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Some Brachyuran Megalopa¹

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INTRODUCTION

This paper is occasioned by Sadayoshi Miyake's published description of a crustacean under the name of *Xenocarcinus esakii* (9)² and purported to be a new species of the family Majidae. The holotype from Kusaie, Caroline Islands, is strikingly similar to a crustacean taken at various localities about the Hawaiian Islands and in the central Pacific area, sometimes in considerable numbers. I have long considered the Hawaiian organism to be a megalops of some brachyuran crab, probably a common one, the advanced larval stage of which has not yet been recognized.

This apparent resemblance of *Xenocarcinus esakii* Miyake to the Hawaiian form (fig. 1, a-d), believed to be a megalops, has led to a more complete examination of brachyuran larvae in the collections of Bishop Museum. Among the collections are large numbers of zoeae but comparatively few megalopa. Of the latter, however, four distinct forms of a peculiar type are recognized and are made the subject of this paper. Since they cannot be referred with certainty to any known crabs, they are here designated as megalops *alpha*, *beta*, *gamma*, and *delta*. It is the *alpha* form which apparently is identical with *Xenocarcinus esakii* Miyake, and the one frequently seen about Hawaii.

Descriptions of these four megalops are given in some detail, with the hope that collectors may procure living specimens of the curious forms and make it possible, in some laboratory or aquarium where circulating sea water is available, to carry their development through into the adult stage. To definitely refer these peculiar larvae to specific brachyuran crabs would be a scientific achievement of considerable interest.

¹ The funds for printing this paper were contributed by the Juliette M. Atherton Trust.
² Numbers in parentheses refer to the Literature Cited, p. 246.

If the crustacean form described by Miyake were an adult crab, it would seem to be somewhat remote from the genus *Xenocarcinus* as specified by White (15), Miers (8), Alcock (1), and others. However, its identity with material at hand believed to consist of crab megalopa, cannot be doubted. The description and accompanying figures by Miyake could well have been based upon any one of more than 100 Hawaiian specimens.

A critical examination of the Hawaiian megalopa here considered place them within the "*Monolepis*" group. The term *Monolepis* was suggested by Say (13) as a genus to accommodate *M. inermis* and *M. spinitarsus*, believed by him to be adult crabs and described from the shores of Maryland and South Carolina, respectively. The simple character of the lamellae on each side of the terminal segment of the abdomen of these forms gave rise to the generic term *Monolepis*. Although Say was in doubt as to the exact position of his suggested genus in the crustacean scale, he recognized its close relationship to the Brachyura.

Dana (3), following the belief of Say that these organisms were adult crustaceans, accepted *Monolepis* as a valid genus, reported *M. inermis* Say and described a new species, *M. orientalis*, taken from the Sooloo [Sulu] Sea. The latter form is close to, if not identical with, specimens in Bishop Museum from Hawaiian and Philippine Island localities. I have designated this organism as megalops *beta*.

Not until 1873 was the authenticity of the genus *Monolepis* questioned. Observations by Smith (14) on the shores of Long Island established beyond a reasonable doubt that *Monolepis inermis* was a stage in the development of *Ocypode arenaria* Milne Edwards (= *Ocypode arenarius* Say = *Ocypode albicans* Bosc). This conclusion was based not only upon anatomical features but upon the seasonal appearance of the larvae, followed a month later by adult crabs.

More recent investigators have generally accepted the views of Smith, regarding monolepoid forms as megalopa of brachyuran crabs, but usually hesitating to refer them to definite species for want of precise information. Kemp (7) describes and figures the megalops of *Ocypode macrocera* Milne Edwards which resembles, in some degree, a monolepoid form. Kemp regards the larva as remarkable because of the deep cavities at the postero-lateral angles of the carapace into which the last pair of walking legs can be folded.

In a number of articles, Mary J. Rathbun (10, 11, 12) described larval stages of brachyuran crabs which bore considerable likeness to monolepoid forms. In 1918, Miss Rathbun referred to *Monolepis inermis* as a developing phase of the sand crab, *Ocypode albicans* Bosc. And in 1923, she described and figured megalopa of several known brachyuran crabs from the west coast of Mexico as well as those of some doubtful species. In certain of these, monolepoid features are observed. Again in 1924, among crabs from the Galapagos Islands, Miss Rathbun described a megalops so closely allied to *Monolepis inermis* that it was referred by her to the sand crab, *Ocypode gaudichaudii* Milne Edwards and Lucas, as this species was the only representative of the genus in the locality. More recently, Boone (2) also recognized this megalops and definitely assigned it to the Galapagan species of *Ocypode*.

In a bibliography of larval stages of decapod crustaceans Gurney (5) has compiled a comprehensive list of references to crab megalopa, including monolepoid forms.

GENERAL FEATURES OF MONOLEPOID MEGALOPA

These curious larval forms possess a convex, well-rounded carapace with high sides and the front more or less turned down. The chelipeds and walking legs are capable of being held closely against the carapace resting in impressed areas and grooves. As a result of this close contact of appendages with the carapace, the rotundity of the body presents an environmental adaptation. Some megalopa are doubtless pelagic during the greater part of their existence, whereas others live at greater depths. Most of them, however, have been taken on sandy shores after having been washed ashore, where they may be rolled about like tiny balls without appreciable injury.

No reference is made either by Say (13) or Dana (3) to the sex of the specimens of *Monolepis* examined by them. Miyake (9), however, states that the holotype of *Xenocarcinus esakii* is a female. This conclusion is probably based upon the general appearance of the pleopods. It is well known, however, that the sexual characters of decapod crustaceans remain undifferentiated throughout the larval stage. If the sex of the monolepoid megalopa in Bishop Museum were judged by features of adult crabs, they might well be considered to be females, as their abdominal appendages are quite female-like. Each individual possesses four pairs of strikingly similar biramous pleopods, regard-

less of the type of megalops. In this stage, however, the pleopods are well-developed swimming organs rather than sexually differentiated appendages. It is quite unlikely that all of the 136 specimens of megalops *alpha* before me are females, or would have developed into that sex, though their abdominal appendages are similar in form.

I found (4) that the sexes of *Atya bisulcata* (Randall) could not be distinguished by the pleopods until the organism had attained a length of 15 to 18 mm. During his notable work on the development of the fiddler crab, Hyman (6) observed that the megalops, unlike the zoea, did not molt during its existence of nearly a month. Changes in the organism, however, did take place, the most striking in the pleopods. These appendages, toward the close of the megalops phase, became smaller and shriveled, no longer being functional swimming organs. Even after hatching into the crab stage, several molts were required before the sexual characters of the organisms were distinguished.

So in examples of monolepoid megalopa such as those under consideration we may assume that sexual differentiation does not occur during the larval condition, and probably not until some time after the crab stage has been reached.

Key to Hawaiian Monolepoid Megalopa

- A. Surface of carapace smooth; chelipeds shorter than carapace.
 - B. Upper surface of carapace deeply and extensively furrowed; chelipeds stout; third walking leg not reaching the orbit.....**Megalops alpha.**
 - BB. Upper surface of carapace not deeply or extensively furrowed; chelipeds slender; third walking leg hooked over the orbit.....**Megalops beta.**
- AA. Surface of carapace granular; chelipeds longer or shorter than carapace.
 - B. Chelipeds longer than carapace; areas of carapace not well-outlined**Megalops gamma.**
 - BB. Chelipeds shorter than carapace; areas of carapace well-outlined.....**Megalops delta.**

Megalops alpha (figs. 1, *a, b, e-g*; 2, *a-d*).

Xenocarcinus esakii Miyake, Rec. Oceanographic Works in Japan
10(2): 168-247, 1939.

Carapace of typical specimen 8 mm. long from posterior border to level of eyes where front begins to turn down; upper surface smooth, highly convex, laterally and postero-anteriorly; areas distinctly outlined and bounded by deep

furrows. Front sharply curved down, border tricuspid; rostrum broad, toothlike, obtusely pointed, separated on either side by a deep notch from a shorter supraocular lobe which curves down in front of eye. Eyes large, stalks short, orbits incomplete, lower border of each formed by carpus of folded cheliped. Basal segment of antenna rests in narrow rim of orbit with flagellum directed forward between rostrum and supraocular lobe.

Mandible with 3-jointed palp; outer maxillipeds not completely closing buccal cavity, length of merus about one-half that of ischium, directed mesially, exognath with a well-developed flagellum. Chelipeds short, stout, the right slightly larger than the left; carpus with flattened upper border against which eye rests; hand broadened proximally; fingers of right hand toothed, those of left hand without distinct teeth but with sharp cutting edges. Surface of chelipeds, although apparently smooth, present a microscopic reticulate pattern well-pronounced on hand and merus.

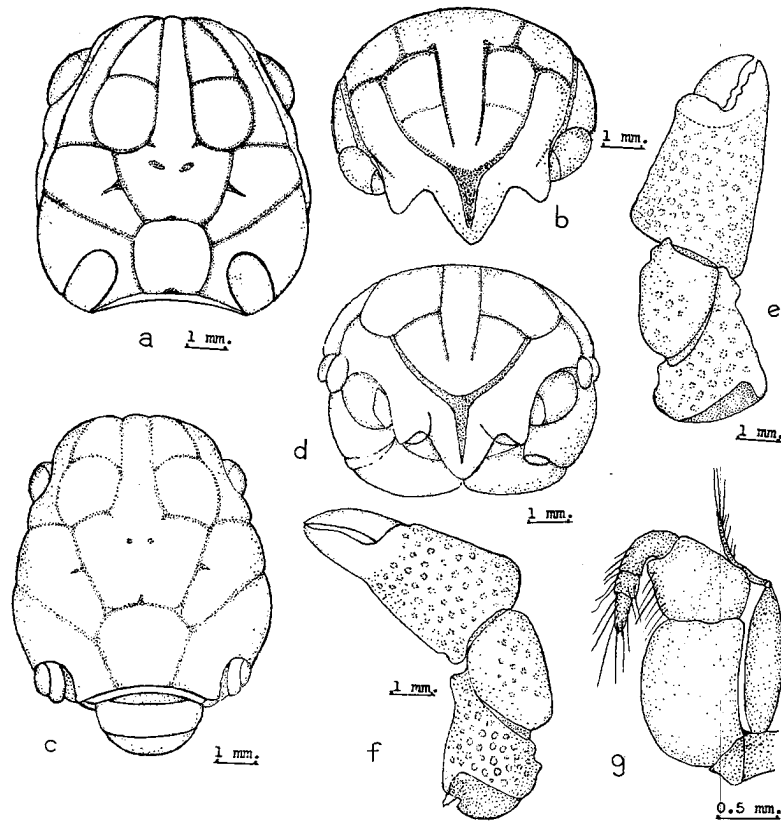


FIGURE 1.—a, b, e-g, megalops *alpha*: a, dorsal surface of carapace; b, front view of carapace; e, right cheliped; f, left cheliped; g, outer maxilliped. c, d, form described as *Xenocarcinus esakii* Miyake: c, dorsal surface of carapace (after Miyake's fig. 11, B); d, front view of carapace (after Miyake's fig. 11, A).

Sides of carapace high, impressed and grooved for reception of folded walking legs. First and second walking legs directed forward and bent abruptly down at carpal joints and held close to body in impressed areas. Third walking leg normally directed forward in a groove extending toward orbit, dactylus of appendage falling short of eye. Fourth walking leg, somewhat smaller than others, folded in an impressed area on postero-lateral border of carapace. Abdomen with 7 segments, second to sixth large and convex, terminal one thin, flat. Pleopods biramous, endopodite a short pointed lobe with a row of hooked setae near tip; lamellae of last abdominal segment single on each side, oval, fringed with long hairs.

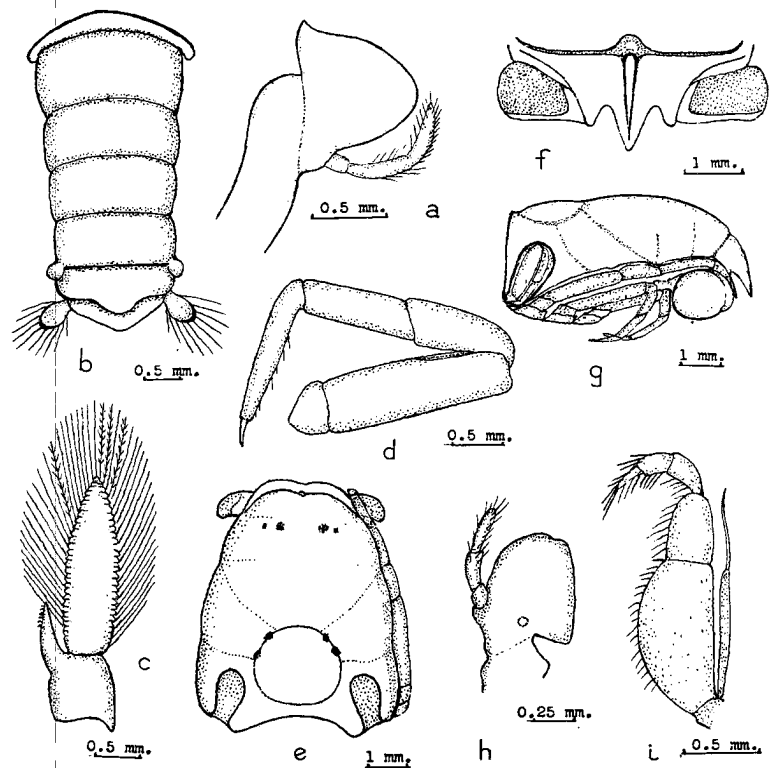


FIGURE 2.—*Megalops alpha*, a-d: a, mandible; b, abdomen; c, first pleopod; d, fourth leg. *Megalops beta*, e-i: e, dorsal surface of carapace; f, front view of carapace; g, side view of carapace, with position of walking legs; h, mandible; i, outer maxilliped.

Specimens of this crustacean, believed to be a brachyuran megalops, in Bishop Museum now number 136, most of them having been collected from the shores of Oahu. Localities from which the specimens came are as follows: Waikiki, Oahu, 1 collected by W. A. Bryan

sometime prior to 1919; Nihoa Island, 30, by the Tanager Expedition, June 1923; Sand Island, near Johnston Island, 1, by the Tanager Expedition, July 1923; Lanikai, Oahu, 1, by H. L. Kelly, July 25, 1932; Waikiki, Oahu, 92, by Jared Smith, August 1933. From the stomach contents of a fish, *Cirrhitus pinnulatus* (Schneider), known as the *po'opoa'a*, caught near Koko Head, Oahu, 11 specimens were collected by Takeo Sugiyama, June 14, 1941. (Bishop Museum collection nos. 1370, 1507, 2180, 3719, 3929, 5268.)

An attempt has been made to correlate the form of the mandibles and outer maxillipeds of the megalopa considered in this paper with corresponding mouthparts of adult brachyuran crabs of the Hawaiian region. Little success, however, has attended efforts to refer the larvae to known species of crabs by this comparative method. In some specimens, the mandibles of the megalops suggest those of a certain crab but the maxillipeds show little similarity. In others, the maxillipeds compare favorably but the mandibles do not. Hyman (6) reports that in the megalops of *Gelasimus* the mandibles practically attained the adult form, but the outer maxillipeds of the crab showed somewhat greater change from those of the megalops. The endopodite of the maxilliped becomes larger in the crab, due to an increase in size of the proximal two segments.

Miyake (9) in a check list of crustaceans from Micronesia includes about a dozen brachyuran crabs from Kusaie, the locality of *Xenocarcinus esakii*, which are common species in Hawaii. The mouthparts of these crabs, and many others, have been compared with the mouthparts of megalops *alpha* without disclosing any close relationship.

Megalops beta (figs. 2, *e-i*; 3, *a-d*).

Monolepis orientalis Dana ?, U. S. Exploring Exped., Crustacea, 13: 492-493, 1852; pl. 31, figs. 5, 6, 1855.

Carapace of typical specimen 6 mm. long, measured from posterior border to a point in line with eyes where front begins to curve down sharply. Rostrum triangular, separated on either side by a notch from a shorter supraocular lobe. Upper surface of carapace convex, smooth, few areas delineated; a prominent transverse postfrontal furrow; cardiac and mesobranchial areas lightly bounded by shallow grooves. Upper surface marked by a pair of depressions on each side of the mid-line in front of middle, the more conspicuous depression of each pair nearer the mid-line and slightly anterior to other; also two depressions on each side in furrow bounding cardiac area. Eyes prominent, outer border of each sloping backward; orbits incomplete. Mandible with straight cutting edge; outer maxilliped with merus about one-half as long as ischium, distal extremity rounded, exognath narrow, with flagellum. Chelipeds slender, equal, smooth, normally held in a folded position against the under surface of the carapace;

fingers longer than palm, without teeth. First and second walking legs folded close together in depressions in side of carapace. Third walking leg resting in a groove in side of carapace, extending straight forward and hooked over eye. Fourth walking leg folded in a depression on the postero-lateral border of carapace, dactylus straight, terminating in 3 long setae. Abdomen with 6 segments, the first 4 convex, inflated; lamellae of last segment single, fringed with long hairs. Pleopods 4 pairs, similar to those of megalops *alpha*.

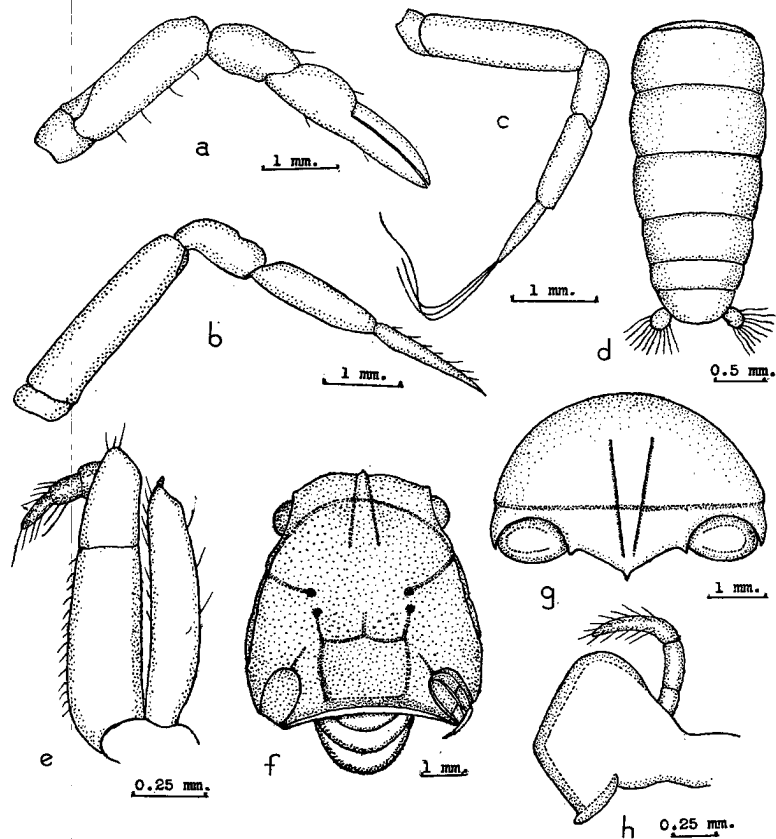


FIGURE 3.—*Megalops beta*, a-d: a, right cheliped; b, second walking leg; c, fourth walking leg; d, abdomen. *Megalops gamma*, e-h: e, outer maxilliped; f, dorsal surface of carapace; g, front view of carapace; h, mandible.

Only six specimens of this peculiar form are among the collections of Bishop Museum, from the following localities: Oahu, 1, collected by W. A. Bryan, sometime prior to 1919; Makena, Maui, 1, by Mrs. J. K. Skinner, 1926; Waikiki, Oahu, 1, by Adna G. Clarke, Jr., June

15, 1928; Keaau, Oahu, 1, by E. Y. Hosaka, July 1, 1934; Cavite, Philippine Islands, 2, by J. G. Johnson, February 18, 1935. (Bishop Museum collection nos. 2595, 3141, 3928, 3959, 5265.)

These six specimens are remarkably similar in size and structural features, with the exception of the specimen taken by Adna G. Clarke, Jr. It is smaller than the others, only 4 mm. long.

This megalops is, without doubt, closely allied to both *Monolepis inermis* Say and *Monolepis orientalis* Dana, apparently being somewhat nearer the latter. Dana (3) points out features of the sternum as a chief difference between *M. inermis* and *M. orientalis*. In the latter, there is a triangular tubercle, pointed in front and rounded behind, between the buccal area and the sternal fossa. In *M. inermis*, three small tubercles occupy this position, two of the three being slightly in front of the other.

Regarding most features, including those of the sternum, Bishop Museum specimens compare favorably with *M. orientalis*. The principal difference seems to be fewer punctures or depressions marking the upper surface of the carapace of specimens I have examined than in Dana's form from the Sulu Sea.

The similarity of this megalops to that of *Monolepis inermis*, recognized as a larval stage of *Ocypode albicans*, might seem to link it closely with *Ocypode ceratophthalma* (Pallas), the common sand crab of the Pacific area, though we have no direct evidence of such a connection. Few of this particular type of megalops have been taken. However, this apparent paucity in Hawaii, where the crab is plentiful, does not preclude this relationship, as we have no information on the late larval stages of the crab. Some slight similarity is seen in the maxillipeds of *O. ceratophthalma* and megalops *beta* (figs. 2, *i*; 4, *e*), but the mandibles of the two are not in close agreement (figs. 2, *h*; 4, *d*). Data regarding the habits of the megalopa are too scanty at this time to draw conclusions relative to a possible succession of larvae and adults.

Megalops gamma (figs. 3, *e-h*; 4, *a-c*).

Carapace of specimen 8 mm. long, measured from posterior border over curve of front to tip of rostrum. Front turned down; rostrum broadly triangular, terminating in a small sharp point; supraocular lobes small, toothlike. Upper surface of carapace convex, granular, few areas delineated. A pair of shallow longitudinal grooves traverse the frontal area of the carapace, one on either side of the mid-line, converging on the rostrum. A prominent transverse, postfrontal furrow passes above the orbits. Gastric area incompletely defined; mesobranchial

and postbranchial areas combined, bounded in front by a furrow; cardiac area rectangular, convex, outlined by grooves. A pair of punctate depressions occupy positions corresponding to each lateral boundary of gastric area. Eyes prominent, orbits incomplete. Mandible with angular cutting edge; outer maxillipeds straight, closing buccal cavity; length of merus one-half that of ischium; palp arising from inner (upper) surface of merus; exognath broad, flagellum rudimentary.

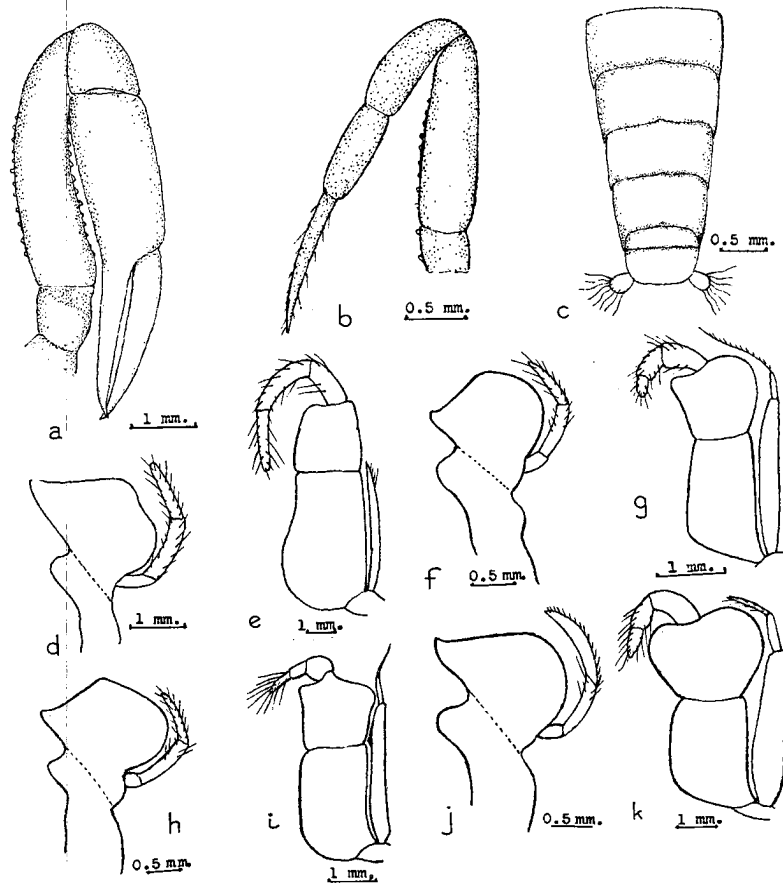


FIGURE 4.—*Megalops gamma*, a-c: a, right cheliped; b, second walking leg; c, abdomen. Mouthparts of crabs, d-k: d, mandible of *Ocypode ceratophthalma*; e, outer maxilliped of *O. ceratophthalma*; f, mandible of *Pachygrapsus plicatus*; g, outer maxilliped of *P. plicatus*; h, mandible of *Pseudozius caystrus*; i, outer maxilliped of *P. caystrus*; j, mandible of *Planes minutus*; k, outer maxilliped of *P. minutus*.

Chelipeds long, slender; upper and lower borders of merus bluntly toothed; fingers straight, about as long as palm, tips crossed, cutting edges without teeth. Walking legs long, slender, merus bluntly toothed on lower border, dactylus longer than propodus. Chelipeds normally held close to under surface of carapace in a folded position, fitting into impressions adapted for their reception. First and second walking legs rest close together in a bent position in depressions in side of carapace. Third walking leg resting in a groove in side of carapace is directed toward orbit but falls short of eye. Fourth walking leg folded in a depression on postero-lateral border of carapace. Abdomen with 6 segments; pleopods, 4 pairs, similar in appearance to those of megalops *alpha*; lamellae of terminal segment simple, bordered by long hairs.

A single example of this megalops was recovered from the stomach contents of a specimen of *Euthynnus alletteratus* (Rafinesque), the *kawakawa*, also known as the bonito or little tunny. It was obtained in a Honolulu fish market by Yoshio Kondo, June 2, 1947. (Bishop Museum collection no. 5272.) This would establish a pelagic habit for the megalops, as the bonito is a fish of the open sea, although it is known to approach close to shore during the summer months.

The special features separating this form from other megalopa observed include the granular surface of the carapace, the broadly triangular rostrum and the greatly elongated chelipeds. The chelipeds, when folded under the carapace, extend backward along either side of the abdominal fossa, the margins of which are ridged and toothed.

In megalops *gamma* the mandible somewhat resembles that of *Pachygrapsus plicatus* (Milne Edwards) and that of *Pseudozius caystrus* (Adams and White) in the angular cutting edge (fig. 4, *f*, *h* respectively), but the outer maxillipeds of the crabs differ from each other and also from that of the megalops (figs. 3, *e*; 4, *g*, *i*). The outer maxillipeds of the megalops which bear broad exognaths and close the buccal cavity suggest relationship with some grapsoid form of the subfamily Varuninae. The mouthparts of all available species of crabs of this group were examined. In none, including the pelagic *Planes minutus* (Linnaeus), shown in figure 4, *j*, *k*, did both mandible and outer maxilliped approach in appearance the mouthparts of megalops *gamma*.

The complete life histories of few crabs are known. Because of the difficulty of determining species of crustaceans by larval forms taken in the tow or otherwise, it becomes increasingly important to procure both zoeae and megalopa alive and, by carefully devised technique, attempt to develop them into the adult stage. In this way more complete information about our common crabs may be obtained.

Megalops delta (fig. 5, a-h).

Carapace of specimen 4 mm. long, measured in a midline from the posterior border to the tip of the rostrum. Front abruptly turned down; rostrum broadly triangular, terminating in a sharp point; supraocular lobes minute. Upper surface of carapace convex laterally and longitudinally; areas delineated by well-defined grooves. Protogastric area triangular; mesogastric region divided into three lobes by two furrows diverging posteriorly; postogastric area divided into two small, rectangular lobes; branchial region divided by a longitudinal furrow; postbranchial and cardiac areas united, extending the entire breadth of the carapace.

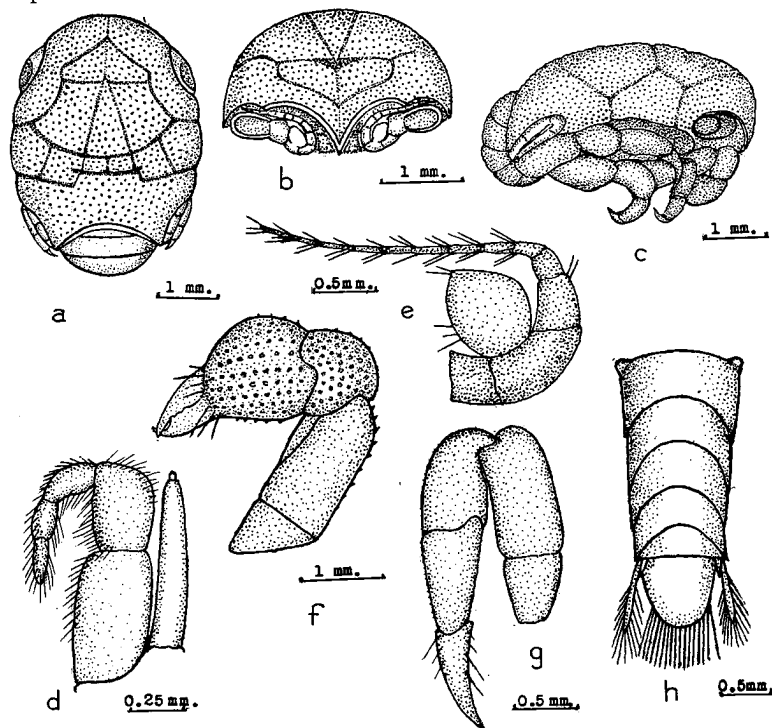


FIGURE 5.—*Megalops delta*, a-h: a, dorsal surface of carapace; b, front view of carapace; c, side view of carapace; d, outer maxilliped; e, antenna; f, cheliped; g, second walking leg; h, abdomen.

Orbits incomplete; eyestalks prominent, elongate. Antenna recurved with flagellum lying in orbit above the eye, a winglike process developed from the second segment. Outer maxillipeds narrow, straight, closing the buccal cavity; palp stout, long; exognath with rudimentary flagellum. Chelipeds stout, subequal, carpus and palm inflated; fingers thin, cutting edges toothed, tips crossing when closed. Minute granules, some of which are sharp, cover the outer surface of carpus and palm, arranged in longitudinal rows on the latter surface; a row of small teeth on the upper border of the merus.

First three walking legs stout, surface as chelipeds, dactylus strong, about as long as propodus. Chelipeds, first and second walking legs folded closely under the carapace when at rest; third walking leg normally resting in a longitudinal groove in the side of the carapace extending forward toward the orbit, curving ventrally just before reaching the eye. Fourth walking leg very small, folded in a depression of the postero-lateral border of the carapace which is confluent with the longitudinal groove supporting the third leg. Abdomen broad, with six segments, the last very thin and bordered with long hairs. A narrow lamella on either side arising at the junction of the fifth and sixth segments is also densely haired.

A single specimen of this megalops was recovered from a coral head dredged off Waikiki, Oahu, at a depth of about 16 fathoms on May 30, 1948, by Charles Allen and Vernon Smith. (Bishop Museum collection no. 5351.)

The specimen is bright red in life, but the color soon fades in alcohol to pale yellow. In the granular ornamentation of the surface and the broadly triangular rostrum it bears some resemblance to megalops *gamma* (p. 241). Features of the chelipeds, antennae and abdomen, however, mark this smallest of the megalops here recorded as a distinct form. Its reference to any known brachyuran crab is uncertain.

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