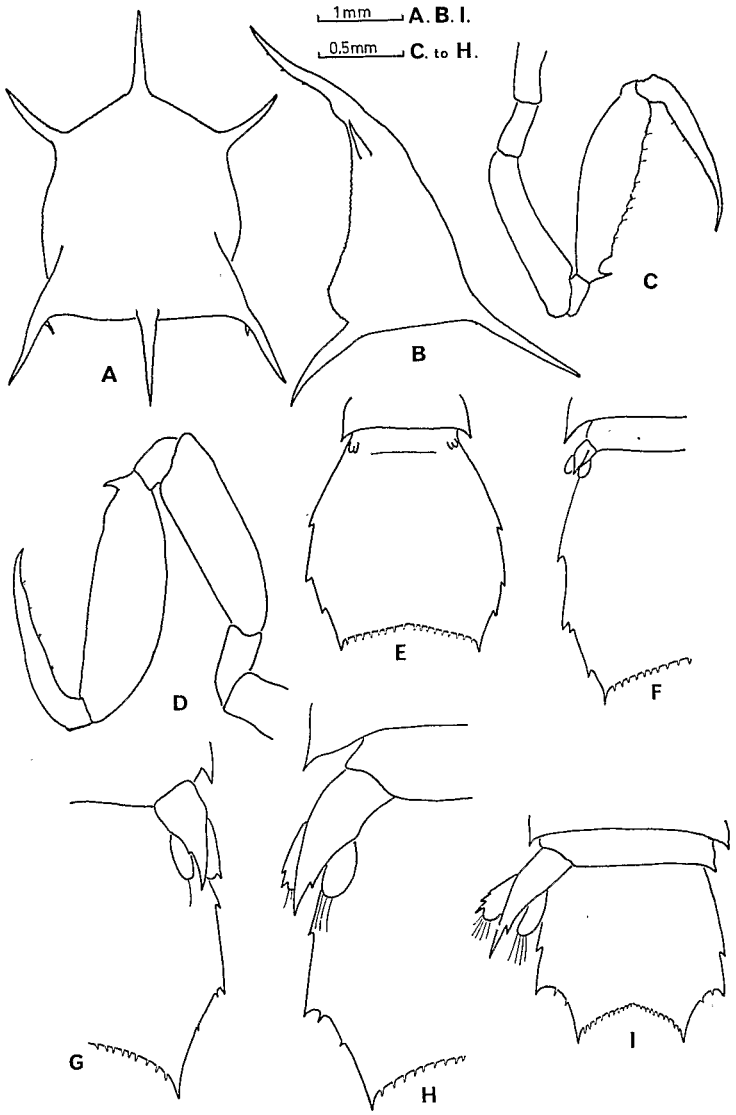

Fig. 1. *Chorisquilla tuberculata* (Borradaile, 1907). A and B, carapace stage n-7; C, raptorial claw stage n-8; D, raptorial claw stage n-7; E to I, telson and uropods stages n-7 to n-3.

In n-4, the third and fourth end in a claw whereas the fifth is pointed. In n-3 all 3 claws are functional. The epipods appear in n-6.

Walking legs (fig. 2A to E; fig. 4C). — These also have a characteristic development: they are absent in n-7, appear as buds in n-6, and as finger-like projections with the appearance of the endopod as a bud in n-5. The endopod and exopod are more elongate in n-4, but in n-3 the exopod appears constricted and in n-2 it is segmented. In n-1 the articulation between the proximal and distal exopod segments is clearly visible.

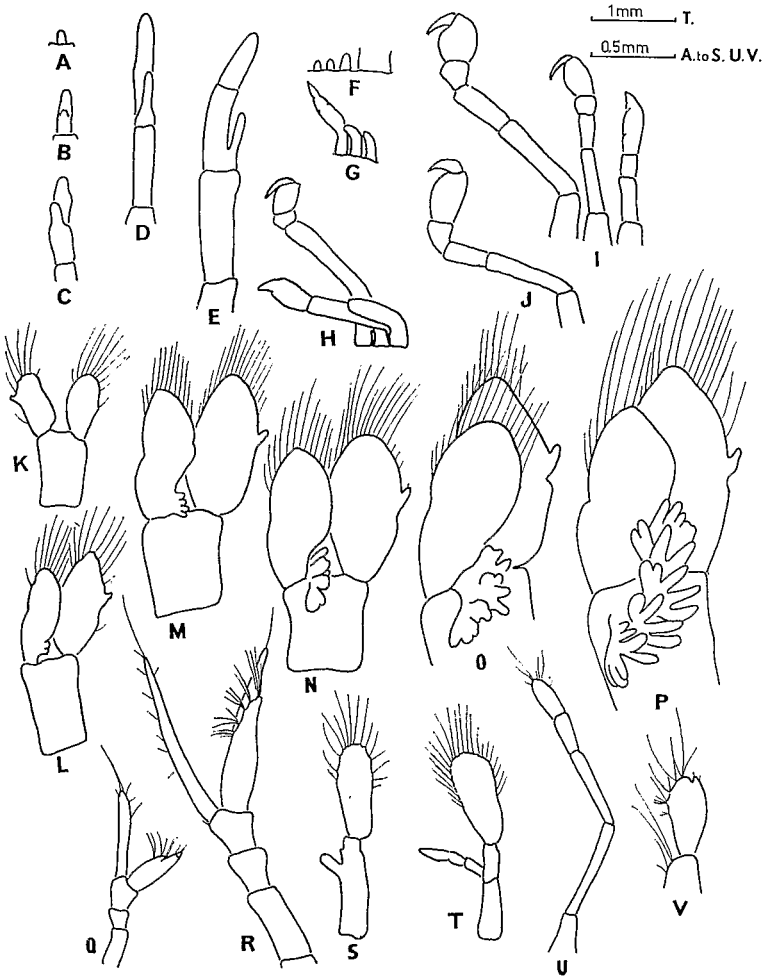

Fig. 2. *Chorisquilla tuberculata* (Borradaile, 1907). A to E, 6th thoracic appendage stages n-6 to n-2; F to J, 3rd, 4th, 5th thoracic appendages stages n-7 to n-3; K to P, pleopods stages n-7 to n-2; Q and R, antennule stages n-7 and n-3; S and T, antenna stages n-7 and n-5; U and V, first maxilliped stages n-7 and n-4.

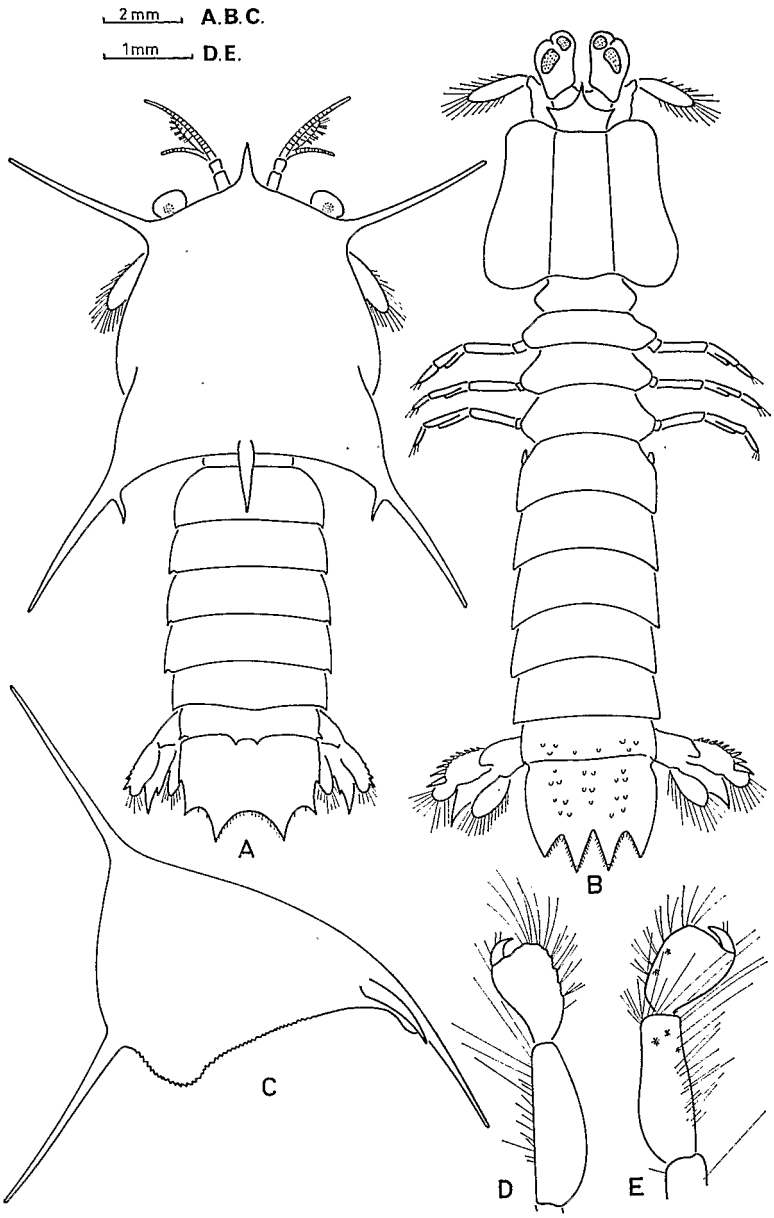

Fig. 3. *Chorisquilla tuberculata* (Borradaile, 1907). A and C, last larva; B, postlarva; D and E, first maxilliped last larva and postlarva.

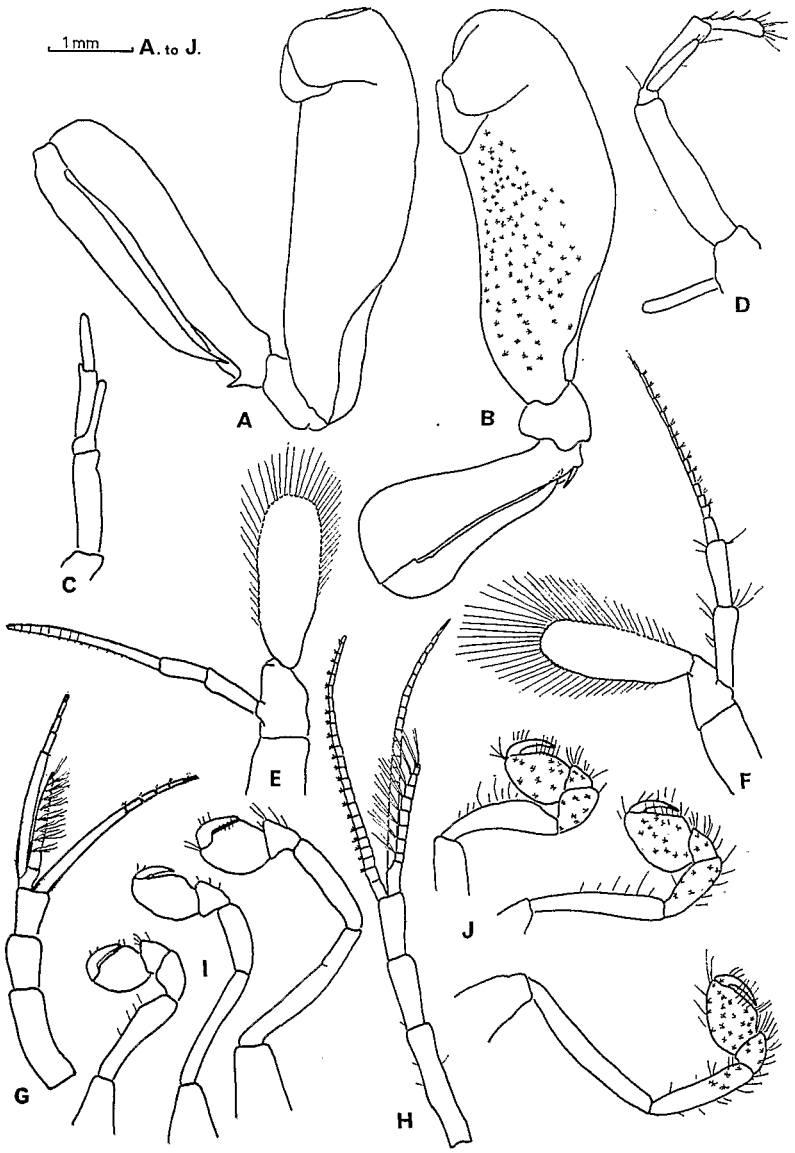

Fig. 4. *Chorisquilla tuberculata* (Borradaile, 1907), last stage and postlarva. A and B, raptorial claw; C and D, 8th thoracic appendage; E and F, antenna; G and H, antennule; I and J, 3rd, 4th, and 5th thoracic appendages.

The male organ appears in stage n-2 at the base of the eighth pair of thoracic appendages.

Abdomen. — The abdomen is five-segmented in n-7; the sixth is separated from the telson only in n-6. The pleura of the abdominal somites terminate in posteriorly directed spines. Submedian spines of the sixth segment appear in n-7. Five pairs of biramous pleopods, each with a functional appendix interna comprising 2 small hooked spines, are present from stage n-8. The gills appear in n-6 and increase in size with development (fig. 2K to P; fig. 5A).

Uropods (fig. 1E to I; fig. 5B, F). — The uropods are absent in n-8, but small, bilobed buds appear in n-7. In n-6 the basal process has only 1 spine and

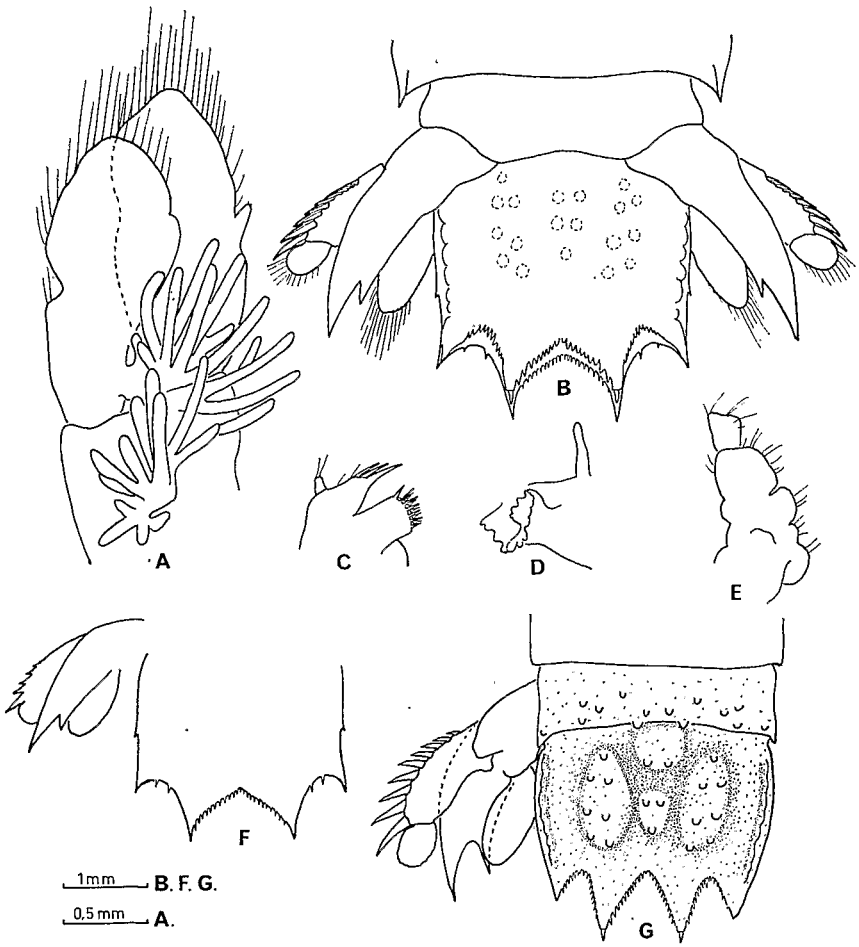

Fig. 5. *Chorisquilla tuberculata* (Borradaile, 1907). A, pleopod stage n-1; B, telson and uropods stage n-1; C to E, first maxilla, mandibula, and second maxilla stage n-1; F and G, telson and uropods of the metamorphosed specimen (F from the cast).

the exopod and endopod both lack setae. In n-5 an internal spine appears on the lateral margin of the basal process, 1 spine is visible on the external exopod margin, and 1 seta is present on the endopod. In n-4 there are 2 spines and 2 setae on the exopod and 3 setae on the endopod; the uropods reach the level of the first lateral tooth of telson. In n-3 there are 3 spines and 5 setae on the exopod and 4 setae on the endopod and in n-2 4 spines are visible on the exopod and the number of setae increases. In n-1 5 or 6 spines are visible on the exopod and the uropods reach the level of the second lateral tooth.

Telson (fig. 1E to I; fig. 5B, F). — There are three pairs of fixed lateral teeth and one pair of fixed submedian teeth on the telson in n-7. In n-6 a denticle appears at the base of the second lateral tooth; in subsequent stages only the second pair of lateral teeth and the submedian pair will undergo any great changes. In the last stage the first pair will be represented only by small spines, and 2 denticles are present between the intermediate and submedian teeth. There are on each side 8 to 9 submedian denticles in the early stages and 10 to 12 in the late stages.

The illustrations were drawn from a single specimen of each stage; there are some minor variations between the larvae of the same stage, the meaning of which will be discussed below. The most easily recognizable characters for the determination of stages n-8 to n-1 are the form of the posterior six pairs of thoracic appendages.

COMPARISON BETWEEN LAST LARVA AND POST LARVA

During metamorphosis comparatively great transformations occur in the Stomatopoda (figs. 3, 4, 5). In the last stage some postlarval characters appear under the cuticle, including the outline of the future carapace, the teeth of the uropodal exopod, and the denticles between the submedian and intermediate teeth of the telson. The most striking change is the loss of the large larval carapace, with its long spines and fixed rostrum, and its replacement by a short carapace bearing a movable rostral plate with a strong median spine and angled anterolateral corners. The eyes become clearly bilobed.

There are no significant changes in the antennules and antennae except for the clear segmentation of the flagellum. The maxillae and maxillipeds 1 to 5 do not change in shape but differ through the appearance of chromatophores. The propodus and dactylus of the raptorial claw become broader and the fixed spine at the basis of the propodus becomes movable. Numerous black chromatophores appear on the external and internal side of the merus of the claw. The pereiopods are ornamented with spines and setae.

Abdominal somites 1 to 5 have their pleura rounded, without posterior spines. The anterolateral plates of abdomen become articulated. The internal spine of the basal process of the uropod remains shorter than the external. In the post-

larva, the sixth abdominal somite and telson present great changes. The ornamentation of the telson appears as four dorsal bosses, the submedians not extending posteriorly beyond the apex of the median excavation in the posterior margin. The surface of all dorsal bosses is tuberculate with 4 + 3 tubercles for the submedian, 3 for the median posterior and 2 for the median anterior. The posterior margin is divided into four triangular teeth, 2 submedians, with movable apices, and 2 intermediates; 14 to 15 intermediate and 11 to 12 submedian denticles are present on each side. The first pair of lateral teeth disappear. The lateral margin of the telson is provided with a carina which shows a series of 7 tubercles. The sixth abdominal somite has four tuberculate bosses. The development of these characters in the postlarva allow its identification with the adult *Chorisquilla tuberculata* described by Borradaile (1907) and Komai (1938).

Coloration. — The larvae are strikingly transparent when alive except for the green eyes, a feature which allows their ready recognition in unsorted plankton samples. Postlarvae are also almost transparent, with the pigmentation appearing lightly on the carapace, thoracic and abdominal somites, and telson.

DISTRIBUTION

The larvae were collected along the meridian 170°E from 20°S to 02°N; they seeem to originate from the neighboring island groups, the New Hebrides, Santa Cruz, Ellice, and Gilbert Islands. They also were collected along the great barrier reef of New Caledonia and in the western area of the Marquesas Islands.

It appears that *C. tuberculata* described previously from Providence Island, western Indian Ocean, and Japan, has a wide geographic range as a result of its long pelagic life.

As most of the other stomatopod larvae, the young of *C. tuberculata* live during the day in the upper layer, 0-100 m, with a night vertical migration to near or at the surface. We also point out the occurrence of postlarvae far from islands over depth of 4000 to 5000 meters.

DISCUSSION

Brooks (1886) mentioned a single larva taken near Kandavu Island, Fiji, and refered it to *Lysioerichtus* group. From his figure it seems that this larva is similar to one of the stages of *C. tuberculata.*

In stage n-8 *C. tuberculata* presents the same characters of development as the stage IV of *Gonodactylus oerstedii* Hansen described by Manning & Provenzano (1963): no vitellus, first maxilliped terminating in setae, and mandibles and maxillae 1 to 2 present. If the development is similar for these two species of the same family, *C. tuberculata* would go through 11 stages from hatching to the last pelagic stage, the first three stages being propelagic. This is comparable to the results of Giesbrecht (1910) who reported 8 stages for *Squilla mantis* (Lin-

naeus) and 9 stages for *Platysquilla eusebia* (Risso); Komai & Tung (1929) reported 9 stages for *Oratosquilla oratoria* (De Haan). Gohar & Al-Kholy (1957) described 6 stages for *Gonodactylus falcatus* (Forskål), but as noticed by Manning & Provenzano (1963) the appearance of the postlarval characters under the cuticle was not mentioned; this suggests that these authors might have overlooked some stages.

Among the larvae and postlarvae we have examined separately a group originating from the offshore stations and another originating from the stations near the coast. Of particular interest is the observed difference in the number of groups of setae on the flagella of the antennules. All the late larvae and postlarvae collected near the Marquesas Islands or near New Caledonia have 8 to 9 groups of setae, but the late stages and postlarvae collected off offshore have 10 to 11 groups (table III); in some early stages, the offshore specimens have supplementary groups in comparison with specimens of the same stages from the nearshore series. These observations lead us to believe, as suggested by Michel (1968), that the development of stomatopod larvae does not normally occur offshore: some supplementary molts may take place without change in length and these can be detected by the number of groups of setae. Probably the delay between consecutive molts is also increased and would explain the occurrence of early stages far from the coast.

TABLE III

Number of groups of setae on the antennule

	Offshore group	Coastal group
Last larval stage	10 larvae: 10-11	5 larvae: 8-9
First postlarval stage	8 postlarvae: 10-11	34 postlarvae: 8-9 *)

*) Post-larvae of the coastal group originate from the Marquesas Islands and New Caledonia.

This phenomenon is similar to the findings of Robertson (1968) in the development of the phyllosoma larvae of *Scyllarus americanus*. He showed that the temperature and the amount of available food were important factors for larval development. He described seven stages and, depending upon the conditions of rearing, he obtained the postlarva after stage VI or with a poor diet after stage VIII or IX. He found similar morphological differences between the reared larvae and planktonic material. The duration of intermolt also differed with temperature and available food. Costlow (1965) found evidence that molting and growth were independent and controlled by separate endocrine systems and that the diet or the presence or absence of some trace elements would delay or even stop development. These factors impart variability in the number of stages as well as in the duration of intermolts, and are evident in the form of minor morphological differences in the larvae.

It appears that for the pelagic larvae, drifting by oceanic currents far from

the coast is often the rule and not the exception. Prevailing conditions may change rapidly, and the amount of food in the open sea is generally poorer than in coastal waters. Temperature may vary greatly during the drift and some trace elements may be absent. All of these factors could result in the observed variation in morphological features of larvae presumably of the same stage and may affect the numbers of stages as well.

RÉSUMÉ

Le maintien en aquarium d'une larve de Stomatopode et l'obtention après sa métamorphose d'une post-larve identifiable ont permis d'attribuer une série larvaire comprenant 8 stades pélagiques à l'espèce *Chorisquilla tuberculata.* Larves et post-larves sont décrites. Il semble que les légères différences morphologiques que l'on peut observer chez les spécimens d'une même stade soient à attribuer à un développement anormal dans les eaux du large.

LITERATURE CITED

ALIKUNHI, K. H., 1944a. Growth stages of Lysiosquilla tigrina Nobili. Current Science, **13**: 18-19.

——, 1944b. Final pelagic larva of Squilla hieroglyphica Kemp. Current Science, **13**: 237-238.

——, 1950. Observations on some larval and post-larval stomatopods. J. Bombay nat. Hist. Soc., **49** (1): 101-107.

——, 1952. An account of the stomatopod larvae of the Madras plankton. Rec. Indian Museum, **49**: 239-319.

——, 1959. Notes on a collection of stomatopod larvae from the Bay of Bengal, off the Mahanadi estuary. Journ. zool. Soc. India, **10**: 120-147.

——, 1967. An account of the post-larval development, moulting and growth of the common stomatopods of the Madras coast. Symposium Crustacea, **2**: 824-939, figs. 1-194, pls. 1-3. (Marine Biological Association of India).

ALIKUNHI, K. H. & R. G. AIYAR, 1942. On some Squilla larvae from the Madras plankton. Current Science, **11** (2): 56-58.

BORRADAILE, L. A., 1907. Stomatopoda from the western Indian Ocean. Trans. Linn. Soc. London, (2) **12**: 209-216.

BROOKS, W. K., 1886. Report on Stomatopoda collected by H.M.S. Challenger during the years 1873-1876. Rep. sci. Res. Challenger (Zool.), **16**: 1-116, pls. 1-16.

——, 1892. The habits and metamorphosis of Gonodactylus chiragra. Mem. nation. Acad. Sci., **5** (4): 353-360.

COSTLOW, J. D., 1965. Variability in larval stages of the blue crab, Callinectes sapidus. Biol. Bull., **128** (1): 58-66.

GIESBRECHT, W., 1910. Stomatopoda. Fauna Flora Golfes Neapel, **33**: 1-239.

GOHAR, H. A. F. & A. A. AL-KHOLY, 1957. The larval stages of three stomatopod Crustacea. Publ. mar. biol. Sta. Al-Ghardaqa, **9**: 85-130.

GURNEY, R., 1937. Notes on some decapod and stomatopod Crustacea from the Red Sea, III-IV. Proc. zool. Soc. London, **107** B (3): 319-336.

——, 1946. Notes on stomatopod larvae. Proc. zool. Soc. London, **116** (1): 133-175.

KOMAI, T., 1924. Development of Squilla oratoria de Haan, 1. Change in external form. Mem. Coll. Sci. Kyoto imp. Univ., (B.) **1** (3): 272-283.

——, 1938. Stomatopoda occurring in the vicinity of Kii Peninsula. Annot. zool. Japon., **17** (3-4): 264-275.

KOMAI, T. & Y. M. TUNG, 1929. Notes on the larval stages of Squilla oratoria, with remarks on some other stomatopod larvae found in the Japanese seas. Annot. zool. Japon., **12**: 187-237.

MANNING, R. B., 1962. Alima hyalina Leach, the pelagic larva of the stomatopod crustacean Squilla alba Bigelow. Bull. mar. Sci. Gulf Carib., **12** (3): 496-507.

——, 1968. A revision of the family Squillidae (Crustacea, Stomatopoda), with the description of eight new genera. Bull. mar. Sci. Gulf Carib., **18** (1): 105-142.

——, 1969. Notes on the Gonodactylus section of the family Gonodactylidae with descriptions of four new genera and a new species. Proc. biol. Soc. Washington, **82**: 143-166.

MANNING, R. B. & A. J. PROVENZANO, JR., 1963. Early developmental stages of the stomatopod crustacean Gonodactylus oerstedii Hansen. Studies on the development of stomatopod Crustacea, 1. Bull. mar. Sci. Gulf Carib., **13** (3): 467-487.

MICHEL, A., 1968. Dérive des larves de Stomatopodes de l'Est de l'Océan Indien. Cah. O.R.S.T.O.M., (Océanogr.) **6** (1):

ROBERTSON, P. B., 1968. The complete larval development of the sand lobster, Scyllarus americanus (Smith), (Decapoda, Scyllaridae) in the laboratory, with notes on larvae from the plankton. Bull. mar. Sci. Gulf Carib., **18** (2): 294-342.

SERÈNE, R., 1962. Révision du genre Pseudosquilla (Stomatopoda) et définition de genres nouveaux Bull. Inst. océanogr. Monaco, **1241**: 1-27.

Received for publication 10 June 1970.

4

THE PELAGIC LARVAE OF *CHORISQUILLA TUBERCULATA* (BORRADAILE, 1907) (STOMATOPODA)

BY

A. MICHEL and R. B. MANNING

Reprinted from: CRUSTACEANA, Vol. 22, Part 2, 1972

LEIDEN
E. J. BRILL