

Aloha Also Means Goodbye: A Cryptogenic Stomatopod in Hawaii¹

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ABSTRACT: Two different scenarios are presented that could account for the recent appearance of what has become the most common shallow water *Gonodactylus* in Hawaii. One requires an introduction event, the other posits the lack of discovery of the species until the early 1950s. While both scenarios have historical components and are difficult to falsify, some corollary hypotheses are suggested that would allow a testable differentiation of the two viewpoints.

THE PHENOMENON OF SPECIES introductions was eloquently brought to the attention of ecologists by Elton (1958) in his book on the ecology of invasions. More recently the life history features and the genetics of species which are characteristic invaders have been discussed (Baker and Stebbins 1965). Some have thought to use interactions of introduced species with indigenous forms to test various ecological theories (Simberloff 1981). Obviously systematists and biogeographers must take into account the fact that species introductions, along with other anthropogenic alterations in isolated areas, are accelerating in number and intensity and that the appearance of a previously unrecorded species will necessitate an inquiry into its history.

A case in point is illustrated by two opposing scenarios: (1) Kinzie (1968) and (2) Manning and Reaka (1981), concerning a stomatopod crustacean of the genus *Gonodactylus* which was first noted in Hawaii in the early 1950s. At that time this species was the only large stomatopod found occupying cavities in dead coral heads in Kaneohe Bay (Kinzie 1968). The two scenarios differ in three main aspects which are discussed below.

SPECIFIC IDENTITY

Scenario 1 holds that the Hawaiian form was introduced from the Philippines. The Hawaiian population according to this

scenario is identical with the stomatopod known as *Gonodactylus falcatus* (Forskål, 1775) in the Philippines (Garcia 1981). This species was originally described from the Red Sea.

Scenario 2 holds that the Hawaiian form is a new and endemic species, *Gonodactylus aloha* Manning and Reaka, 1981.

Morphometrics

Manning and Reaka state (1981:196):

It is extremely difficult to characterize *G. aloha* as well as to distinguish it from *G. falcatus* on morphological grounds alone.

That the Hawaiian form is morphometrically indistinguishable from *Gonodactylus falcatus* is borne out by a discriminant function analysis of the lengths of seven body parts (see Table 1 for a list) made on specimens collected from five geographic locations, based on data from material collected or borrowed from museums for my 1968 paper. These particular measurements were chosen for the earlier study; however, a reanalysis of these data was carried out for this paper. Of the 103 Hawaiian specimens, almost 20 percent were incorrectly assigned to geographic locations (Table 2). A canonical discriminant function analysis gave Mahalanobis distances and probabilities shown in Table 3. There is clearly no evidence from these analyses that the Hawaiian form differs, in the characters measured, from the Philippine *G. falcatus*. This supports Manning and Reaka's statement about the difficulty in characterizing *G. aloha* on morphological grounds.

¹ Manuscript accepted 12 June 1984.

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TABLE 1
MEANS (± 1 S.D.) FOR THE SEVEN BODY PARTS WHICH WERE MEASURED FOR THE ANALYSIS IN TABLE 2

	CARAPACE LENGTH	PROPODUS LENGTH	ROSTRUM WIDTH	TELSON WIDTH	DACTYLUS LENGTH	TELSON LENGTH	ROSTRUM LENGTH
Hawaii ($N = 103$)	9.25 \pm 3.20	6.79 \pm 2.41	2.69 \pm 0.77	5.69 \pm 1.99	6.41 \pm 2.26	5.77 \pm 1.94	2.66 \pm 0.64
Lord Howe Island ($N = 50$)	12.91 \pm 2.73	9.40 \pm 1.97	3.65 \pm 0.59	8.66 \pm 1.72	8.94 \pm 1.90	8.34 \pm 1.65	3.40 \pm 0.46
Philippines ($N = 12$)	8.20 \pm 3.37	6.00 \pm 2.42	2.66 \pm 0.86	5.18 \pm 2.11	5.69 \pm 2.29	5.36 \pm 2.12	2.65 \pm 0.83
Queensland ($N = 46$)	9.09 \pm 3.01	6.66 \pm 2.18	2.61 \pm 0.71	5.87 \pm 1.90	6.38 \pm 2.10	5.71 \pm 1.72	2.64 \pm 0.58
Red Sea ($N = 41$)	10.58 \pm 2.76	7.99 \pm 1.93	2.96 \pm 0.56	6.69 \pm 1.60	7.50 \pm 1.74	6.81 \pm 1.66	2.92 \pm 0.46

TABLE 2

PERCENTAGE OF 103 SPECIMENS OF HAWAIIAN
Gonodactylus ASSIGNED TO FIVE GEOGRAPHIC LOCATIONS
FROM WHICH COLLECTIONS WERE AVAILABLE*

LOCATION	PERCENTAGE
Hawaii	81.55
Queensland	2.91
Red Sea	9.71
Lord Howe Is.	1.94
Philippines	3.88

* Discriminant function analysis SPSS. Prior probabilities set equal to sample size. Almost 20% of the Hawaiian specimens were incorrectly assigned.

In their discussion, Manning and Reaka (1981:196) suggest some other morphometric features that may differ between *Gonodactylus falcatus* and *G. aloha*:

(a) Rostral plate usually broader than long in *Gonodactylus falcatus* but usually longer than broad in *G. aloha*. The specimens from the Red Sea agreed with their characterization of *G. falcatus* with 63 percent having rostral length : breadth ratios less than one. The Hawaiian form had length : breadth ratios greater than one in 52 percent of the specimens, which is also in agreement with the characterization of Manning and Reaka. The Philippine specimens were similar to the Hawaiian ones in that they had length : breadth ratios greater than one in 64 percent of the specimens. However, in none of these collections are the ratios significantly different from 50 : 50 (chi square test $\alpha = .05$).

(b) Telson usually about as broad as long in *Gonodactylus falcatus* but usually broader than long in the Hawaiian form. The specimens from the Red Sea differed significantly from a 50 : 50 ratio with 60 percent of the individuals having telsons that were longer than broad. This was also true for 70 percent of the Hawaiian specimens which were highly significantly different from a 50 : 50 ratio, and in a direction opposite to that suggested by Manning and Reaka. The specimens from the Philippines had 64 percent of the specimens with telson length : breadth ratios greater than one, but this collection did not differ significantly from a 50 : 50 ratio.

At any rate the use of ratios can cause further analytical problems (see Atchley 1978), especially as the relative proportions of some body parts vary with age in stomatopods.

Color

Manning & Reaka (1981:196) state that color is an important diagnostic character:

More convincing evidence of the distinctness of the Red Sea and Hawaiian populations previously identified with *G. falcatus* lies in the color in life of specimens from the two areas.

While Manning and Reaka list several color differences, they apparently failed to use any sort of color standards (e.g., Wilson 1941), so the usefulness of their extensive discussion of color is questionable. While they may, in fact, be able to differentiate specimens from different areas, the utility of this character in defining the species, as well as its usefulness to other workers, is of little value.

In order to test the applicability of such subjective color judgments, an experiment was performed using living specimens of *Gonodactylus* from Kaneohe Bay, the type locality of *G. aloha*. These animals were collected in 1983 for this study. Twelve graduate students with no knowledge of the Manning and Reaka paper or of the colors associated with the Red Sea and Hawaiian forms were asked to name the color of six body parts selected from Manning and Reaka as being most diagnostic of the differences between the two forms. The wide range of variability between individual observers and between different specimens makes unequivocal assessment of the color patterns difficult. The results are shown in Table 4. Clearly, such subjective color evaluations are useless in establishing a new species.

With regard to differentiating between the two scenarios a comparison between living Hawaiian and Philippine forms would of course be the most appropriate, but this was not possible.

Larvae

Manning and Reaka (1981:197) suggest that differences between larval stages may differentiate the two forms:

TABLE 3

MATRIX OF MAHALANOBIS DISTANCES AND ASSOCIATED PROBABILITIES OF DISTANCES FOR THE FIVE COLLECTIONS*

	HAWAII	LORD HOWE IS.	PHILIPPINES	QUEENSLAND	RED SEA
Hawaii	—	0.00	.8163	.0001	.0065
Lord Howe Is.	3.492	—	.001	.0000	.0000
Philippines	1.732	3.321	—	.0000	.0000
Queensland	1.542	2.653	2.467	—	.0000
Red Sea	1.331	3.128	2.394	1.505	—

* Canonical discriminant function analysis SAS. Values below diagonal are Mahalanobis distances between samples. Values above diagonal are the associated probabilities. The analysis suggests that the Hawaiian and the Philippine collections cannot be differentiated.

Such differences between the same larval stage from two different regions seem to us to be of far greater magnitude than might be attributable to variation within a species.

Manning and Reaka (1981:196) use five differences between Hawaiian (data from an unpublished report of mine and specimens supplied to R. B. Manning) and Red Sea (Gohar and Al-Kholy 1957) stage V larvae as "additional evidence, although incomplete, that the Hawaiian and Red Sea populations represent distinct species."

1. Rostrum exceeds antennules in the Red Sea specimens but not in the Hawaiian specimens.
2. Rostrum with five ventral spines in the Red Sea larvae, but with four in the Hawaiian form.
3. Posterolateral spines of the carapace extend to the middle of the fifth abdominal somite in the Red Sea larvae but not beyond the second abdominal somite in those from Hawaii.
4. Antennal scale with 12 marginal setae in Red Sea larvae and with 14 setae in those from Hawaii.
5. Articulation of the sixth abdominal somite with the telson is complete in larvae from the Red Sea but not in the Hawaiian larvae.

There are several problems with the analysis of larval characters given by Manning and Reaka. Comparisons using mass reared larvae (as were those studied by Gohar and Al-Kholy 1957) may be misleading since larval stages may be missed or misidentified (Williams 1982). Certainly differences in charac-

ters of larvae reared under different conditions at different locations should not be given too much significance since inconsistencies in rearing methods, temperature, food, and so on can all cause modifications in the development, timing, and recognition of larval stages (see Reese and Kinzie 1968 for some examples). Furthermore, fixation may cause swelling and thus obscure real differences or similarities in the length of body parts (see Manning and Provenzano 1963).

With regard to the specific points made by Manning and Reaka: Points 2 and 4 refer to the number of rostral spines and marginal setae of the antennal scale respectively. The ranges in these counts from two studies conducted by two different workers using very different rearing conditions is less than or equal to the range for the same body parts of *Gonodactylus oerstedii* larvae in a single experiment from the same population (Provenzano and Manning 1978, table 3). This clearly contradicts Manning and Reaka's statement (1981:197): "variation of that magnitude was not seen in larvae of that [*G. oerstedii*] species." Clearly such small meristic differences should not be used to split one species while being considered part of the normal range of variation in another.

Points 1 and 3 could well be problems of fixation or proper identification of larval stage (see above).

With regard to point 5, Provenzano and Manning (1978, table 3) indicate that the completeness of the articulation of the sixth abdominal somite in the Red Sea form is questionable.

TABLE 4

COLORS OF THE SIX BODY PARTS USED BY MANNING AND REAKA (1981) TO DIFFERENTIATE *Gonodactylus falcatus* FROM *G. aloha*

	DISTAL PROMINENCE*	WALKING: LEGS	ANTENNAL SCALE	ENDOPOD OF UROPOD	UROPOD OVERALL	POSTERIOR LINING OF ABDOMINAL SOMITE
MALES						
<i>G. falcatus</i>	brown	red	scarlet proximally blue distally	crimson or scarlet	blue or blue-green crimson setae	red
1	v	gr-pr	cl	pr	pr	t
2	dkr/pr	pk/gr	gr/bl	bl-gr	r	br/dkr-br
3	bk	r/m	br/gr/pk	r	gr/r	r-y/m
4	bk	pr/pk	gr	bl/t	pk/pr	y-br/br
5	br/bk	l	bl-gr/pk	bl/bl-gr	l	l
6	bk	pk/l	r-br/gr	gr	pk/r	br
7	bk	pk/r	pk-br/y-gr	gr/bl	r/bl-gr	br/dkgr
8	br/bk	r-br/v	r/gr	r/gr	gr/r	br/r-br
9	bk/br	v/o	gr	pk/l	pk/l	br
10	bk	o/pk	o-gr	gr/t	o/t	br/dk-gr
11	bk	pk	r-bl	pr-pk	pk-gr/bl	y-gr/lt-gr
12	bk	o/pr	y-pk	bl-gr	pk-o	gr/dk-gr
<i>G. aloha</i>	bl-gr	bl or bl-br or bl-br	m proximally lt-bl distally	p-o basically y distally	no bl	red

FEMALES

<i>G. falcatus</i>	brown	yellow	brownish proximally yellow distally	yellow w/ crimson setae	(not given)	red
1	v	r-br	br	br	lt-br	same as rest of somite
2	dk-br/bk	r	o-gr	gr	r-br	r-br/dk-br
3	br/bk	o/br	o/gr	o	o-gr	bk/o
4	br	br/o	gr/br	gr	pk/o	o
5	g	o	y-gr	bl-gr	o	o
6	bk	o/r	o/y	gr	o	br
7	bk	r	o/y	gr	r-gr	br/dk-gr
8	dk-br/v	r-br	o/y	r-o/gr	gr/r	dk-o/dk-br
9	br-bk	o-r	o/y	gr	o-r	br
10	br-bk	o/r	o-y	br-gr	gr/br	b/bk-br
11	r-bk	pk	r/y	pk	pk/y	same as rest of somite
12	bk	bl/pr	y-pk/o	bl-gr	pk/r	gr/dk-gr
<i>G. aloha</i>	bl-gr	y or y-gr (merus only)	m proximally p/o than y distally	p-o basically y distally	no bl	not red

NOTE: At the head of each part of the table is the color of the tabled body part for *G. falcatus*, then follow color evaluations made by 12 observers. At the bottom of each part is the color diagnostic of *G. aloha*. A dash (-) indicates an intermediate color, a slash (/) indicates differences between specimens. r = red, br = brown, sc = scarlet, y = yellow, bl = blue, bk = black, gr = green, o = orange, pk = pink, pr = purple, l = lavender, t = turquoise, g = grey, m = maroon, bg = bluegreen, dk = dark, lt = light, v = violet, cl = clear, t = tan.

*Manning and Reaka 1981:196.

Point 3 seems to be the most pronounced difference between the Red Sea and the Hawaiian larvae. Gohar and Al-Kholy's figures depict larvae of all planktonic stages (IV thru "VI") with long carapace spines relative to those of the Hawaiian form. Provenzano and Manning state (1978: 309): "The excessive length of the carapace spines in Gohar and Al-Kholy's stage VI larvae was not matched in Gurney's [1937] stage VI also from the Red Sea, in Kinzie's larvae from Hawaii or in our larvae of *G. oerstedii*."

Caution should be used in making the comparison of stage V larvae from the Red Sea and those from Hawaii because the stage V larvae of Gohar and Al-Kholy appeared 21 d after hatching while the stage V Hawaiian larvae ran from day 11 through day 16. This period overlaps stages III and IV of Gohar and Al-Kholy. The Hawaiian larvae reached stage VI by day 16 when the Red Sea larvae were still in stage IV. These differences in timing and length of carapace spines could be due to real differences in the larval stocks as suggested by Manning and Reaka but could equally well be due to the very different rearing conditions (see Williams 1982). Perhaps it is best to follow the caution of Provenzano and Manning (1978: 309) in their discussion of the later stage VI larvae: "The apparent differences between Kinzie's specimens and those from the Red Sea indicate that direct comparisons based on published works are unreliable."

Taking into account the adult morphological and color characters and the larval descriptions, there is little in Manning and Reaka to support the contention that the Hawaiian form is different from *Gonodactylus falcatus* and nothing at all that addresses the Philippine-Hawaiian connection set out in scenario 1.

HISTORY OF THE FORM IN HAWAII

Scenario 1 holds that the Hawaiian form is an introduced specialist species that replaced an indigenous generalist, *Pseudosquilla ciliata* (Fabricius, 1787), from part of the latter's habitat—the dead bases of corals and dead corals.

Scenario 2 holds that the Hawaiian form is native to Hawaii and that it is the habitat which is new. This scenario holds that dead corals have significantly increased in abundance in Kaneohe Bay.

The Existence of Dead Corals in Hawaii

The suggestion that dead corals were not common on Hawaiian reefs until the 1950s seems a peculiar assumption for anyone familiar with coral reefs anywhere in the world.

The fact that not only were dead corals common in Kaneohe Bay, but that patch reefs with tops of dead corals—the typical *Gonodactylus* habitat in Kaneohe Bay—were present in the early part of this century, is clear from early accounts of the bay. Writing of *Leptastrea* MacKaye (1915) states: "It spreads over the surfaces of other varieties of dead corals on both the inner and outer reefs," and of *Favia*: "It forms rather large colonies by spreading over the dead colonies of other species." MacKaye (1916) also describes a trip in a glass-bottom boat in Kaneohe Bay: "And here we come to the second reef, one which is partly dead on one side but alive on the other." Photographs as early as 1928 show the typical patch reef environments in Kaneohe Bay (Devaney et al. 1982).

Lack of Searching in the Dead Coral Habitat

It might be maintained that although the dead coral habitat existed in sufficient abundance to support the endemic stomatopod, the animal remained unnoticed until the 1950s.

It is difficult to support this contention in view of the extensive collections and publications of C. H. Edmondson who began his research in Hawaii in 1920 (Banner 1977). Edmondson was a typical biologist of his day, rarely working deeper than the shallow subtidal except with a dredge. Primarily a specialist in decapod crustaceans, he made exhaustive collections in dead and living coral heads in the intertidal and shallow subtidal (A. H. Banner, pers. comm.), as evidenced by the following:

Many [xanthid crabs] seem to be dispersed without reference to any particular environment within a given area, wandering at random seeking concealment under stones or in crevices of dead coral heads. (Edmondson 1962:216)

Type locality Waikiki reef Oahu in shallow water in a dead coral colony.... (Edmondson 1930:7)

Type locality, island of Maui, collected by Mrs. F. K. Skinner in shallow water among dead coral heads.... (Edmondson 1930:7)

Blocks of dead coral when broken into pieces, may yield some of the more unusual forms of swimming crabs which hide in the crevices of coral. (Edmondson 1959:154)

As a carcinologist, Edmondson was not likely to miss such a large, conspicuous member of the fauna. Edmondson certainly did collect other stomatopods (Edmondson 1923, Edmondson et al. 1925), and he was clearly aware of the occurrence of *Pseudosquilla ciliata* which he termed "The most common species about local shores [it] is found in shallow water under stones or in holes in dead coral blocks" (Edmondson 1933:208). Edmondson also described a very small stomatopod (*Coronida sinuosa* Edmondson 1921) less than 20 mm long from Hawaii.

In addition to the extensive work of Edmondson, the Banners began their intensive work on alpheid shrimps, common inhabitants of dead coral heads, in 1937. While countless dead coral heads were broken open in search of the alpheid shrimps, no gonodactylid stomatopods the size of *Gonodactylus falcatus* were ever seen (A. H. Banner, pers. comm.).

In addition to the work of these carcinologists in Hawaii, S. J. Townsley in 1948 began his research, which focused specifically on stomatopods. Although he found stomatopods as inconspicuous as *Coronida sinuosa*, the only large stomatopods he found in dead coral in shallow water were *Pseudosquilla ciliata* and *P. oculata* (Brullé 1836) (Townsley 1953 and pers. comm.). The comparison of the well-studied coral head habitat and that of the anchialine ponds in Hawaii (Manning and Reaka 1981:199) is totally misleading since the latter habitats had not been examined until the 1970s (Maciolek and Brock 1974).

Thus neither the contention that the habitat was not abundant nor that it was insufficiently

searched can be supported. While negative evidence such as this can never unequivocally establish the fact that the stomatopod was truly absent, the weight of the data indicates that the burden of proof lies on supporters of the second scenario. That is, since dead corals were a common habitat element in Kaneohe Bay for many years before the appearance of the species, some explanation for its apparent absence must be put forth.

REPLACEMENT OF *Pseudosquilla ciliata* BY *Gonodactylus*

Scenario 1 holds that the more aggressive coral cavity specialist, *Gonodactylus*, competitively displaced the habitat generalist, *Pseudosquilla ciliata*, from the dead coral habitat. Scenario 2 holds that there was no competitive displacement; rather, *Gonodactylus aloha* simply moved into a habitat that had increased in availability (Manning and Reaka 1981:199).

To support their scenario Manning and Reaka make three points from a dissertation by Hatziolos (1979):

1. In a field experiment *Pseudosquilla ciliata* did not move into suitable cavities which were experimentally provided.
2. Additions of burrows to a study site did not increase the density of *P. ciliata*.
3. When *Gonodactylus* is less than 80 percent of the size of *Pseudosquilla*, the latter dominates the interactions.

From these points Manning and Reaka (1981:197) conclude:

- (A) that coral rubble is not the primary preferred habitat of *P. ciliata*.

This appears to be a straw man that has nothing to do with the fact that *P. ciliata* did in fact occupy coral head rubble in Hawaii until the 1950s (Edmondson 1933, Townsley 1953). Scenario 1 says nothing about coral rubble being "the primary preferred habitat of *P. ciliata*." Both Kinzie and Hatziolos state explicitly that *P. ciliata* is a generalist:

Its [*P. ciliata*] occurrence in hard and soft substrates, in cavities of coral rubble or U-shaped burrows it fashions out of sediment and algae, further qualify it as a generalist. (Hatzios 1979:13)

Since *P. ciliata* can be found in burrows in muddy bottoms and walking freely on the bottom, and since, prior to 1953 it was taken from coral heads, this species seems to have a wider range of possible habitats than does *Gonodactylus falcatus*. (Kinzie 1968:473)

But as Hatzios (1979:17) also states, other things being equal *P. ciliata* will tend to occupy dead coral: "*P. ciliata* prefers the less vulnerable coral cavities as shelters when available."

The second conclusion made by Manning and Reaka (1981:197) is:

(B) The availability of burrows (or inavailability [*sic*] as the result of their occupation by *Gonodactylus*) does not regulate population densities of *P. ciliata*.

Like point (A) this is a straw man since there was no statement in Kinzie (1968) that the introduction of *Gonodactylus* regulated the population density of *P. ciliata*. In fact I stated (Kinzie 1968:474): "It can be further predicted that the presence of *G. falcatus* in Hawaii will not affect those populations of *Pseudosquilla ciliata* utilizing habitats other than coral heads." However, it is interesting that Hatzios (1979) states:

The agonistic coil [intense mutual escalation] is frequently observed among Hawaiian individuals [of *P. ciliata*] most often associated with burrow defense; (p. 117)

Under conditions of extreme environmental rigor, such as, for example, when the ratio of population to resource density is high, aggressive behavior may reach its full potential; (p. 118)

The fact that intense escalation during burrow defense occurred more frequently in Hawaii than in Jamaica suggests that the payoff in fitness gain from burrow acquisition may be much higher in the former site. (p. 120).

It appears from Hatzios' dissertation that at the time she was doing her research in Hawaii, there was markedly more intraspecific competition for burrows among Hawaiian *Pseudosquilla ciliata* than in Jamaica: It would be impossible at this time to determine if this pressure was due to the activities of *P. ciliata* individuals evicted by *Gonodactylus*, or to other factors. At any rate Manning and

Reaka's conclusions (A and B) neither refer to necessary components of Scenario 1, nor are they actually supported by the data they cite from Hatzios. Their third conclusion is:

(C) that *P. ciliata* frequently may dominate *G. aloha* behaviorally due to the larger body size of the former. (Manning and Reaka 1981:198)

They go on to state that Hatzios (1979:120) found that:

Among Hawaiian animals, *P. ciliata* residents succeeded in defending their burrows against intruders in 95% of the encounters indicating strong territoriality and willingness to defend.

Manning and Reaka neglect to state that these were intraspecific encounters and thus irrelevant to the question of interspecific aggression. In fact, Hatzios (1979:112) states: "Without exception, Hawaii individuals [of *P. ciliata*] inhabiting cavities in preference to artificial burrows were evicted by intruding *Gonodactylus* admitted to the tank." These were size-matched encounters. To support their contention that *P. ciliata* may dominate the Hawaiian *Gonodactylus* behaviorally due to the large body size of the former, Manning and Reaka refer to Hatzios (p. 112 and fig. 4, p. 109) and conclude: "In contrast, when the individual *Gonodactylus* was less than 80% of the size of its larger *Pseudosquilla* opponent, the latter dominated the interaction" (Manning and Reaka 1981:197). Manning and Reaka then state that since these data were obtained from Thailand where the *P. ciliata* are less aggressive, their conclusion is conservative. They neglect to mention that the *Gonodactylus* species that Hatzios studied in Thailand were *G. viridis* and *G. chiragra* as well as *G. falcatus* and were not treated separately in her dissertation (Hatzios 1979:110); so Manning and Reaka's conclusion is not conservative—it is invalid.

As a qualification of their statement about the aggressive nature of *Pseudosquilla ciliata* Manning and Reaka (1981:198) state:

However, Caldwell and Dingle (1975:220) reported that in laboratory experiments *P. ciliata* was always driven from a burrow (a glass vial) when *G. falcatus* was introduced into the same tank, but the reverse was never observed.

In fact the information presented by Caldwell and Dingle are from my earlier paper (Kinzie 1968, table 2) where, interestingly, in 50 percent of the winning encounters, the *Gonodactylus* individual was less than 80 percent of the size of the losing *P. ciliata*. While my sample sizes were not as large as those of Hatziolos, these data should not be ignored.

Manning and Reaka present data showing that in Hawaii *Gonodactylus* is 58–60 percent the size of *Pseudosquilla ciliata*. No extensive tests matching individuals of these relative sizes have been made in Hawaii, nor has it been shown that the largest *P. ciliata* can even physically fit into crevices of the size inhabited by the Hawaiian *Gonodactylus*.

DISCUSSION

Both scenarios have historical components that are untestable. In support of Scenario 1 it could be argued that Hawaii has received and is continuing to receive numerous exotics.

Large numbers of this crustacean [a grapsid crab] were recovered from the fouling on the hull of a barge in Pearl Harbor dry dock April 5, 1950. The barge served in Guam during World War II, but had been anchored in Pearl Harbor for the past two years. Apparently this species has not been recorded previously from the Hawaiian area. The adults of this crab may have been transported from Guam but the myriads of juvenile specimens observed indicate that propagation of the species has taken place since reaching Pearl Harbor. (Edmondson 1951:212)

Observations in the local drydocks indicate that many exotic forms of marine life may be introduced into new environs in this manner. How many of them become established under altered conditions it is impossible to say, but there is evidence that some of them do. (Edmondson 1959:154)

Elton (1958:100) makes the point that oyster culture is "the greatest agency of all that spreads marine animals." In 1939, 210 cases of *Crassostrea gigas* spat from Japan were sown in Kaneohe Bay (Devaney et al. 1982:101). In addition Kaneohe Bay has been sown with Japanese little neck clams (*Tapes japonica*), Japanese clams (*Meretrix meretrix*), and Australian oysters (*Ostrea cuculata*) (Devaney et al. 1982). The bait wells of commercial fishing boats are another source of accidental immigrants. Fishes from the South and

Central Pacific have been either introduced in baitwells or accidentally mixed with intentional introductions (Randall and Kanayama 1972). Introductions of octocorals from the Caribbean (Thomas 1979), sponges of the fouling community (Bergquist 1967), marine algae from the Philippines and elsewhere in the Pacific (Russell 1981), and scyphozoans from the Philippines (Cooke 1984) support the idea that Hawaii is receiving many successful marine introductions.

It is interesting to note that *Gonodactylus hendersoni* Manning, 1967, a much smaller stomatopod, was also first noticed in Hawaii about the same time that the large *Gonodactylus* was reported. I suggested (Kinzie (1968:474) that "*Gonodactylus falcatus* and *G. hendersoni* came to the Hawaiian Islands from the area of the Philippines or the South China Sea by means of concrete barges." Nonetheless, it could always be argued (as one reviewer of this paper did) that had Edmondson turned over one more stone or split one more coral head the elusive *G. aloha* might have been found.

Support for Scenario 2 might come from the fact that new species are being described from Hawaii, and this is evidence that some species have simply gone unnoticed until now. It has, however, been shown above that the habitat of the Hawaiian *Gonodactylus* is not new, nor has that habitat gone unsearched. At this point the two scenarios remain, each with untestable historical components. Do any of the three points discussed above suggest falsifiable hypotheses generated by either of the two viewpoints?

Specific Identity

A cladistic analysis of the *falcatus* group of *Gonodactylus* (Manning 1978) has not been carried out. However, such an analysis could differentiate between Scenario 1, which predicts that the Hawaiian and Philippine forms share an immediate common ancestor (Figure 1A), and Scenario 2, which predicts a more distant relationship (Figure 1B). Should the Hawaiian and a Philippine population in the *falcatus* group prove to be the same or sister groups, Scenario 1 would be supported. A

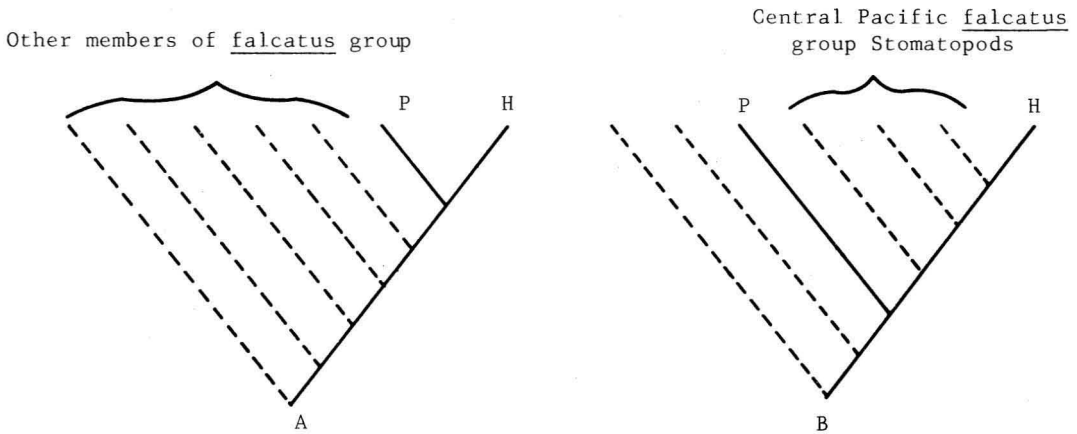


FIGURE 1. Cladograms of the *falcatus* group of *Gonodactylus* as predicted by Scenario 1 (A) where the Hawaiian form (H) and the Philippine form (P) share an immediate common ancestor, and by Scenario 2 (B) where the Hawaiian form is more closely related to Central Pacific forms. In A the two forms may in fact not be distinguishable. The position and number of dotted lines represent unknown relationships.

closer relationship of the Hawaiian population to Pacific Basin species would be evidence for Scenario 2. This is because much of the native Hawaiian marine fauna is most closely allied with forms from the Pacific Basin (Edmondson 1940, Gosline 1968) as delineated by the Pacific plate (cf. Springer 1982). There is a further interaction between biogeography and systematics in situations like the one described in this paper. Carlton (1982) pointed out that the rapidly increasing number of introduced species being discovered can result in a new species being described not from the area where it is endemic, but rather from an area to which it has been introduced. The probability of such an occurrence is significant because source areas of undescribed species are often remote, while areas that are arrival points for undescribed species are frequently the nexus of shipping (and also have a higher probability of having biological institutions). Thus, the chances of an undescribed species being detected could be greater where it is exotic than where it is native. As Carlton noted, it is important to clearly identify, if possible, the suspected biological source area for such species—as distinct from the source of the type specimens. In many cases this may not be possible.

The Hawaiian *Gonodactylus* discussed in this paper may be an example of the latter

situation. The Philippine source population may represent a good species in the *falcatus* group (see Garcia 1981, who differentiates between Philippine *G. falcatus* and *G. glabrous* Brooke [1886]) but one distinct from the Red Sea population (and also, as the evidence presented here suggests, distinct from the southern hemisphere populations as well). This possibility was not addressed by Manning and Reaka. As to the specific identity of the Hawaiian form, it is unlikely that the concept of a species held by a taxonomist responsible for one superfamily, nine families, 31 genera, and more than 100 species in the past 20 years would be congruent with that held by a biogeographer trying to work out patterns of distribution in space and time.

History of the Form

Both scenarios require that the Hawaiian form went through a population bottleneck due either to a founder effect following the introduction of a few individuals or to the rapid increase in numbers as the habitat expanded and the previously rare form became the coral head dominant. Whether the genetic consequences of an expanding founder population, randomly selected from a large co-adapted parent population, would differ from those of a small isolated endemic population

that was suddenly released and subsequently expanded in numbers in situ is not clear but deserves investigation. An examination of mitochondrial DNA may be a suitable method of investigating this question (A. Templeton, pers. comm.).

A characteristic of many introduced species is that they go through a period of very rapid increase in numbers followed by a marked decline. This has been shown for aquatic plants [*Elodea* (Elton 1958), *Eucheuma* (Russell 1981)] and several terrestrial organisms in Hawaii [*Argyrope appensa* (Gosline 1968), *Achatina fulica* (Mead 1961), and *Oryctolagus cuniculus* (Tomich, Wilson, and Lamoureux 1968)]. It is interesting to note that as of 1983 the population densities of *Gonodactylus* in Kaneohe Bay appear to me to be about one-third of what they were in the 1960s. However, more intensive work is needed to verify this. Changing conditions in Kaneohe Bay would also have some effect on the populations of the two stomatopod species. It is noteworthy, however, that dead coral heads are still very abundant in many parts of the bay (Evans, Holthus, and Maragos, in press; Aliño, in press).

Replacement

Experimental encounters between specimens of the critical sizes suggested by Manning and Reaka as well as intensive field studies in Hawaii could clarify the question of whether appropriate size ratios of *Gonodactylus* and *Pseudosquilla* give competition outcomes supporting Scenario 1 or 2. Not only is the density of *Gonodactylus* in Kaneohe Bay lower than in the 1960s but there appears to be an increase in density and average size and a change in coloration of the *Pseudosquilla ciliata* populations in the bay. A repetition of Hatzios' study could shed light on the sequelae of the intense interactions that she observed in Hawaii. Whichever scenario is correct, there has been a marked alteration in the stomatopod situation in Kaneohe Bay since the time of her study.

We are left with two scenarios each with an untestable historical component; the first requires an act of introduction that cannot be

documented, and the second requires the existence of a previously unnoticed species. Since situations of this nature are likely to become more and more common, it does not seem appropriate to create new specific entities for populations with dubious historical pedigrees. Carlton (1982) has proposed the term "cryptogenic" for situations of this sort. I suggest that the Hawaiian *Gonodactylus* be considered a cryptogenic species until either its specific identity and relationship with other stomatopods can be clearly determined, or its situation in Hawaii can be clarified.

ACKNOWLEDGMENTS

A. H. Banner and S. J. Townsley graciously shared with me their experiences on Hawaiian reefs from the 1930s until today. Their knowledge and observations are the foundation of this paper. Both they and L. Eldredge read the manuscript and their comments improved it. Thanks are also due to the U.S. National Museum, the Queensland Museum, the Australian Museum, the Rijksmuseum van Natuurlijke Historie, and the Mauritius Institute Museum for the loan of specimens used in the 1968 study.

The observers for the data in Table 3 were participants in the 1983 Hawaii Institute of Marine Biology Summer Program in Coral Reef Biology.

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