

HAWAIIAN ATYIDAE

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INTRODUCTION

Fresh-water crustaceans of the family Atyidae, because of their phylogenetic development, structural features, and distribution, are of special interest to the investigator.

It seems clear from the evidence presented by Ortmann (15)¹ and Bouvier (6) that the Acanthephyridae, now widely distributed in tropic and temperate seas down to at least 3,000 fathoms, and the Atyidae had common ancestors inhabiting the littoral zone, whence some migrated into the abyssal regions and others ascended rivers, adapting themselves to fresh-water habitats.

The invasion of fresh water by ancestors of the Atyidae probably had its beginning in an early geologic period. Ortmann (17) considered this family among the oldest of fresh-water decapods and, although no fossils have been positively identified, reckoned their origin to have been during the Jurassic period. He did not believe that the Atyidae, themselves, immigrated from the sea, but concluded from the circumtropical distribution of the family that their progenitors invaded fresh water during a period when a tropical climate prevailed throughout the world.

Although the family is not a large one, during its long habitation and extensive distribution in fresh waters of continental and island areas, it has become widely specialized. In a comprehensive treatment of the family, Bouvier (10) recognized 16 genera with fully 100 species and divisions, more than half of which were included under one genus. Calman (13) has recently described an additional genus and species.

Although confined chiefly to tropical and subtropical regions the known range of the family is from about 43° S., near Christchurch, New Zealand, to approximately 50° N., in France. In the Northern Hemisphere representatives have been taken from the Mammoth Caves, Kentucky; Sonoma County, California; Central Japan; Northern China; and numerous localities in countries bordering the north shores of the Mediterranean Sea, all well within the Temperate Zone.

The Atyidae also show wide altitudinal distribution. In Hawaii a species of the genus *Caridina* may be taken a few feet above sea level, and a sub-

¹ The numbers in parentheses refer to Literature Cited (p. 36).

species of *Paratya compressa* has been reported in Japan from an altitude of about 9,000 feet.

Members of the family vary greatly in size. Calman (11) described a species of *Caridella* from Lake Tanganyika but 4 mm. in length, and Bouvier (10) records a specimen of *Atya gabonensis* from Senegal, West Africa, 124 mm. long.

The characteristics of the family are fully detailed by Bouvier (10) and need not be repeated here. General features, however, by which the collector may be assisted in distinguishing representatives of the family are as follows: first two pairs of legs chelate, their carpi simple; posterior maxilliped terminating in a claw; mandible without a palp but with a masticating lobe; telson without a median spine on the posterior border; epipodites typical of basal segment of chelipeds and walking legs.

With the exception of the most primitive genus, *Xiphocaris*, which shows affinities for the Acanthephyridae and is known only from the West Indies, all Atyidae are characterized by well-developed tufts of setae extending forward from the tips of the pincers.

In Hawaii 3 genera of the family have been recognized. Of these, *Caridina* is the most generalized. Bouvier (10) fully describes the genus and reports about 50 species and varieties from African and Indo-Pacific regions in tropical and subtropical latitudes. Roux (21) records 5 species and varieties from Australia.

Rathbun (20) tentatively referred specimens collected in pools near the sea on the island of Hawaii to *Caridina brevirostris* Stimpson. Similar specimens have been collected more recently from widely separated localities on Oahu and it is probable that the species inhabits all the larger islands of the Hawaiian group. It is to be found in shallow pools on the elevated coral plain near the sea. When living it is vermilion in color and reaches a length of about 15 mm.

Although the Hawaiian species of *Caridina* shows considerable variation in the chelipeds, typical examples have well-developed palms with short dactyli. The carpi of both pairs of chelipeds are elongated, those of the second pair being the longer. (See fig. 1, *a*, *b*.)

The species *Caridina brevirostris* was inadequately described by Stimpson (23) from the Loo Choo Islands. Bouvier (10) recognizes great variation and plasticity in this species but expresses doubt that either specimens from the Seychelles, referred to *Caridina brevirostris* by him, or the Hawaiian form studied by Rathbun, are identical with Stimpson's species.

Representatives of two other genera of the family, *Atya* and *Ortmannia*, have been described from Hawaii. The genus *Atys* was introduced by Leach in 1815 but changed to *Atya* by him two years later, the earlier name having been preoccupied. Twelve species of the genus are now recognized, 11 re-

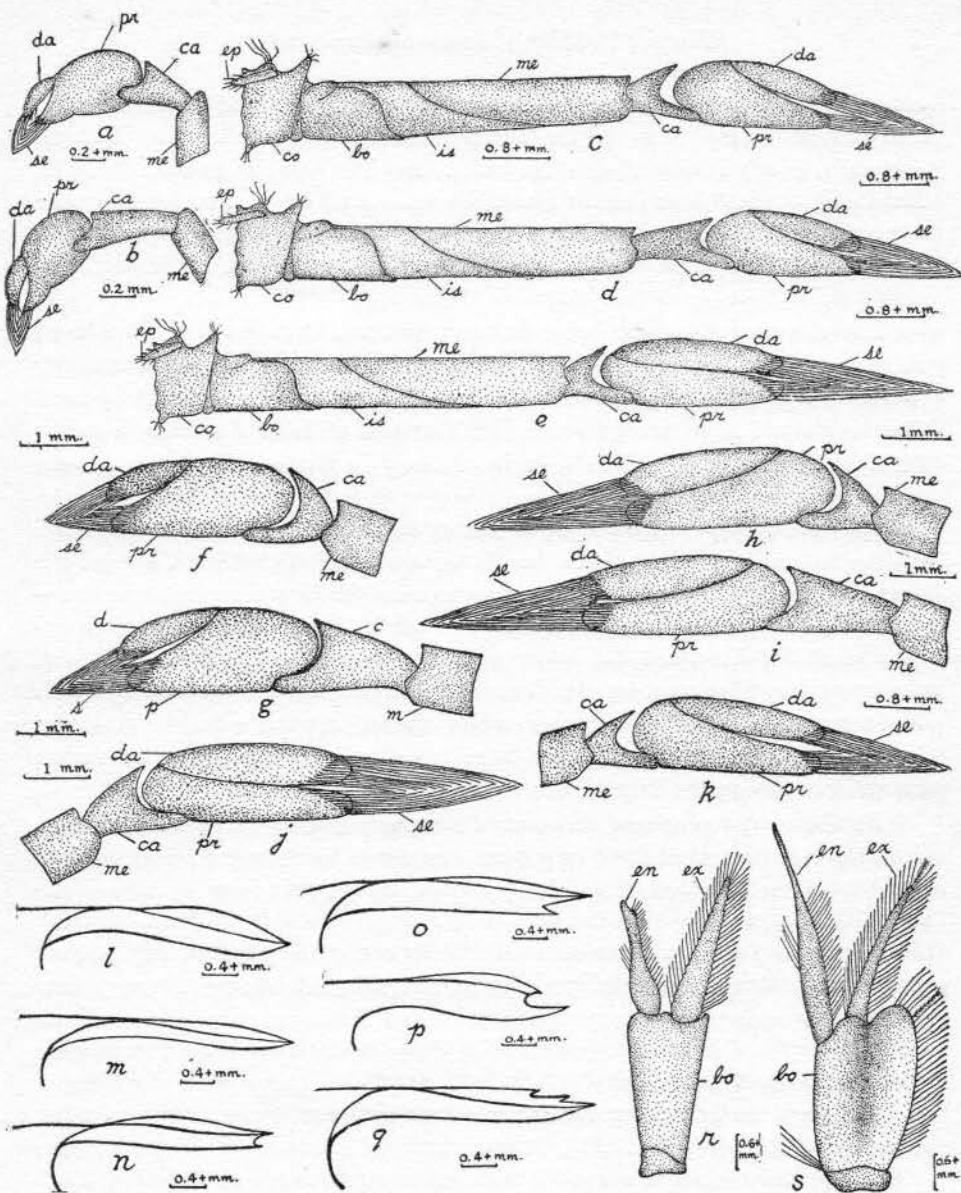


FIGURE 1.—Morphology of Atyidae: a, b, extremities of first and second left chelipeds, respectively, of *Caridina brevisrostris*; c, d, extremities of first and second right chelipeds, respectively, of *Ortmannia henshawi*; e, first right cheliped of *Atya bisulcata* (second cheliped resembles the first in *Atya*); f, g, extremities of first and second left chelipeds, respectively, of a long-palmed form of *Ortmannia henshawi*; h, i, the same of a short-palmed form; j, k, extremities of second right chelipeds of two forms intermediate between *Ortmannia henshawi* and *Atya bisulcata*, j, with a long dactylus and short carpus, k, with a distinct palm but carpus as in *Atya*; l, m, rostra of female and male specimens, respectively, of *Atya bisulcata*; n-g, variations in armature of rostra; r, first swimmeret on the left side of a male specimen of *Atya bisulcata* (posterior view); s, first swimmeret on left side of a female specimen of *Atya bisulcata* (posterior view). (bo, Basopodite; ca, carpus; co, coxopodite; da, dactylus; en, endopodite; ep, epipodite; ex, exopodite; is, ischium; me, merus; pr, propodus; se, setae.)

corded by Bouvier (10) and 1 described by McCulloch and McNeill (14). They range from West Africa through the Indo-Pacific region, Malaya, Australia, South Pacific islands, Hawaii, to tropical America and the Antilles. Randall (18) first described an Hawaiian species of Atyidae under the name *Atyoida bisulcata*. Rathbun (19) determined Randall's type specimen to be a true *Atya*, the species, therefore, now being known as *Atya bisulcata* (Randall).

In order to clear up confusion in nomenclature, Rathbun (19) introduced the generic term *Ortmannia* to include those members of the Atyidae which showed slight variations from *Atya*. The chief difference between the genera *Ortmannia* and *Atya*, recognized by Rathbun and all later observers, is in the form of the chelipeds. (See Pl. I; fig. 1, *c-e*.) In *Ortmannia* the hand has a palm, by reason of the dactylus being shorter than the propodus; in *Atya* the dactylus is as long as the propodus, thereby eliminating the palm. The carpi of the second pair of chelipeds in *Ortmannia* are longer than those of the first, but in *Atya* the carpi of the two pairs of chelipeds are short and approximately equal in length. In chelipeds of both genera the carpus is excavated at the distal end, this segment articulating with the lower border of the propodus. The setae at the tips of the pincers are longer in *Atya* than in *Ortmannia*. In both genera epipodites are lacking from the fifth pair of legs, and in some species of *Atya*, not Hawaiian, they are also absent from or rudimentary on the fourth pair.

Rathbun (19) proposed the name *Ortmannia henshawi* for the Hawaiian form, previously listed by Sharp (22) as *Atya bisulcata* and by Ortmann (16) as *Atyoida bisulcata*, and designated it as an atavic form of *Atya bisulcata* (Randall).

The term *Ortmannia* has been universally accepted by authorities, at least as a convenience in the classification of the Atyidae. Bouvier (10) recognizes *Ortmannia* as having true generic status and lists 6 species ranging from West Africa and Mauritius through the Indo-Pacific area, including Hawaii, to tropical America and the West Indies.

Although the Hawaiian forms known as *Ortmannia henshawi* and *Atya bisulcata* (Pl. I, *A-D*) have long been recognized as having distinct characteristics, they have also been known to be closely associated ecologically. Both may be taken in the same stream and under the same stone. They are typical of the cool mountain waters, having been collected from altitudes of at least 1,800 feet above sea level. Although not descending to the seashore they have been taken in Nuuanu Stream, in the vicinity of School Street, Honolulu, about 15 feet above sea level and less than a mile from the ocean.

It is impossible to determine accurately the relative proportion of specimens of *Ortmannia henshawi* and *Atya bisulcata* in Hawaii from small collections. Full-grown females of both forms may reach 50 mm. in length, being

larger than mature males. Females are more numerous than males in *Atya* and vice versa in *Ortmannia*. (See below.) Because some collectors take the larger specimens, overlooking or discarding the smaller ones, a greater number of the *Atya* form may appear in some collections. Methods of collecting also vary results in this regard. When taken by hand the larger specimens only are likely to be secured, but when nets or traps are employed specimens of various sizes are more frequently collected.

Calman (12) reports that of the two lots of Atyidae procured by the Challenger Expedition at the Fish Market in Honolulu, one consisted of 42 *Atya*, 46 *Ortmannia*, and a specimen with 3 chelipeds of the *Atya* form and one of the *Ortmannia* type. The other lot included 38 *Atya* and 9 *Ortmannia*. Among 74 specimens collected in 1927 by C. S. Judd in Waiahole Valley, Oahu, 36 were *Ortmannia* and 38 *Atya*. Otto Degener collected 197 specimens on Maui in 1927, 172 of which were *Ortmannia* and 25 *Atya*. I have taken more than 2,000 specimens from the small streams of upper Manoa Valley, Oahu, collecting all specimens observed. Of these fully 80 per cent were *Ortmannia henshawi*.

A collection of 1,784 specimens taken near Hilo, Hawaii, consisted of 1,300 typical examples of *Ortmannia*, 465 *Atya*, and 19 individuals which clearly showed characteristics intermediate between *Ortmannia henshawi* and *Atya bisulcata*. One specimen had 3 chelipeds of the *Ortmannia* form and 1 like *Atya*.

Transitional forms have also been observed among those taken from the streams of Oahu. In some specimens the dactyli of the chelipeds are greatly lengthened, reducing the palms to a minimum, and the carpi of the second pair of chelipeds are little longer than those of the first. (See fig. 1, *j*.) In others the dactyli are not shortened so much, but the carpi of the second pair of chelipeds are like those of the *Atya* form. (See fig. 1, *k*.) In all these specimens is seen an increase in the length of the setae extending from the tips of the pincers, over those of a typical example of *Ortmannia henshawi*. Although still retaining characteristics of the *Ortmannia* form these individuals show a near approach to *Atya bisulcata*. Bouvier (8) recognized specimens of *Ortmannia alluaudi* which showed characteristics like *Atya* and designated them "preatyien."

A numerical lack of balance between the sexes is clearly seen in both Hawaiian forms. Among more than 2,000 specimens of *Ortmannia henshawi* examined, approximately 90 per cent were males, and in *Atya bisulcata* the opposite sex prevails in a correspondingly large proportion. Bouvier (8) found a similar disparity of sexes in specimens of *Atya serrata* and *Ortmannia alluaudi*. He reports that in a lot of 154 specimens of *Atya serrata* 14 were males, and of 157 specimens of *Ortmannia alluaudi* 118 were males.

Although typical specimens of *Ortmannia henshawi* and *Atya bisulcata*

are clearly differentiated by the form of their chelipeds, there is considerable variation of these appendages in the former. Two extremes in the form of the hand are seen. One is represented by a short dactylus and a long, well-developed palm, features that are more pronounced in the anterior pair of chelipeds. The hand of this form approaches that of the *Caridina* type. (See fig. 1, *f, g*.) The other extreme is represented by a much shorter palm, the dactylus being proportionately longer. This variety more nearly approaches *Atya* in the form of the hand. (See fig. 1, *h, i*.) Between these extremes in *Ortmannia henshawi* intermediate forms exist, the proportionate length of the dactylus and the propodus being an exceedingly variable feature. In all typical examples of *Ortmannia henshawi*, however, the elongated carpi of the second pair of chelipeds is constant.

There is considerable variation in the length, degree of curvature and armature of the rostrum in the Hawaiian forms. Typically the rostrum is unarmed and in full-grown females may have a greater depth and curvature than in males. (See fig. 1, *l, m*.) It is not uncommon, however, to find specimens in which the rostrum bears one or more spines on its upper or lower border. (See fig. 1, *n-q*.)

The sexes may be distinguished by a difference in the form of the first pair of swimmerets. In the male the endopodite is shorter than the exopodite and slightly curved, but in the female the endopodite is straight, tapering, and slightly longer than the exopodite. The basopodite is broader in the female than in the male and is bordered by long hairs serving for the attachment of eggs. (See fig. 1, *r, s*.) The morphological features of the swimmerets are identical in the corresponding sexes of *Ortmannia henshawi* and *Atya bisulcata*. In the young the sexual characteristics are not distinguished by the first swimmerets until the animal has reached a length of from 15 to 18 mm. (See fig. 4, *m-o*.)

In discussing the status of the genus *Ortmannia*, Bouvier (4) called attention to the presence of both *Ortmannia* and *Atya* among specimens of Atyidae in the Museum of Paris collected near Honolulu in 1877, and cited a parallel example of *Atya serrata* Bate, which in its geographical range bears the same relation to *Ortmannia alluaudi* Bouvier that *Atya bisulcata* does to *Ortmannia henshawi* in Hawaii. Bouvier expressed the opinion that these two species of *Atya* and of *Ortmannia* were to be considered as showing evolution by mutation, *Ortmannia* the more primitive form giving rise to *Atya* the more specialized and stable one.

In order to test this hypothesis Bordage (1), at the suggestion of Bouvier, conducted some experiments with *Atya serrata* and *Ortmannia alluaudi* in the island of Reunion. Although the investigations were limited in extent and carried on under adverse conditions certain definite conclusions were announced.

Bordage procured ovigerous females of *Atya serrata* and *Ortmannia alluaudi* and hatched young specimens from the eggs of both. From the eggs of 2 specimens of *Atya serrata* 27 young were obtained. All, according to the report, were like their parents. Larvae developing from the eggs of a specimen of *Ortmannia alluaudi*, 16 in number, were, however, dimorphic, 10 being true to the parental form and 6 like *Atya*.

These results were in accord with the hypothesis of Bouvier and convinced that investigator that *Ortmannia* gave rise to *Atya* by sudden mutation, the latter reaching the status of a fixed species and breeding true.

In the course of his experiments Bordage (2) removed the chelipeds from one side of a specimen of *Atya serrata* and observed the progress of their regeneration. The appendages were at first like those of *Ortmannia*, the dactylus of the hand being shorter than the propodus. On molting the chelipeds assumed the normal form of *Atya*. Bordage explains that mutilation stimulated regression to a more primitive type, the regression, however, being only partial and transitory. This, the investigator called "régénération hypotypique."

In describing the regenerating process, Bordage (2) illustrates the various steps by text figures, the accuracy of which may well be questioned. Setae are shown projecting from the tips of the pincers and a very adult-like carpus is figured characterizing the early stages of regeneration, presumably before the molt occurred. If these figures accurately represent the early phases in the regeneration of a cheliped in *Atya serrata* the procedure is quite unlike that in *Atya bisulcata*. (See p. 19 and fig. 2, a-d.)

Calman (12), in reviewing the work of Bordage, considered the experiments of that investigator insufficient as a basis for the conclusions reached and suggested the need of further work along parallel lines. Calman pointed out that if, as Bordage states, *Atya* always breeds true and *Ortmannia* produces both *Atya* and *Ortmannia*, the latter would tend to disappear, which does not seem to be in accord with general observations.

In the same review Calman suggests that the apparent dimorphism may be due to heteromorphic regeneration of the chelipeds as a result of mutilation; but at the same time he considers this explanation improbable, as all four chelipeds would rarely, if ever, be removed at the same time.

Believing that the work of Bordage should, if possible, be verified and elucidated by more complete details, I began in April 1927, a series of experiments with *Atya bisulcata* and *Ortmannia henshawii*. My experiments were initiated with the view of extending our information regarding the general ecology of these unique fresh-water forms, as well as reexamining the interrelations of members of the two recognized genera, *Atya* and *Ortmannia*.

The scope of the investigations included observations on the responses of the animals to normal and altered conditions of environment, a detailed study

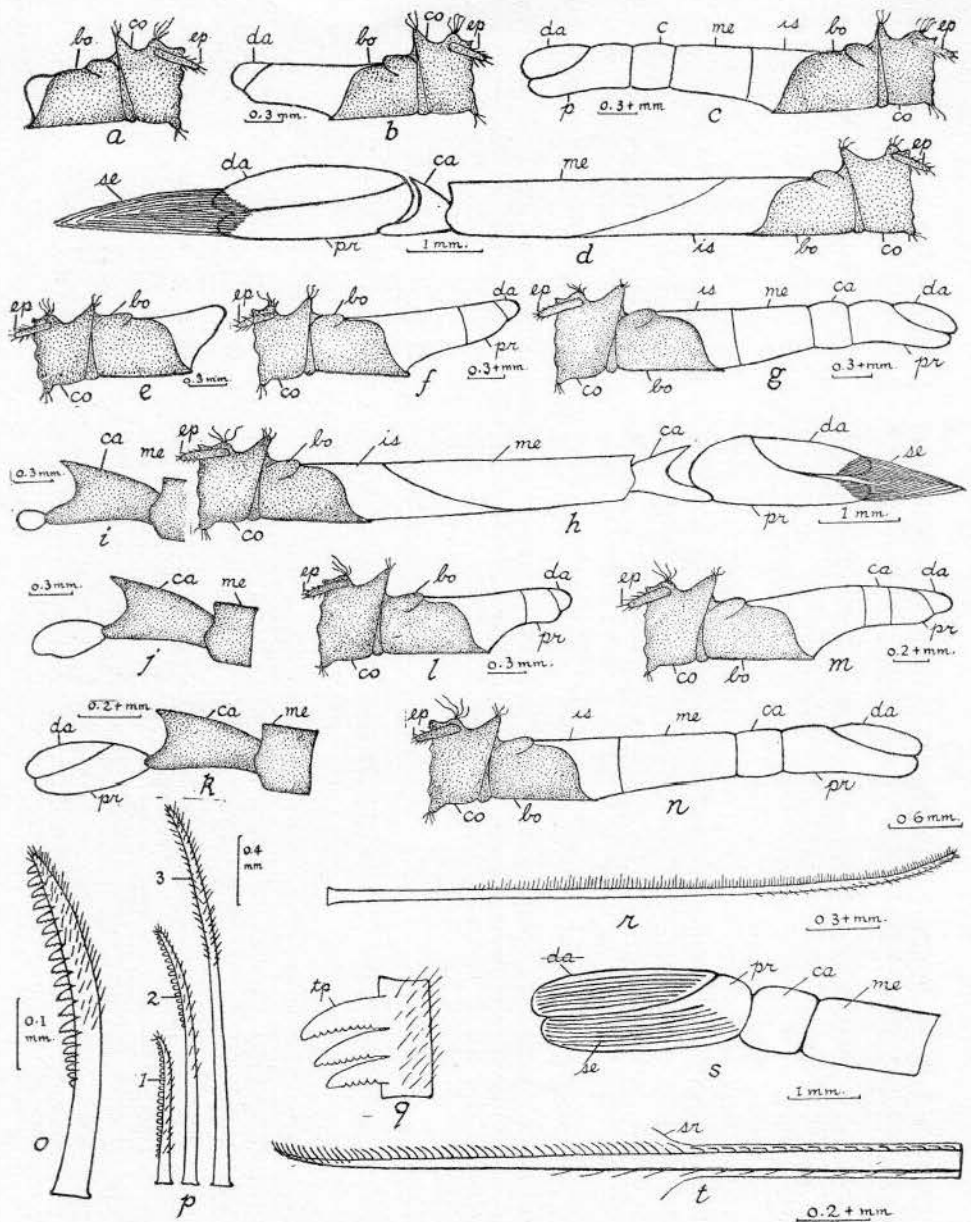


FIGURE 2.—Regeneration and morphology of Hawaiian Atyidae (unshaded areas of chelipeds represent regenerated portions of appendages). *a-d*, Typical regeneration of the first left cheliped of *Atya bisulcata* after mutilation: *a*, 2 days after mutilation, the beginning of the appendage shown as a clear, rounded lobe; *b*, 4 days after mutilation; *c*, 8 days after mutilation; *d*, fully formed cheliped, immediately following molt, 25 days after mutilation. *e-h*, Typical regeneration of first right cheliped of *Ortmannia henshawii* after mutilation; *e*, 3 days after mutilation; *f*, 5 days after mutilation; *g*, 9 days after mutilation; *h*, immediately following molt, 21 days after mutilation. *i-k*, Regeneration of the hand of left cheliped of *Ortmannia henshawii* after mutilation; *i*, 5 days after mutilation, showing beginning of regeneration; *j*, 8 days after mutilation; *k*, 11 days after mutilation. *l-n*, regeneration of the second right cheliped of the same specimen; *l*, 4 days after mutilation; *m*, 3 days later; *n*, 11 days after mutilation. *o*, A short seta borne at the tip of the pincers of *Ortmannia henshawii*, showing the toothed margin. *p*, Setae of *Ortmannia henshawii*, showing the reduction of toothlike processes with the increasing length: 1, a short seta with many teeth; 2, a longer seta with fewer teeth; 3, a long seta with no teeth. *q*, A section of a short seta of *Ortmannia henshawii* (greatly enlarged). *r*, A typical seta from the tip of the pincers of *Atya bisulcata*. *s*, Extremity of a cheliped of *Atya bisulcata*, 24 hours before molting, with the setae formed in the dactylus and propodus. *t*, A seta dissected from the propodus, showing the sheath (*sr*) ruptured. (*bo*, Basopodite; *ca*, carpus; *co*, coxopodite; *da*, dactylus; *ep*, epipodite; *is*, ischium; *me*, merus; *pr*, propodus; *se*, setae; *sr*, ruptured sheath of seta; *tp*, toothlike process.)

of the regeneration of the chelipeds of *Atya bisulcata* and *Ortmannia henshawii*, and the culture of young hatched from eggs of both forms.

EFFECT OF ECOLOGICAL FACTORS

RESPONSE TO INCREASED SALINITY

There is no record of *Ortmannia henshawii* or *Atya bisulcata* having been taken in brackish water or in waters of the coastal plain near the sea. These forms are, at the present time, strictly confined to fresh-water habitats. The lowest altitude at which they have been collected on Oahu is about 15 feet above sea level. (See p. 6.) They have been reported at altitudes of at least 1,800 feet above the sea and probably have a much higher range. Experiments were conducted to ascertain how complete has become the adjustment of the animals to the cool, fresh waters of the higher altitudes and how readily they may be readapted to the warmer waters of the coastal plain and the brackish water near the sea.

That *Ortmannia henshawii* and *Atya bisulcata* have long been established in a fresh-water environment is indicated by their sensitiveness to a medium of normal sea water. When transferred directly to sea water most adults die within 12 hours. Larvae 10 days old are less resistant to normal sea water than are adults, most of them dying within 4 hours.

Both young and adult specimens readily adapt themselves to a slightly saline solution consisting of 9 parts of fresh water to 1 part of sea water. In this medium, changed daily, they exist for an indefinite period. Molting occurs in as regular a manner and the rate of regeneration of lost appendages is as rapid as in normal fresh water.

Some specimens show a high degree of accommodation when transferred abruptly from fresh water to a solution of 3 parts of fresh water to 1 part of sea water. Adults have lived more than 5 months under these conditions with the medium changed daily. Molting occurs in a regular manner. One specimen survived 104 days and another 75 days, each having molted 4 times. Although great variation in the degree of resistance of both adults and young to this medium is seen, specimens from 8 to 10 mm. in length have, in general, lived 4 or 5 times longer than adults. In some specimens subjected to standing solutions of this medium, changed daily, the rate of regeneration of chelipeds seemed to be retarded but in others development proceeded in a normal manner. (See fig. 3, *a, b*.)

On subjecting adult shrimps to a solution consisting of 2 parts of fresh water to 1 part of sea water, changed daily, great variation in their sensitiveness was observed. One specimen lived for more than 6 months, molting 7 times during the period. Frequently adults have lived from 1 to 3 months and molted at normal intervals. Young specimens show a slightly greater resist-

ance to this medium than do adults. There is a marked effect on the rate of regeneration of lost appendages in this solution. Approximately twice as long may be required for the development of a cheliped to a length of 3 mm. as when in normal fresh water. (See p. 20.) Frequently from 12 to 21 days are required for the appendage to regenerate to the extent of 2 or 3 mm., when the animal is exposed to this saline medium, and occasionally a length of not more than 1 mm. is reached in 12 days. The re-formed cheliped following a molt may also be subnormal in size. (See fig. 3, *c-e.*)

Adult and young specimens were subjected to a solution consisting of 1 part of fresh water to 1 part of sea water, changed daily. One adult survived 118 days, molting 5 times. Others lived from 40 to 60 days, molting once or twice. A young specimen 10 mm. long endured these conditions 3 months, and others have survived from 40 to 56 days. Young specimens do not show a more ready accommodation to this medium than do adults. The rate of regeneration of chelipeds is clearly affected by this solution. At least 12 days are usually required for chelipeds to develop to a length of 2 mm. and from 19 to 22 days frequently elapse before a length of 3 mm. is reached, a growth normally attained in from 8 to 12 days. (See fig. 3, *f, g.*)

When transferred directly to a medium consisting of 1 part of fresh water to 2 parts of sea water, changed daily, both adults and young are capable of maintaining themselves for at least 30 days. One adult lived 34 days without molting. A young specimen lived 59 days. Regeneration of appendages in adults when subjected to this medium is clearly retarded. Usually not until the fifth day after mutilation is the beginning of regeneration observed, and later development is very slow. A regenerating cheliped attained a length of but 0.75 mm. in 9 days. (See fig. 3, *h.*)

In a solution consisting of 1 part of fresh water to 3 parts of sea water both young and adult animals die usually within 5 days.

That a slightly saline medium is not deleterious to the embryonic development of these crustaceans is indicated by the eggs of *Atya bisulcata* being hatched and vigorous larvae developed in a circulating solution consisting of approximately 3 parts of fresh water to 1 part of sea water.

It is obvious that my laboratory experiments were carried on under somewhat abnormal conditions in that, for the most part, standing solutions were used, whereas in their natural habitat the animals are subjected to strong current. The experiments indicate, however, that although *Ortmannia hen-shawi* and *Atya bisulcata* are not readily accommodated to normal sea water they are capable of maintaining themselves in water of a higher degree of salinity than that which they frequent and may, if other conditions are favorable, approach much nearer the sea than they actually do.

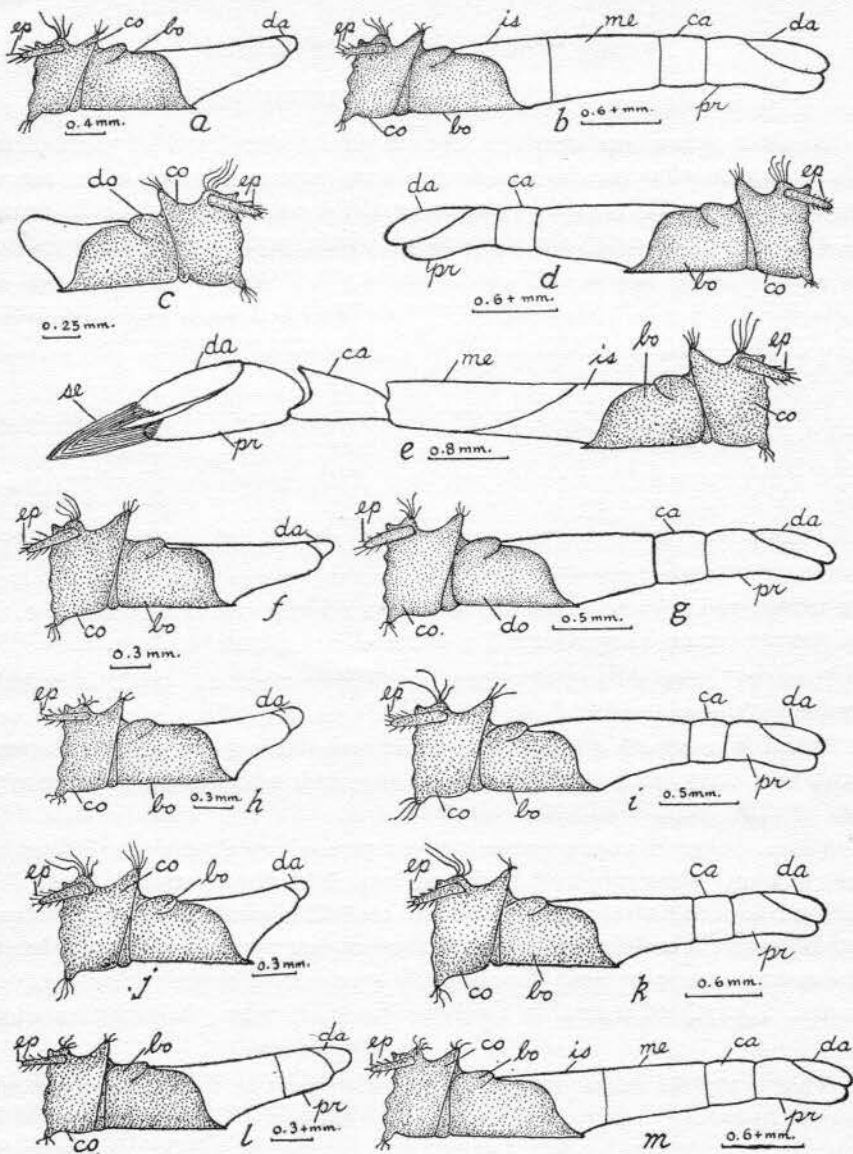


FIGURE 3.—Regeneration of the chelipeds of *Ortmannia henshawi* under abnormal conditions (unshaded areas represent regenerated portions of appendages). *a, b*, In a solution consisting of 3 parts of fresh water and 1 part of sea water: *a*, 4 days after mutilation; *b*, 10 days after mutilation. *c-e*, In a solution consisting of 2 parts of fresh water and 1 part of sea water: *c*, 3 days after mutilation; *d*, 15 days after mutilation; *e*, immediately following molting, 22 days after mutilation. *f, g*, In a solution consisting of equal parts of fresh and sea water: *f*, 5 days after mutilation; *g*, 11 days after mutilation. *h*, In a solution consisting of 1 part of fresh water and 2 parts of sea water, 9 days after mutilation. *i*, At a constant temperature of 30°C., 11 days after mutilation. *j, k*, Under constant subjection to a temperature ranging from 15°C. to 18°C.: *j*, 12 days after mutilation; *k*, 21 days after mutilation. *l*, After 10-days' treatment by ultra-violet rays from Cooper Hewitt Uviarc 110-watt lamp (illumination of ventral surface 5 minutes daily, 42 cm. from arc). *m*, Untreated control, 10 days after mutilation. (*bo*, Basopodite; *ca*, carpus; *co*, coxopodite; *da*, dactylus; *ep*, epipodite; *is*, ischium; *me*, merus; *pr*, propodus; *se*, setae.)

RESPONSE TO ALTERED TEMPERATURE

In their natural environment *Ortmannia henshawi* and *Atya bisulcata* inhabit waters of mountain streams the temperature of which often ranges from 8°C. to 10°C. lower than the water of the coastal plain near the ocean. At 2 p.m., July 20, 1927, the temperature of the surface water of a shallow stream of leeward Oahu, 50 yards from the sea, was 31°C. Twenty minutes later, in Manoa Valley at an elevation of 200 feet, 3 miles from the ocean, the temperature of a stream inhabited by the crustaceans was 23°C. Both readings were taken in shaded localities.

Numerous experiments were carried on to determine the resistance of adult and young shrimps to high and low temperatures. The temperature of fresh water surrounding an adult specimen of *Ortmannia henshawi* was gradually raised from 25.3°C. to 33.8°C. in 27 minutes. On reaching the higher temperature the animal became greatly agitated, swimming rapidly on its side and back. After a few minutes the temperature was raised to 35.5°C. when the animal suddenly fell upon its back in a sharply contracted condition. It did not recover on being removed to water of normal temperature.

Repeated tests showed that heating to approximately 35°C. is quickly fatal to both young and adult animals. No appreciable difference was observed in the behavior of *Atya bisulcata* and *Ortmannia henshawi* under high temperature. Young specimens from 8 to 12 mm. in length showed a response to rapid heating parallel with that of adults.

When subjected to a constant temperature of 30°C. the metabolism of the adult animals seems to be affected in a deleterious manner. One adult survived this condition, which is from 6° to 8°C. above normal, for 60 days, but died without molting. The regeneration of lost appendages is retarded at this constant temperature. In an adult specimen a regenerating cheliped reached a length of 2 mm. in 11 days (fig. 3, *i*) when the animal molted. The cheliped assumed the adult form immediately after the molt but was subnormal, being but 4.5 mm. in length as compared with 7 mm. for the original appendage. Another adult lived 53 days at 30°C. but died without molting. A mutilated cheliped of this specimen regenerated to the extent of 3 mm. in length in 32 days, which is much slower than normal. (See p. 20.) All adults subjected to a constant temperature of 30°C. have died within a few days, or have shown the effects of a disordered metabolism in delayed molting or retarded regeneration of appendages.

Although young specimens from 8 to 12 mm. in length have shown great variation in resistance to a constant temperature of 30°C., none has survived longer than some adults. In some experiments vigorous young specimens endured these thermal conditions for 2 months, but on the average did not show greater resistance than did adults.

Many attempts were made to hatch larvae from the eggs of ovigerous females exposed to a constant temperature of 30°C. but without success. It is probable that a failure of ready adjustment to temperatures of about 30°C. is a factor of considerable importance in preventing the animals from becoming established in the lower levels of streams near the ocean.

The lower thermal endurance of *Ortmannia henshawi* and *Atya bisulcata* was also determined. Water in which an adult specimen of *Ortmannia* was placed was gradually reduced from 25.3°C. to 12°C. in 30 minutes. As the lower temperature was reached the animal turned on its back and remained in a partially paralyzed condition, only slight twitching of the appendages being observed. The temperature was reduced to 10°C. when movements ceased. After 2 minutes the specimen was returned to water of normal temperature, and in 7 minutes it had completely recovered. In all temperature experiments *Atya bisulcata* showed responses parallel with those of *Ortmannia henshawi*.

Two adult specimens exposed to a temperature fluctuating from day to day between 12°C. and 14°C. were paralyzed after 9 hours. One, on being returned to normal temperature, recovered; the other was stimulated mechanically, revived, and lived 5 days in the cold environment. Numerous similar tests were made but no specimen lived longer than 8 days at a temperature ranging from 12°C. to 14°C.

Under sustained exposure to temperature ranging from 15°C. to 18°C. adult specimens have been maintained for more than 2 months and doubtless are capable of enduring such thermal conditions for a much longer period. This low temperature, however, retards the regeneration of lost appendages (fig. 3, *j*, *k*) and probably has a deleterious effect on the general metabolism of the animals.

One adult specimen, under thermal conditions ranging from 15°C. to 18°C., lived 61 days, when it molted and immediately died. Mutilation of a cheliped occurred 17 days before molting but no regeneration took place. In a similar environment, another adult specimen molted in 27 days, a regenerating cheliped having reached a length of 2 mm. in this time. The adult form was assumed by the appendage immediately after the molt but was 2 mm. shorter than the original. Another specimen lived 60 days without molting, which indicates a disordered metabolism, as this process is of more frequent occurrence under normal conditions. (See p. 27.) A regenerating cheliped in this specimen required 60 days to reach a length of 3 mm., which also shows a retardation of function. (See p. 20.)

The circulating fresh water of the Marine Biological Laboratory at Waikiki, Honolulu, in which the animals seem to develop normally, ranges in temperature from approximately 22°C. to 25°C. during the year, with a lesser daily variation.

Although during the cooler season of the year the temperature of the mountain streams in Hawaii is somewhat lower than during the summer months, it probably seldom falls below 18°C . where the *Atyidae* live. The temperature of a small stream in Manoa Valley, Oahu, at an elevation of 450 feet above sea level, was 21.5°C . at 3 p.m., December 31, 1928, and 19.1°C . at 7:30 a.m., January 26, 1929, the latter record being taken during an unusually cool period. The thermal range within which these animals develop best is probably from approximately 20°C . to 26°C .

RESPONSE TO LIGHT

When hatched in standing water, under laboratory conditions, the young *Atyidae* pass through a free-swimming zoea stage, during which they show a strong positive phototropism. If a transformation into the mysis stage occurs under these conditions, the phototropism is altered, becoming negative, a condition which is maintained throughout the life of the animal. On hatching in a strong current of water the zoea stage seems to be passed in the egg, as the young are released in the mysis form, showing at once a strong aversion to light.

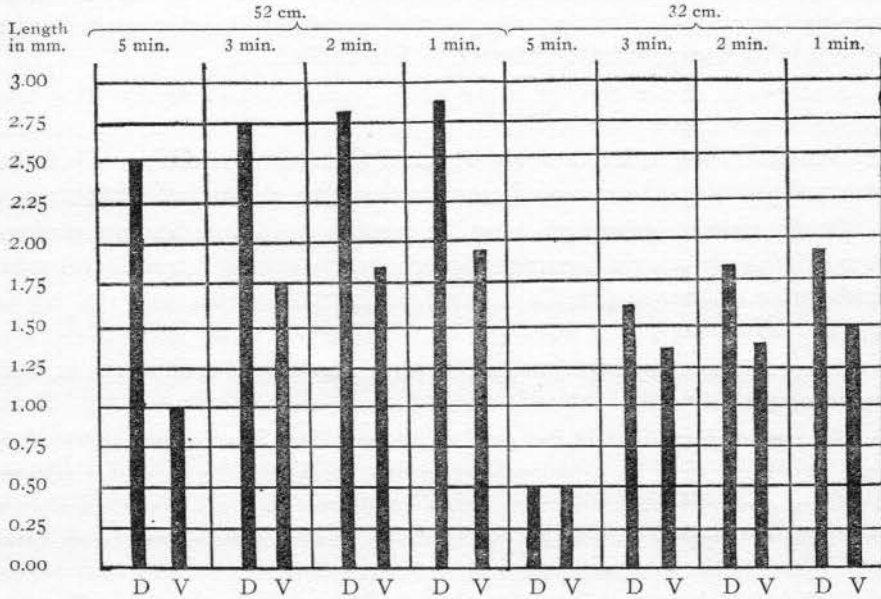
In their natural habitat the animals secrete themselves under stones during the day or cling to submerged vegetation along the borders of a stream, avoiding strong light. Under laboratory conditions they are quiescent during daylight, concealing themselves in available shaded places, but show great activity at night. In aquaria with sand-covered bottoms, as dusk approaches, the shrimps become actively engaged in rolling the sand grains about, using the setae at the end of the pincers for this purpose and by means of them transferring food particles to the mouth.

A series of experiments was conducted to determine the effect of ultra-violet rays on the metabolism of the animals as expressed in the regeneration of chelipeds. A device was employed by means of which the specimens could be held in any position desired by the investigator in order to compare the influence of the rays when thrown upon the ventral and dorsal surfaces of the animals. Treatments ranging from 1 to 5 minutes daily were given with the specimens at various distances up to 52 cm. from the arc, a Cooper Hewitt 110-volt Uviarc lamp being used.

Almost without exception the experiments indicated a pronounced retardation of regeneration of the chelipeds, especially when the ventral surface of the specimen was illuminated. (See fig. 3, *l*.) In this position the rays fell directly upon the mutilated surfaces where the appendages had been removed. At distances of 52 cm. (Table 1) and 42 cm. from the arc, dorsal irradiation did not seem to slow up regeneration to any great extent. When brought within 32 cm. of the arc (Table 1) and 22 cm., in other experiments, there

was a marked effect on the rate of regeneration regardless of whether the ventral or dorsal surface of the specimen was exposed to the rays.

TABLE 1. EIGHT-DAYS' REGENERATION OF CHELIPEDS OF *ATYA BISULCATA* TREATED 1, 2, 3, AND 5 MINUTES DAILY WITH ULTRAVIOLET RAYS, 52 CM. AND 32 CM. FROM THE ARC. D, DORSAL EXPOSURE; V, VENTRAL EXPOSURE.



Heat as a possible factor in retardation was eliminated by illuminating specimens in an air temperature of from 20°C. to 24°C. maintained by circulating ice water. Under these conditions, at 52 cm. from the arc an exposure of 5 minutes daily, for 10 days, resulted in a regeneration of 1 mm. for a ventral and 2.50 mm. for a dorsal treatment. The latter rate is normal for untreated controls.

The effect of heat on regeneration was also determined by a Mazda lamp of 250 watts so arranged as to produce, at a given distance, the same amount of heat in a similar time as that developed by the Uviarc lamp at 52 cm. Specimens illuminated under the Mazda lamp showed little variation in the rate of regeneration from untreated controls.

RESPONSE TO ALTERED PH

Many laboratory tests were made to determine the comparative rate of regeneration of chelipeds under altered conditions of hydrogen-ion concentration for a range of pH 5.4 to pH 9.

Although considerable variation is shown in the rapidity of regeneration in solutions on both sides of neutrality, repeated experiments indicate that an alkaline reaction between pH 8 and pH 9 presents an optimum condition for the regenerative process.

Determinations of the pH of a stream flowing from the mountains through Manoa Valley, Oahu, were made at 5 stations throughout its course ranging from one-half to one mile apart, the readings being taken the same afternoon during a period of 3 hours. (See Table 2.)

Station A, at the foot of a mountain waterfall and representing one source of the valley stream, showed a pronounced alkaline reaction, as did Station E, about 4 miles nearer the sea. Intermediate localities indicated a lower alkalinity reaching neutrality at an elevation of 170 feet (Station D).

In this stream shrimps are found in greatest abundance between stations A and B. They occur in lesser numbers between stations B and C, and some doubtless go below station C. I have not found any between stations D and E.

In some laboratory experiments the animals have lived indefinitely, molted, and showed the normal rate of regeneration of chelipeds in pH 5.4. None of the fresh-water streams of Oahu approaches pH 5.4, but field tests have shown that the water in which shrimps are living is as slightly alkaline as pH 7.2. The shrimps are apparently capable of adjusting themselves to a considerable range in pH, which doubtless occurs in all mountain streams on Oahu.

Although I have not found shrimps in Manoa Valley stream as low as station E (Table 2), they have been taken in Nuuanu Valley stream at a much lower altitude. (See p. 6.) The fact remains, however, that the shrimps are more abundant near the headwaters of mountain streams, and it is probable that here the higher degree of alkalinity together with the relatively low temperature effects the most favorable environment for the metabolic processes of these animals.

TABLE 2. ELEVATION, TEMPERATURE, AND pH OF 5 STATIONS IN THE COURSE OF A STREAM IN MANOA VALLEY, OAHU, MARCH 19, 1929, 1 P. M TO 4 P. M.

| Station | Elevation above sea, in feet | Temperature °C. | pH |
|---------|------------------------------|-----------------|-----|
| A | 700 | 19.8 | 8.2 |
| B | 400 | 22.0 | 7.2 |
| C | 300 | 23.0 | 7.2 |
| D | 170 | 24.4 | 7.0 |
| E | 65 | 25.0 | 8.0 |

MORPHOLOGICAL CHANGES

THE REGENERATION OF CHELIPEDS

Up to the present time no experimental work with the *Atyidae* has supplemented that of Bordage (2) on the regeneration of the chelipeds of *Atya serrata*. The announcement of that investigator that regenerating chelipeds of *Atya serrata* were like those of *Ortmannia alluaudi* until the first molt, when they took on the original form, was evidence supporting the view of Bouvier that *Atya* developed from *Ortmannia*. In its development, preceding a molt, the cheliped of *Atya* showed a temporary return to an ancestral form which Bordage described as a partial regression. Unfortunately the experiments of Bordage were limited, and details of important phases of the regeneration process were omitted in his report.

Believing that the work of Bordage should be verified and efforts undertaken by him extended along parallel lines, I began a series of experiments on the regeneration of the chelipeds of *Ortmannia henshawi* and *Atya bisulcata*, following mutilation.

On removing the cheliped from a living specimen, the point of natural separation is the articulation between the basopodite and ischium. (See fig. 1, *c*.) By lightly grasping the appendage with a pair of dissecting forceps it is readily detached. In some specimens the hand only was removed and the progress of the regeneration of this organ followed. The separation of the hand from the carpus is not accomplished so easily as is the detachment of the cheliped at the junction of the basopodite and ischium, but fine pointed scissors may be used to clip the narrow union between the propodus and carpus, allowing the proximal segments of the cheliped to remain undisturbed.

My experiments were carried on in the Marine Biological Laboratory, the circulating fresh water being supplied from the mains of the city of Honolulu. It was found that algae and other fresh-water plants usually furnished the animals with adequate nourishment, although other foods were frequently offered, among which bread and bananas were readily ingested.

Under normal laboratory conditions the beginning of the regeneration of a cheliped in the adult shrimp may be observed within 48 hours after the loss of the appendage. The first appearance is a nipple-like, clear lobe at the distal extremity of the basopodite. (See fig. 2, *a*.) After 3 or 4 days, as the lobe becomes finger-like, a depression appears on the ventral surface near the tip, from which a diagonal suture is continued, differentiating the distal portion, or dactylus, from the remainder of the appendage. (See fig. 2, *b*.)

A few days later, the carpus, or wrist, is differentiated from the propodus and the merus. (See fig. 2, *c*.) On reaching a length of approximately 3 mm. in from 8 to 12 days after mutilation, the merus is marked off from the ischium by a suture which is transverse at first, assuming a diagonal course

after a molt. The regenerating cheliped has now acquired all the segments of an adult appendage, but the dactylus is still fused throughout its length with the propodus. The appendage is smooth, the carpus has not assumed the adult form, and no setae have appeared at the distal extremity of the hand. (See fig. 2, c.)

The differentiation of segments in the regenerating cheliped proceeds from the tip toward the base, the distal extremity, or dactylus, representing the oldest portion of the new appendage. There is no difference observed in the form of the regenerating chelipeds of *Ortmannia henshawi* and *Atya bisulcata* during the early stages and up to the time of molting. (See fig. 2, c, g.) In both forms the dactylus is shorter than the propodus, and, as observed by Bordage (2), the chelipeds of *Atya* during regeneration are like those of *Ortmannia*.

Having reached a length of approximately 3 mm. in from 8 to 12 days after mutilation the regenerating cheliped remains in this condition until a molt occurs, immediately after which the adult form is assumed. The most obvious changes brought about by the molt are as follows: the dactylus is separated from the propodus except for its proximal articulation, the two segments now forming a pincer; setae appear at the tips of the pincers; the carpi become altered in form and size; and the suture between the merus and ischium takes on a diagonal course. (See fig. 2, d.)

Usually the form of the original cheliped is assumed immediately after the molt, although the new appendage may be slightly subnormal in size and occasionally other significant morphological differences occur. (See p. 22.)

If a cheliped is removed within approximately 8 days preceding a molt the appendage does not assume the adult form immediately following the molt, although regeneration may have proceeded to some extent. If mutilation occurs 3 or 4 days preceding a molt usually no regeneration is observed until after the molt has taken place. The metabolic preparation for the process of molting seems to have a retarding effect upon regeneration.

The effect of repeated mutilation and regeneration of a cheliped is seen in a marked reduction in the size of the appendage. The second cheliped on the left side of an adult female specimen of *Atya bisulcata*, the hand of which was 3.5 mm. long, was removed December 19, and after each of 3 successive molts. The length of the hand, following the molts of January 7, January 28, and February 12 was 3 mm., 2.5 mm. and 2 mm., respectively. The opposite cheliped, which was mutilated in a similar manner, did not assume the adult form after the last molt.

In young specimens from 10 to 12 mm. long mutilated chelipeds often completely regenerate and assume the normal form without a molt intervening. I have but 2 records of this occurring among adults in experiments involving several hundred mutilations.

A correlation is seen between the rate of regeneration of a hand and that of an entire cheliped in the same animal. The second cheliped on the left side and the hand only of the opposite appendage were removed from a specimen of *Atya bisulcata*. In 11 days the cheliped had regenerated to a length of 3 mm. and the hand had reached a length of 0.5 mm. (See fig. 2, *i-n*.) In 25 days, just before the specimen molted, the cheliped had increased to 4 mm. and the hand to 1.25 mm. in length. Although the regenerating tissue in the cheliped was more than 3 times the volume of the opposite hand, the rate of growth was so proportioned that, in the two appendages, the hands were identical in form and size immediately after the molt.

Most of the Atyidae are characterized by tufts of setae projecting from the tips of the pincers. (See p. 4.) In regenerating appendages of adults these setae do not usually appear until the molt has occurred. In *Ortmannia henshawi* and *Atya bisulcata* the length of the setae is correlated with the length of the dactylus. Relatively short setae are borne on long-palmed specimens of *Ortmannia*, and on the progressive shortening of the palm the setae are correspondingly lengthened, as is the dactylus. A transformation from forms like *Ortmannia* to forms like *Atya*, or vice versa, is accompanied by a modification in the length of the setae.

There is a distinction in form between the setae of typical specimens of *Ortmannia henshawi* and those of *Atya bisulcata*. In the former all setae bear fine hairs, and in addition the shorter ones carry on their medial borders toothlike processes, which when well developed are notched on one edge and longer near the middle of the row. (See fig. 2, *o, q*.) These processes are fewer in number on setae of medium length and are entirely absent from the longer ones. (See fig. 2, *p*.) In typical forms of *Atya bisulcata* the setae bear fine hairs, which are more numerous on the medial border, variable in length, and directed at right angles to the surface. (See fig. 2, *r*.) No toothed setae are present in this form. In intermediate forms which clearly show characteristics of both *Ortmannia* and *Atya*, some of the shorter setae of the pincers are toothed. It is significant that on the reversion of *Atya bisulcata* to *Ortmannia henshawi*, as a result of the regeneration of chelipeds (p. 22), many of the shorter setae assume a toothed form after the molt, quite unlike those of the original appendage.

A regenerating cheliped in adult specimens rarely assumes the normal form until a molt occurs. (See p. 20.) As the immature appendage is drawn from the molted skin, preformed setae are suddenly thrust from the tips of the dactylus and propodus.

The setae are formed in place, appearing 24 hours before a molt occurs as distinct elements within the substance of the dactylus and propodus. (See fig. 2, *s*.) A seta was dissected from the propodus before a molt occurred. (See fig. 2, *t*.) It tapers from a truncated base to the distal extremity, which

is slightly curved. Numerous fine hairs occupy one border, and similar but fewer ones are borne on the opposite side. Each seta is provided with a sheath, which when intact prevents the hairs from becoming erect. When the sheath is ruptured by dissecting needles (fig. 2, *t*) or the seta thrust out through the tip of the dactylus or propodus on molting, the hairs assume a more erect position.

The suggestion of Calman (12) that mutilation and regeneration may account for the morphological difference between the chelipeds of *Atya* and *Ortmannia* has not been given a thorough experimental test up to the present time.

In preliminary work on mutilation and regeneration of chelipeds in *Ortmannia henshawii* I observed that adult specimens originally having long palms, that is, relatively short dactyli, after a molt usually possessed short palms and relatively long dactyli. This frequent shift of the point of articulation of dactylus and propodus led me to undertake a quantitative study of the effect of mutilation in both *Ortmannia henshawii* and *Atya bisulcata*.

Experiments were carried on in which 1, 2, 3, or all 4 chelipeds were removed. In some specimens the anterior pair of chelipeds only was detached, in others the posterior pair. In some the chelipeds on the right side were removed and in others those on the left side.

My early results clearly showed that the regenerating chelipeds of adult specimens of *Atya bisulcata*, following a molt, did not always assume the form of the original appendages, but frequently appeared as in a typical example of *Ortmannia henshawii*. The change included an elongation of the carpi of the second pair of chelipeds, and a shortening of the dactyli and of the setae borne at the tips of the pincers. A long series of experiments fully established the fact that *Atya bisulcata* may revert to the *Ortmannia* form after the first molt following mutilation of the chelipeds. (See fig. 4, *a, b*.) It was also shown that age is an important factor in this reversion. In a lot of 50 young specimens, 20 to 25 mm. in length, approximately 75 per cent were converted into typical examples of *Ortmannia henshawii* following the mutilation of all chelipeds. One lot of 6 young specimens all reverted to the *Ortmannia* form on the first molt after mutilation. Older specimens, as females 50 mm. in length, are not transferred into *Ortmannia henshawii* with the same readiness as are younger ones. It is obvious that through age the specialized character of the cheliped of the *Atya* form reaches a greater stability, which the stimulus of mutilation does not readily overcome.

Similar experiments with specimens of *Ortmannia henshawii* showed that a transformation of this form into typical examples of *Atya bisulcata* may result from the mutilation and regeneration of chelipeds. (See fig. 4, *c, d*.) This change, however, occurs more frequently in adults than in young specimens. Among 125 adult specimens, approximately 10 per cent shifted from

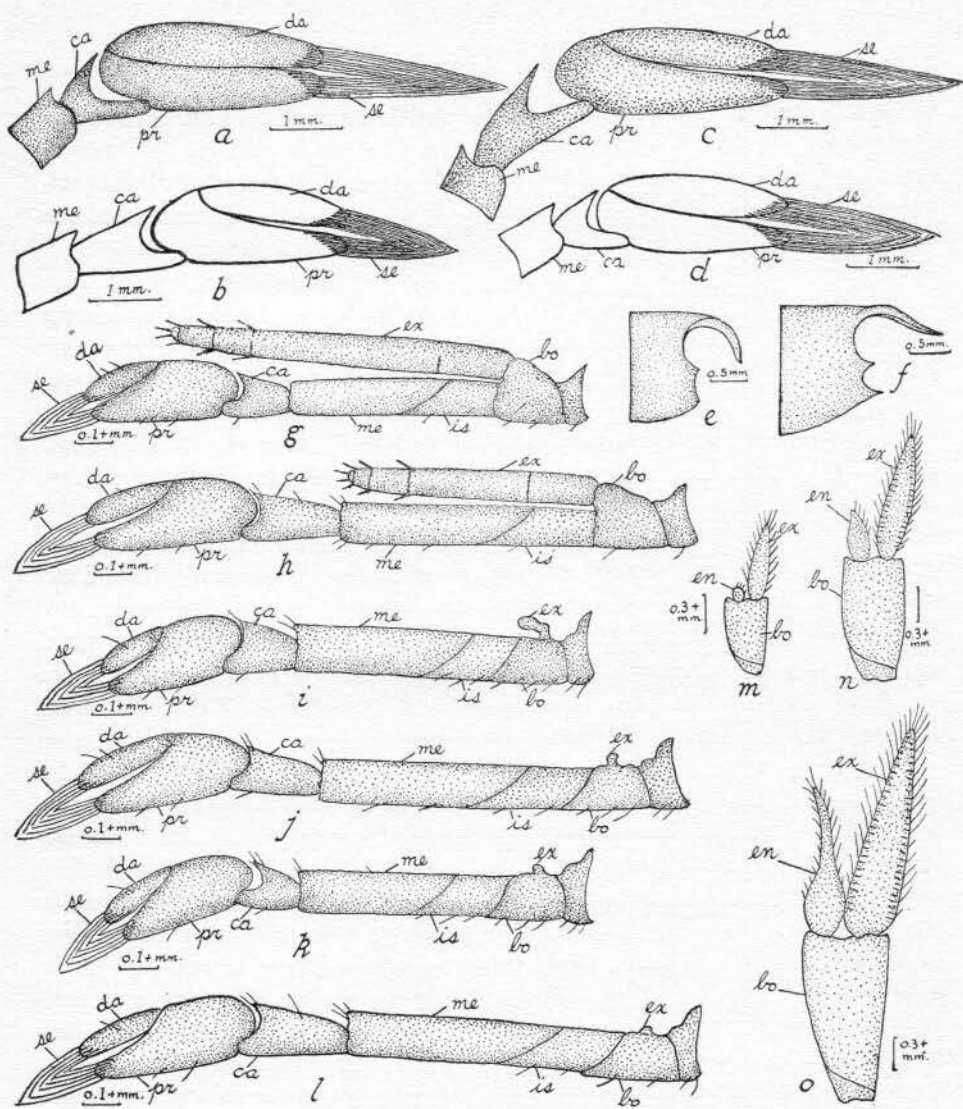


FIGURE 4.—Morphological changes in chelipeds following mutilation (a-d) and larval development (e-o) in Atyidae (unshaded areas of chelipeds represent regenerated portions of appendages). a, b, Conversion of *Atya bisulcata* into *Ortmannia henshawi* by mutilation of chelipeds: a, extremity of second right cheliped of *Atya* before mutilation; b, the same appendage after the first molt following mutilation, showing conversion to the *Ortmannia* form. c, d, Transformation of *Ortmannia henshawi* into *Atya bisulcata* through mutilation of chelipeds: c, second right cheliped of *Ortmannia* before mutilation; d, the same appendage following the first molt after mutilation, showing the *Atya* form. e, f, Form of rostrum and front margin of carapace of young specimens: e, specimen one month old; f, specimen four months old. g-l, First and second left chelipeds of a young specimen hatched from *Atya bisulcata*, showing disappearance of exopodites: g, h, first and second chelipeds, respectively, of a specimen about five days old, after molt of May 22; i, j, the same after molt of June 3; k, l, the same after molt of June 11. m-o, Development of swimmerets of a young specimen: m, posterior surface of first left swimmeret of specimen 8 mm. long; n, the same when the specimen has reached a length of 14.5 mm.; o, the same when the specimen has attained a length of 16 mm., the male characteristic now being indicated. (bo, Basopodite; ca, carpus; da, dactylus; en, endopodite; ex, exopodite; is, ischium; me, merus; pr, propodus; se, setae.)

the *Ortmannia* form into that of *Atya* on the first or second molt after mutilation.

A large series of specimens illustrating the transformation of *Atya bisulcata* to *Ortmannia henshawii* and vice versa are among the collections of the Bernice P. Bishop Museum.

The completeness of the change from one form to the other depends upon the number of chelipeds removed. I have developed specimens in which the anterior pair of chelipeds is as in *Atya* and the posterior pair as in *Ortmannia* and vice versa. Specimens have also been produced with chelipeds typical of *Atya* on one side and of *Ortmannia* on the other. The unique specimens noted by Calman (p. 7) and by me (p. 7) may be accounted for, in the light of my experiments, by the loss in each specimen of a single appendage, which on regeneration failed to assume the form of the other three.

The change from one form to the other, when it occurs, usually follows the first molt after mutilation. Occasionally, however, only a transitional form results, and a second mutilation is necessary to obtain a complete conversion. Most specimens, after such a transformation, remain true to the acquired form of cheliped through successive molts. My records show, however, some examples in which the change was temporary. Specimens of *Atya bisulcata* have reverted to *Ortmannia henshawii* on the first molt following mutilation and returned to the *Atya* form after the next molt, whether preceded by mutilation or not. This observation only emphasizes the plasticity of the organisms and points to the possibility of a shifting back and forth from one form to the other in the natural course of molting.

Because experimental mutilation obviously stimulates a modification in the form of the chelipeds, the chance of the animals losing these appendages in their natural environment is an important consideration. Although the ready detachment and rapid regeneration of the chelipeds indicate that accidents may be encountered, these appendages are well protected from injury and loss. The walking legs immediately posterior to the chelipeds are larger and stronger than those appendages and serve as a shield to them. When disturbed, the animal holds the chelipeds straight forward, parallel with and close against the third maxillipeds, in which position they are well protected.

Among more than 1,000 adult specimens examined directly after having been taken from their native habitat, less than 1 per cent showed recent mutilation of chelipeds, and evidently none had lost more than 2 chelipeds at the same time.

During molting of adults, one or more chelipeds are occasionally pulled off, but mutilation from this cause, under laboratory conditions, usually occurs in specimens physically weakened by lack of food or by having been kept in unnatural situations for a long time. Appendages are occasionally injured or destroyed by enemies. In a small aquarium a female had 2 chelipeds torn

off in fighting with a male. Another specimen when taken from its natural habitat had the palms of 2 chelipeds severed transversely near the middle. That adult specimens may lose their chelipeds from various causes is clearly shown, but quantitative studies indicate that mutilation of these appendages is of rare occurrence among mature individuals.

Among young shrimps, however, chelipeds are more frequently mutilated during molting than in the adult stage. In an experiment, 100 young specimens, ranging in age from 10 days to about 4 months, were isolated, each in a container by itself. From 25 of these specimens the second pair of chelipeds was removed at the beginning of the experiment and after each successive molt. The experiment continued 6 weeks, the specimens molting from 1 to 4 times. Of the 75 normal animals 7 were self-mutilated while molting, 4 of them losing all chelipeds at the same time. Fifteen specimens died in the process of molting, all of them being very young individuals. Of the 25 experimentally mutilated specimens 8 showed complete restoration of chelipeds, at one time or another during the observation, without the intervention of a molt. My observations show that the chance of self-mutilation during molting is many times greater among young specimens than among adults.

To determine the probability of a change of form of chelipeds in young specimens, 152 young *Ortmannia henshawi*, ranging in length from 8 to 15 mm., were isolated from each other and observed during a period inclusive of from 1 to 8 molts. The second pair of chelipeds was removed from 51 specimens at the beginning of the experiment and from 25 of these after each successive molt.

In none of the specimens was there a complete transformation from the cheliped of the *Ortmannia* form to that of the *Atya* form. Experimental mutilation obviously had no influence in causing a shift in the form of the appendages of these specimens. One individual, however, of the unamutilated number, after the first molt was changed from a typical *Ortmannia* into a form near *Atya*. The dactyli and setae became lengthened, and the carpi of the second pair of chelipeds became shortened, indicating a transition toward *Atya bisulcata*. Unfortunately this specimen, which was one of the older individuals, died directly after molting.

It is clearly shown that young specimens are held closely to the *Ortmannia* form, the younger the individual the more intimate this relationship. Mutilation exerts a lesser influence in advancing the cheliped of the *Ortmannia* form to the *Atya* form in young specimens, at least under 4 months of age, than in older ones.

All my experiments show that *Ortmannia* is the basic form, which is in accord with the view of Bouvier (4-10). I cannot agree, however, with that investigator in his assumption that *Atya bisulcata* is a fixed species. It would seem that these two Hawaiian forms represent a single dimorphic

species with variations ranging from the basic *Ortmannia* to the highly specialized *Atya*.

A young male specimen of the *Atya* form, 24 mm. long, was isolated in a container of circulating water and unobserved for 2 months, when the animal was found dead and partially decomposed. The carpi of the second pair of chelipeds were, however, intact and elongated as in a typical example of *Ortmannia*. Sufficient time for 3 molts had elapsed but whether mutilation of the chelipeds occurred, acting as a stimulus for the change of form, is not known.

It is clearly shown that mutilation followed by regeneration may produce not only a "partial regression" as indicated by Bordage (2) but a shift from one form of cheliped to the other, a complete progression as well as a complete regression. A shuttling back and forth in the form of the chelipeds in the same individual, which may be accomplished experimentally and probably occurs normally, points strongly to *Atya bisulcata* and *Ortmannia henshawi* as being highly plastic forms but differing from each other neither generically nor specifically.

An analysis of the collection from Hilo, Hawaii (p. 7), showed that of the 1,300 specimens of *Ortmannia henshawi* 899 ranged in length from 15 to 30 mm. and of the 465 specimens of *Atya bisulcata* 185 came within these measurements. A large proportion of small specimens, in a wild state, seem to be of the *Ortmannia* form, an observation that is in accord with my experimental results that the young are all like *Ortmannia* at first (p. 28) and are not readily transformed into the *Atya* form within the first few months. Of the 185 specimens of *Atya bisulcata* in the Hilo collection, between 15 and 30 mm. in length, few are less than 20 mm. long. It is probable that the fluctuation from *Ortmannia* to *Atya* occurs most readily after the animals have reached a length of about 20 mm. and are from 9 to 12 months of age.

Of the 6 species of *Ortmannia* recorded by Bouvier (10) 4 have no associated species of *Atya* among the collections, and of 12 known species of *Atya* 10 have been reported unaccompanied by *Ortmannia* forms. Bouvier (4) is of the opinion that if *Ortmannia* is alone it has not developed a superior form and if *Atya* is found unassociated with *Ortmannia* the latter has disappeared. I would suggest the possibility, however, of both forms existing in localities where but one has previously been taken, especially where the number of specimens collected has been small. More extensive collecting in certain regions is necessary, I believe, to ascertain whether species of *Ortmannia* or *Atya* exist alone.

I received 63 specimens of Atyidae from the Marquesas, collected by Simeon Delmas. They were sent in 3 separate lots, the first 2 of which consisted wholly of specimens of an undescribed species of *Atya*. The last

lot numbered 35 specimens, of which 33 were similar to those of the previous lots. Two young individuals were typical *Ortmannia* as to the hands, but the carpi of the second pair of chelipeds were no longer than those of the first. In all features except size and form of hands the 2 specimens resembled their associates.

The discovery of *Ortmannia* forms among specimens from the Marquesas is in line with Bouvier's (11) prediction that *Atya serrata* and *Atya bisulcata* may not be the only species with which *Ortmannia* is associated. I am of the opinion, however, that the specimens like *Ortmannia* from the Marquesas represent intermediate forms and that more complete investigations would show that their associates like *Atya* do not represent a fixed species but give rise to young basic forms like *Ortmannia*.

The adult specimens from the Marquesas are identical with a female taken with 17 specimens of *Atya moluccensis* in Fiji by Harry S. Ladd, in August, 1928.

THE MOLTING PROCESS

Molting is a critical process in the life of the Atyidae. If laboratory conditions simulate their natural environment, even in a slight degree, the shrimps probably experience a high rate of mortality during the process of molting.

It has been shown (p. 25) that approximately 15 per cent of young specimens died while molting, during a period of 6 weeks. Many individuals die within a few hours after molting, and though their death cannot be positively ascribed to the effects of molting, the evidence is strongly in its favor. Fewer adult specimens than young die while molting. In efforts to free itself from the old skin the animal may rupture a vital organ, resulting in immediate death, or be injured to such an extent that death may shortly follow.

Self-mutilation of the chelipeds often occurs in young shrimps during the molting process. (See p. 25.) At this time adults, also, may lose their chelipeds, but this rarely takes place under natural conditions. (See p. 24.)

Intervals between molts vary greatly in both young and adult specimens. Young individuals, however, molt more frequently than do adults. Among 62 young specimens of *Ortmannia henshawi*, ranging in age from 6 days to 4 months, extending over a period of from 2 to 8 molts, the average interval between molts was 11.1 days, with a range from 2 to 25 days. In one specimen 6 days old at the beginning of the experiment, the intervals between successive molts were 5, 7, 8, 7, 9, 5, and 5 days. In another specimen of the same age the intervals were 9, 5, 8, 22, 17, and 10 days.

The average interval between molts in adults was 22.6 days, based on 123 specimens over a period of from 2 to 4 molts. The interval range was from 11 to 48 days.

Altered conditions of salinity and temperature, if extreme, greatly affect molting. (See pp. 11-15.) Deprivation of food does not seem to influence the time interval between the first 2 or 3 successive molts but eventually retards or inhibits molting.

THE LARVAL DEVELOPMENT

With the announcement of Bordage (1) that the young of *Atya serrata* were all like *Atya* and that *Ortmannia alluaudi* gave rise to young specimens of both *Atya* and *Ortmannia*, the mutation theory of Bouvier (6) seemed to be verified experimentally, in so far as those forms were concerned.

To give greater weight to this hypothesis, however, experiments similar to those conducted by Bordage in the island of Reunion were carried on in Mauritius with *Caridina richtersi* and *Ortmannia edwardsi*, which are closely associated ecologically. Bouvier and de Charmoy (9), reporting the results of these experiments, found them to be in accord with those of Bordage and entirely supporting the mutation hypothesis. The young of *Caridina richtersi* were of two kinds, one like the parent and the other like *Ortmannia edwardsi*. The young of *Ortmannia edwardsi*, however, were all like that species.

From the results announced a complete progressive evolution by mutation was now apparently clearly established in theory and by experiment. The course of development obviously was from *Caridina* to *Ortmannia* and from *Ortmannia* to *Atya*. According to this view, species of *Atya* have become fixed, breeding true.

With the purpose of paralleling the work of Bordage I began an extensive series of experiments, rearing larvae from the eggs of *Atya bisulcata* and *Ortmannia henshawii*.

A swift current of water is necessary for the proper development of these forms. In aquaria without circulating water eggs may hatch into the zoea stage, but further metamorphosis rarely occurs. Under a strong current the zoea stage seems to be passed in the egg, as the young forms when released from the swimmerets are mysis-like. At this stage the young shrimp is about 6 mm. in length, having a short rostrum curving sharply downward, and chelipeds which bear exopodites as do all of the walking legs.

The larvae, like adults, exhibit a strong negative phototropism and are very secretive in habits. A positive rheotropic response enables them to creep against a strong current of water, and although capable of swimming they are usually in contact with a surface or support.

From the first ovigerous female specimen of *Atya bisulcata* under observation, 32 larvae were hatched and examined. The most significant feature about them was that they were not *Atya*-like but each resembled a young specimen of *Ortmannia henshawii*. The dactyli of the hands and the setae

of the tips of the pincers were short, and the carpi of the second pair of chelipeds were long. (See fig. 4, *g-l*.) Subsequently from about 25 female specimens of *Atya bisulcata*, taken at different times of the year and from various localities on Oahu, I have reared more than 1,000 young shrimps and examined each individual. Shortly after being hatched none has resembled its maternal parent but possessed the typical cheliped of *Ortmannia henshawii*.

Larvae were also reared from the eggs of female specimens of *Ortmannia henshawii*. From 4 specimens 139 larvae were obtained. All possessed chelipeds typical of their parents. An ovigerous female intermediate in form between *Ortmannia henshawii* and *Atya bisulcata* gave rise to *Ortmannia* larvae.

My experiments on regeneration and larval development show that the form called *Ortmannia henshawii* is the basic one, and that the one known as *Atya bisulcata*, by its reversion to the basic type, does not breed true and is not a fixed species. The evidence is sufficient to conclude that the generic or specific separation of the two forms cannot be sustained. It follows, therefore, that the generic term *Ortmannia* as applied to Hawaiian species should be discontinued, the name *Atya bisulcata* (Randall) taking precedence.

Although these conclusions are at variance with those of Bordage (1), I do not assert that his observations were erroneous. It is not impossible that *Atya serrata* may have reached the status of a true species by mutation, while the Hawaiian form, not equally advanced, exhibits only dimorphism, a fluctuation of environmental incitement attained during the life of the individual without sufficient germinal influence to prevent a return to the basic type in reproduction. Yet the close resemblance of the Hawaiian forms to *Atya serrata* and *Ortmannia alluaudi* leads one to believe that their phylogenetic development has reached a similar stage. More complete experimental investigations, however, not only on the species serving as the basis of Bordage's conclusions but on allied ones wherever they exist, would do much to define the relationship of members of the Atyidae.

Many efforts were made to interbreed the two Hawaiian forms but without success. Bordage (3) reported that the sexes of *Ortmannia alluaudi* readily mated but that he did not succeed in getting this form to breed with *Atya serrata*. I do not consider the failure of the crossing of the Hawaiian forms significant, as all attempts to mate the sexes of *Atya bisulcata* and also those of *Ortmannia henshawii*, under laboratory conditions, were equally unsuccessful.

It seems to me very probable that, under natural conditions, a general interbreeding of these forms does occur. Because of the disparity of the sexes (p. 7), it is likely that the males of the *Ortmannia* form mate with the females of *Atya*.

Reproduction is not a seasonal phenomenon, as ovigerous females of both forms may be taken during every month of the year. The smallest ovigerous females I have collected were 25 mm. in length. It would seem that breeding does not begin among the shrimps until they are more than one year of age.

In the mysis stage of the young shrimp the thoracic appendages bear exopodites which diminish in size from the first pair of chelipeds to the last walking legs. Those of the chelipeds (fig. 4, *g, h*) are stout and in the first pair reach almost to the tip of the pincers. Usually by the time the animal is from 15 to 20 days old and 2 or 3 molts have occurred, the exopodites are reduced to rudiments. (See fig. 4, *k, l*.) Another morphological change which marks the transition of larva into adult is the gradual straightening of the rostrum, which assumes the mature position about the fourth month. (See fig. 4, *e, f*.)

In both *Ortmannia henshawi* and *Atya bisulcata* the adult sexes may be distinguished by the first pair of swimmerets. (See p. 8.) For the first 2 or 3 months, however, while the specimens are attaining a length of from 8 to 12 mm., it is impossible to distinguish the sexes by these appendages. In a specimen 8 mm. long the endopodites are minute, rounded lobes. Not until the animal has reached a length of about 16 mm. and is about 4 months old do the first swimmerets become sufficiently differentiated to serve as sex indicators. (See fig. 4, *m-o*.)

ASSOCIATES OF THE ATYIDAE

Experiments were conducted with other animals inhabiting the mountain streams of Oahu to ascertain if there were enemies of Atyidae among them and to determine, if possible, whether other organisms may have been a factor in driving the shrimps from the lower levels near the sea to higher altitudes. Animals associated with the Atyidae in Hawaii, at the present time, include other crustaceans, larvae of insects, fishes, and frogs. Few of these are endemic, and most of them are comparatively recent immigrants.

A native decapod, *Bithynis grandimanus*, much larger than the Atyidae with which it associates, lived peaceably with specimens of *Atya bisulcata*, under laboratory conditions. Specimens of endemic gobies which ascend the mountain streams made no attempt to molest larvae or adults of Atyidae when confined with them in small aquaria. The stomach contents of one of these fishes when taken from the mountain stream consisted of filamentous algae, among which was a larva of a midge. It seems clear that the gobies are not enemies of the shrimps. Dragon-fly nymphs are common inhabitants of the mountain streams. A very large one attacked and almost instantly killed an adult shrimp when the two were released in a small container of water. Adult frogs (*Rana rugosa*), associates of the Atyidae, showed no disposition to destroy young or old shrimps with which they were confined 12 days without food. The shallow streams and standing water of the lowlands of Hawaii are well stocked with "top minnows" or mosquito fish. Experiments showed that the Atyidae could not long maintain themselves in the presence of these fishes. Young shrimps, from 6 to 12 mm. in length, were devoured at once when introduced into aquaria with the minnows. The fishes perceived the movements of the shrimps and attacked from a distance as great as 30 cm.

The Atyidae of the mountain streams of Hawaii obviously have few enemies among native or introduced associates, and general observations indicate that they are in no danger of extermination. Accommodation of the Atyidae, now inhabiting the higher altitudes, to the lowland waters in Hawaii would, at the present time, be prohibited by competition with the mosquito fish, if other conditions were favorable. The recent introduction of these fishes does not, however, explain the natural adaptation of the shrimps to the cool waters of mountain habitats. My experiments seem to show that the chief factor limiting their lower altitudinal distribution is temperature.

MEANS OF DISPERSAL

The extreme age conceded to the family, the extensive geographical distribution of certain of its representatives, and the localization of others offer opportunity for speculation on the probable means of their dispersal.

It is to be assumed that the primitive representatives of the family had a single center of origin, probably in an environment of brackish water, from which invasions of fresher water gradually took place. Where the Atyidae had their beginning and by what means their wide dispersal was accomplished at such an early period as to make possible the high degree of specialization reached is unknown.

That a moist environment is essential to the prolonged life of the Atyidae is obvious. My experiments showed that both young and adults of *Atya bisulcata* die within 8 hours in the air out of water. Under laboratory conditions, the shrimps have a disposition, however, to creep out of water if opportunity permits. This indicates the possibility of short voluntary migrations from one stream to another within very limited distances. An extended transportation, voluntary or involuntary, through the air out of water would be fatal to the life of the animals.

My laboratory experiments (p. 11) showed that normal sea water is quickly fatal to the shrimps. It was shown, however, that they are capable of enduring slightly saline media for several months, the young being more readily accommodated to some degrees of salinity than the adults. (See p. 11.) It is obvious that the Atyidae could not be successfully transported alive for any considerable distance if submerged in sea water or frequently moistened by it. Their dispersal, therefore, must have occurred under conditions insuring a moist environment, the moisture being due to fresh water or but slightly saline water.

The eggs of Atyidae, being attached to the swimmerets of the females until hatched, are capable of being distributed only as the animals voluntarily move about or are transported.

Involuntary dispersal of some aquatic animals, as mollusks and insects, has been accounted for by their being imbedded in mud attached to the feet of migratory birds. It is improbable that specimens of *Atya bisulcata* could be successfully transported long distances in this manner. As the shrimps do not inhabit mud it is unlikely that they would be picked up on the feet of wading birds, but if so they would not long survive. I imbedded a series of young shrimps, 8 to 10 mm. long, in pellets of soft mud and examined them at intervals of 15 minutes. None of the specimens survived one hour, and most of them died in 30 minutes, probably from lack of oxygen. It is less likely that adults could be picked up and successfully carried on the feet of birds.

From the secretive habits of the Atyidae it can readily be understood how their dispersal may be accomplished by human migrations, being carried in fresh water or among moist plants. An endemic species, however, as *Atya bisulcata* in Hawaii, indicates a residence for a very long time. Agents more ancient than early man must have been responsible for the immigration of such forms. What these agents were is problematical.

SUMMARY AND CONCLUSIONS

1. Adult forms of Atyidae known as *Ortmannia henshawi* Rathbun and *Atya bisulcata* (Randall), now inhabiting the mountain streams of Hawaii, die within 12 hours when transferred directly to sea water. Most young specimens die within 4 hours.

2. Young and adult specimens live several months in media consisting of equal parts of fresh water and sea water. In solutions of lesser proportions of sea water young specimens show a greater degree of accommodation than adults.

3. Temperature of 35°C. kills both young and adult shrimps almost instantly, but on constant subjection to temperatures ranging from 12°C. to 14°C. they may live about 8 days. On sustained subjection to 30°C. or to temperatures ranging from 15°C. to 18°C. both young and adults may live at least 60 days. Optimal thermal conditions range from approximately 20°C. to 26°C.

4. Regeneration of chelipeds is retarded by solutions of greater salinity than 3 parts of fresh water to 1 part of sea water, the inhibition becoming more pronounced with increased salinity. On constant subjection to 30°C., or temperatures ranging from 15°C. to 18°C., regeneration is usually retarded and molting often inhibited.

5. Ultraviolet rays of a Cooper Hewitt 110-volt Uviarc lamp apparently retard regeneration of chelipeds under various conditions of illumination, especially when the ventral surface of the animal is irradiated. Rays falling upon the dorsal surface of the animal have little influence unless the specimen is brought near the arc.

6. Water ranging from pH 8 to pH 9 seems to represent the most favorable condition for the regenerative processes of these animals. The higher levels of the streams of Manoa Valley, Oahu, where shrimps abound, show a greater degree of alkalinity than points nearer the sea.

7. In adult specimens, chelipeds after mutilation normally regenerate to a length of about 3 mm. in from 8 to 12 days and assume the adult form immediately after the next molt. The regenerating chelipeds of the form *Atya bisulcata* pass through phases resembling those of *Ortmannia henshawi*. Chelipeds in young specimens are often completely re-formed after mutilation before the next molt. Seldom does this occur in adults.

8. The form *Atya bisulcata* may be converted into that of *Ortmannia henshawi*, as a result of mutilation and regeneration of chelipeds. Young specimens are thus transformed more readily than adults. In a similar manner the form *Ortmannia henshawi* may be converted into that of *Atya bisulcata*, the change occurring more often in old than in young specimens. Although mutilation of chelipeds in adults seldom occurs under natural con-

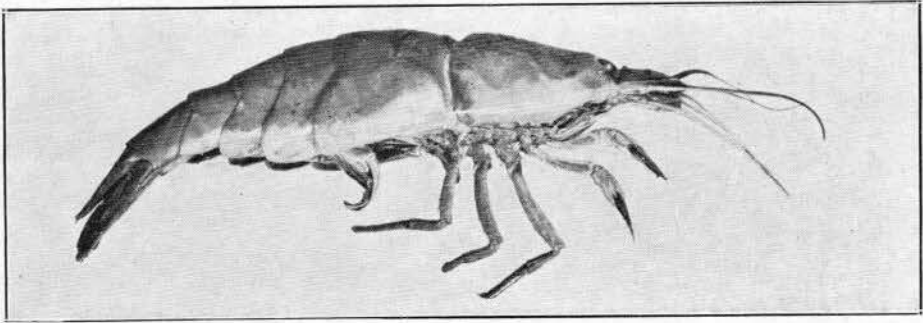
ditions, the presence of forms intermediate between *Ortmannia henshawi* and *Atya bisulcata* as well as laboratory observations indicate that transition from one form to the other may take place without mutilation.

9. All young specimens hatched from the eggs of *Atya bisulcata* and *Ortmannia henshawi* resemble the latter at first. Some seem to be converted into the *Atya* form, following molts in the normal course of development, and occasionally others are transformed as a result of mutilation.

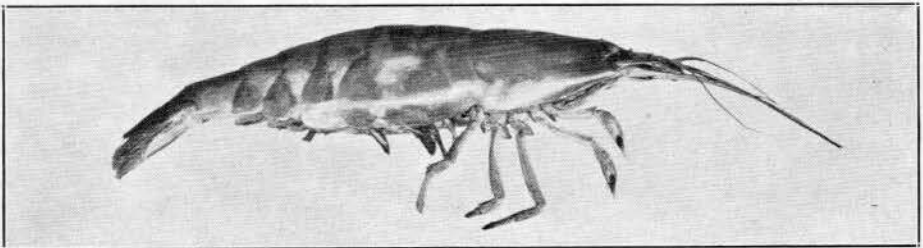
10. The unity of the two forms *Ortmannia henshawi* and *Atya bisulcata*, as shown by regeneration and reproduction, is convincing evidence that the latter is not a fixed species. No generic or specific distinction can properly be made between these Hawaiian forms, and by the law of precedence both should be included under the name *Atya bisulcata* (Randall).

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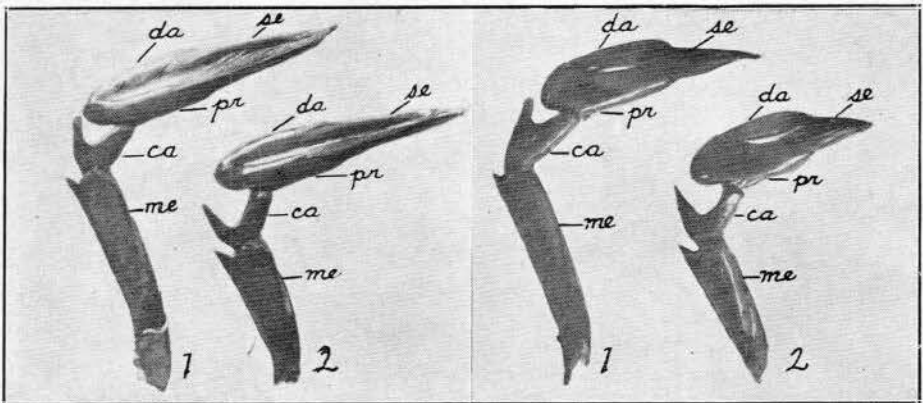
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A



B



C

D

A, B, ADULT FEMALE ATYIDAE, AFTER REMOVING CHELIPEDS AND WALKING LEGS FROM THE LEFT SIDE; A, *ATYA BISULCATA* (RANDALL); B, *ORTMANNIA HENSHAWI* RATHBUN. C, D, CHELIPEDS FROM THE RIGHT SIDE OF TYPICAL SPECIMENS; C, *ATYA BISULCATA*; D, *ORTMANNIA HENSHAWI*: 1, SECOND CHELIPED; 2, FIRST CHELIPED; CA, CARPUS; DA, DACTYLUS; ME, MERUS; PR, PROPODUS; SE, SETAE.