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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

VERNON E. BROCK
Selective Fishing Action of Longline Gear

EDWARD C. ROOSEN-RUNGE
Biology of Sexual Reproduction of Phialidium

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Marine Chlorophyta of Hawaii, I

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(Continued on inside back cover)

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On the Nature of the Selective Fishing Action of Longline Gear

VERNON E. BROCK[1]

FISHERY BIOLOGISTS have, thanks to the magnitude of sampling provided by commercial fisheries, a better quantitative understanding of the populations with which they are concerned than do biologists interested in the quantitative aspects of other marine organisms. However, fishery biologists must be aware of bias that may be introduced by the sampling mechanism, the fishing apparatus. Fishing gear may be more effective in the capture of fish of some sizes or in some areas or seasons. If the nature of the bias is known allowance can be made for it, and its character may supply additional information on the population of fish.

Longline gear, as used for tuna fishing, characteristically takes the larger tuna. It is presently used to harvest a major portion of the world's catch of tuna, especially yellowfin tuna, *Thunnus albacares,* and bigeye tuna, *Thunnus obesus,* from the tropical waters of the Atlantic, Pacific, and Indian oceans. It is apparently the only method useful for the harvest of these species and, largely, of the albacore, *Thunnus alalunga,* in the open ocean far from land.

The present paper is concerned with a hypothesis regarding the basis for the selection of larger fish by longline gear based on the fish schooling theory of Brock and Riffenburgh (1960), together with a discussion of the relationship between availability of fish to longline gear and the age or size composition of the stock.

Only the relationship between yellowfin tuna and longline gear is considered in any detail. While the conclusions reached for this species may be applicable to others, there are certain difficulties involved in further comparisons. The lack of any substantial surface fishery for bigeye tuna makes any comparisons of the character of the catches between fishing methods difficult for this species. Albacore seem to be differentially distributed by size, and skipjack (*Katsuwonus pelamis*) are taken too infrequently by longline to provide useable data. Skipjack catches by longline are possibly analogous to catches of small yellowfin by the same gear.

Bluefin tuna (*Thunnus thynnus*) has not been considered; the occurrence of this species in temperate waters, subject to a variety of changes in the depth of the mixed layer, and its ability to live in both tropical and temperate marine environments, complicate any analysis. Schooling of large bluefin tuna may occur primarily for reproductive purposes.

ACKNOWLEDGMENTS

I wish to thank Mrs. M. L. Godfrey and other staff members of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, who made a special effort in organizing IBM cards containing data on longline catches for machine computation, and Dr. R. H. Riffenburgh, who supervised the programming of a computer and made the tests of the significance of the differences in lengths of yellowfin taken solitarily, in pairs, or in runs of higher numbers.

DESCRIPTION OF LONGLINE GEAR

Longline gear is a floating or drifting fishing device which takes fish by hooking and is made up of a horizontal line, to which are attached droppers ending in baited hooks. While there are modifications of the basic plan, these are not important in terms of the present analysis. Shomura and Murphy (1955) described one of the gear designs employed by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, as follows:

> One unit of gear, called a basket, has 1,260 feet of mainline and six 88-foot branch lines (droppers) attached to the mainline at 30-fathom intervals. Several baskets are joined to make up

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[1] U. S. Bureau of Commercial Fisheries, Honolulu, Hawaii. Manuscript received May 12, 1961.

Now, Biological Laboratory, Washington, D. C.

a set, the entire set being buoyed with floats at basket junctures and at the ends. Fishing at subsurface levels is accomplished by using 10-fathom lines between mainlines and floats and by setting the mainline slack so that it will sag in the water. To this end, the 1,260 feet of mainline is set in about 900 linear feet.

With this gear the minimum fishing depth is 148 feet and, of course, the droppers midway along the mainline between the floats would settle much deeper than this.

SIZE CHARACTERISTICS OF YELLOWFIN TUNA TAKEN BY LONGLINE, PURSE SEINE, AND LIVE-BAIT FISHING

Yellowfin tuna taken in the central Pacific by longline gear (Fig. 1*a*) were caught during the course of experimental and exploratory fishing by the Bureau of Commercial Fisheries. While the lengths range from 40 to 175 cm., the bulk of the fish exceed 120 cm. Figure 1*b* shows a percentage length frequency distribution of yellowfin tuna landed from the eastern Pacific (Hennemuth, 1961: table 1) by live-bait and purse seine fishing. While the lower length limit is about the same for both distributions, the largest sizes taken only infrequently by live-bait and purse seine fishing are about the same as the modal size taken by longline gear.

These distributions of lengths of fish taken by purse seine and live-bait fishing and by longline gear are typical for these fishing methods. Moore (1951) illustrates similar distributional patterns for yellowfin taken by longline and sold in the Honolulu market. Yabuta and Yukinawa (1959) give similar patterns of length distribution for fish taken in the western Pacific by this gear, as does Mimura (1958) for the Indian Ocean. Wilson and Shimada (1955) reported catches of large yellowfin by longline in the eastern Pacific; Mais and Jow (1960) reported on additional experimental longline fishing trials in the eastern Pacific, which also took large tuna, although not as large as those reported by Wilson and Shimada.

While purse seining for yellowfin tuna is largely confined to the eastern Pacific, a small live-bait tuna fishery for yellowfin off Japan takes fish of the sizes characteristic for this fishing method in the eastern Pacific (Yabuta and Yukinawa, 1957), and, from my observations, occasional catches taken by this method in Hawaii are composed of small and medium size fish.

POSSIBLE FACTORS AFFECTING SIZE OF YELLOWFIN TAKEN BY VARIOUS TYPES OF FISHING GEAR

Successful purse seine and live-bait fishing depend upon fish being in schools, and ordinarily upon their being evident on the surface of the water. Schooling fish may not be essential for successful longline fishing; in any event, the gear is ordinarily set without any surface evidence of fish.

The pattern of length distribution found in the purse seine and live-bait fishing catch could be attributed to selection against the smaller sizes (< 50 cm.) by the fishermen and to decreasing abundance of the larger sizes through the effects of both fishing and natural mortality. Comparing length distribution of the central Pacific longline catch with that of the eastern Pacific surface fishery suggests that the former fishing method may be ineffectual for smaller fish. However, there exists a difference in the fishing grounds which may reflect some differences in population structure. In addition, the longline gear fishes at some depth; the other two methods depend upon schooling fish located by signs evident at the surface of the sea. The fish available to longline gear are called the "deep swimming tunas" in fisheries literature (Murphy and Shomura, 1955); they are presumed to be large in contrast to the smaller surface-dwelling fish.

Brock (1959) pointed out that areas which sustained large surface yellowfin tuna fisheries were located on the eastern margins of the tropical Atlantic and Pacific oceans, where the mixed or surface isothermal layer was relatively shoal. For the central and western Atlantic and Pacific and all of the Indian Ocean, where the mixed layer is fairly deep, only longline gear seemed to be effective.

Both purse seine and live-bait fishing depend on surface evidence of schooling fish. Where the isothermal surface layer is deep, schools may appear at the surface less frequently, thus reducing the effectiveness of these methods. Addi-

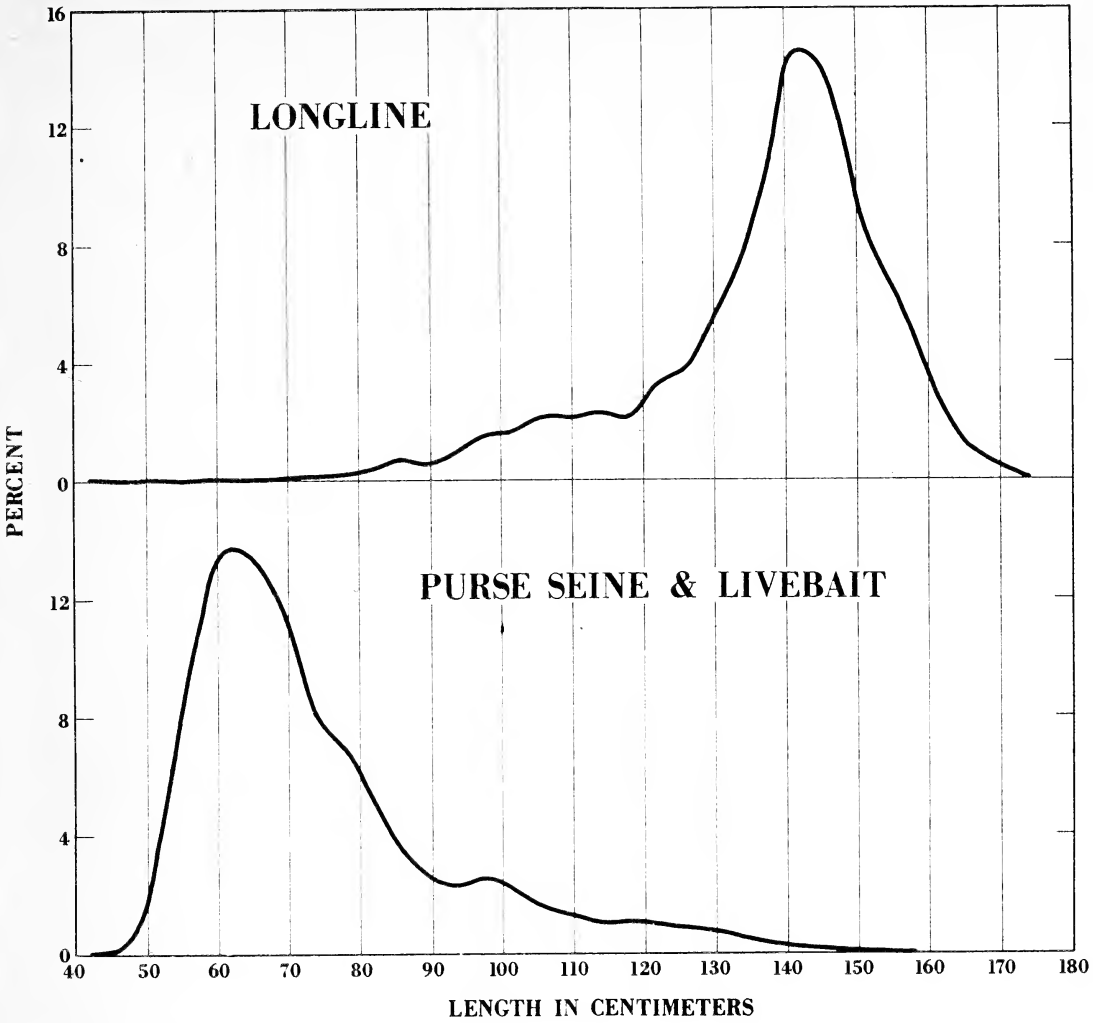

FIG. 1. *a,* Percentage length frequency distribution of yellowfin tuna taken by longline gear in the equatorial central Pacific. *b,* Percentage length frequency distribution of yellowfin tuna taken by both live-bait and purse seine fishing in the eastern tropical Pacific.

tionally, if larger fish tend to form smaller schools, or no schools at all for the largest sizes, the failure of fishing methods dependent on schooled fish to take larger sizes would follow. Conversely, longline gear should be most effective for scattered fish for reasons which will be given.

It may be pertinent, at this juncture, to define a fish school. A number of definitions have been suggested, which are discussed in detail by Breder (1959). A rather simple definition will suffice here. A school is two or more fish of the same species which respond to the others by swimming as a group. The response is assumed to be effected by vision; hence, the distance among fish within a school is less than the visual range, usually much less.

FISH SCHOOLING AND THE SIZE SELECTIVITY OF LONGLINE GEAR

If it is assumed that the number of fish in an average school is some inverse function of fish size, the low proportion of small yellowfin tuna in longline catches would be an expected consequence if longline gear was less effective in catching fish which were schooled than those which were not. Brock and Riffenburgh (1960) show that the anticipated encounter ratio of a predator for schooled or scattered prey of some number is

$$N_e = \frac{r^3 N_f}{\left[r + c \sqrt[3]{\frac{3 N_f}{4 \pi}} \right]^3} \qquad (1)$$

where r is the visual range of the predator, N_f the number of prey, and c the average distance among individual fish in a school of N_f prey.

Equation (1) expresses the ratio of the visual densities of scattered and schooled fish. It would also express the ratio of encounter by scattered or schooled predators with some fixed number of prey, where N_f is the number of such predators and c the average distance among fish in a school of predators.

It contains three variables: (1) the visual range, which is a function of water clarity; (2) the number of schooled and scattered fish; (3) the space occupied by each fish in the school. If the visual range substantially exceeds the distance among fish in a school, then a school will scout through a substantially smaller volume of water than will an equal number of scattered fish, because the visual ranges of a large part of the schooled fishes overlap; this is not true for the scattered ones. For large schools, in clear water, the encounter ratios may range from hundreds to thousands in favor of the scattered fish. These relationships are illustrated in Figures 2 and 3.

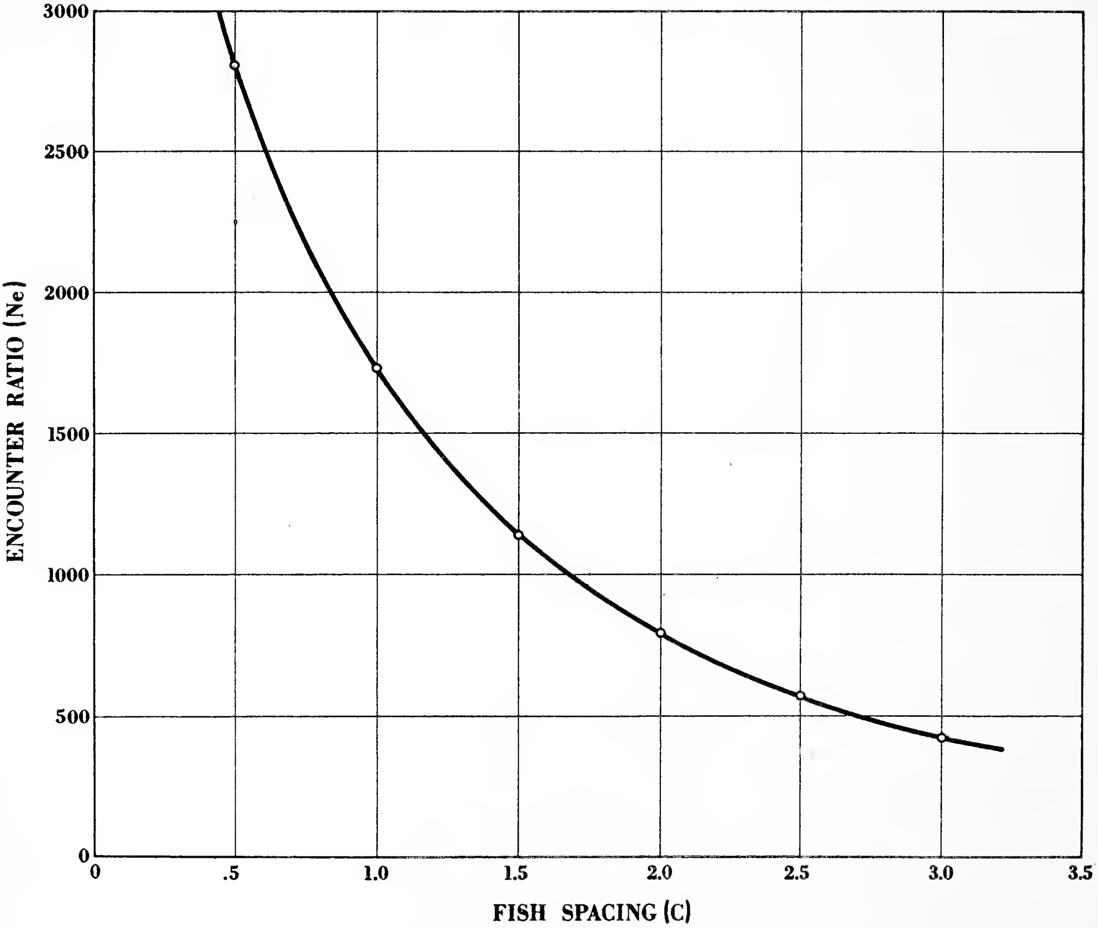

FIG. 2. Effect of increase in distance between fish in a school on the encounter ratio.

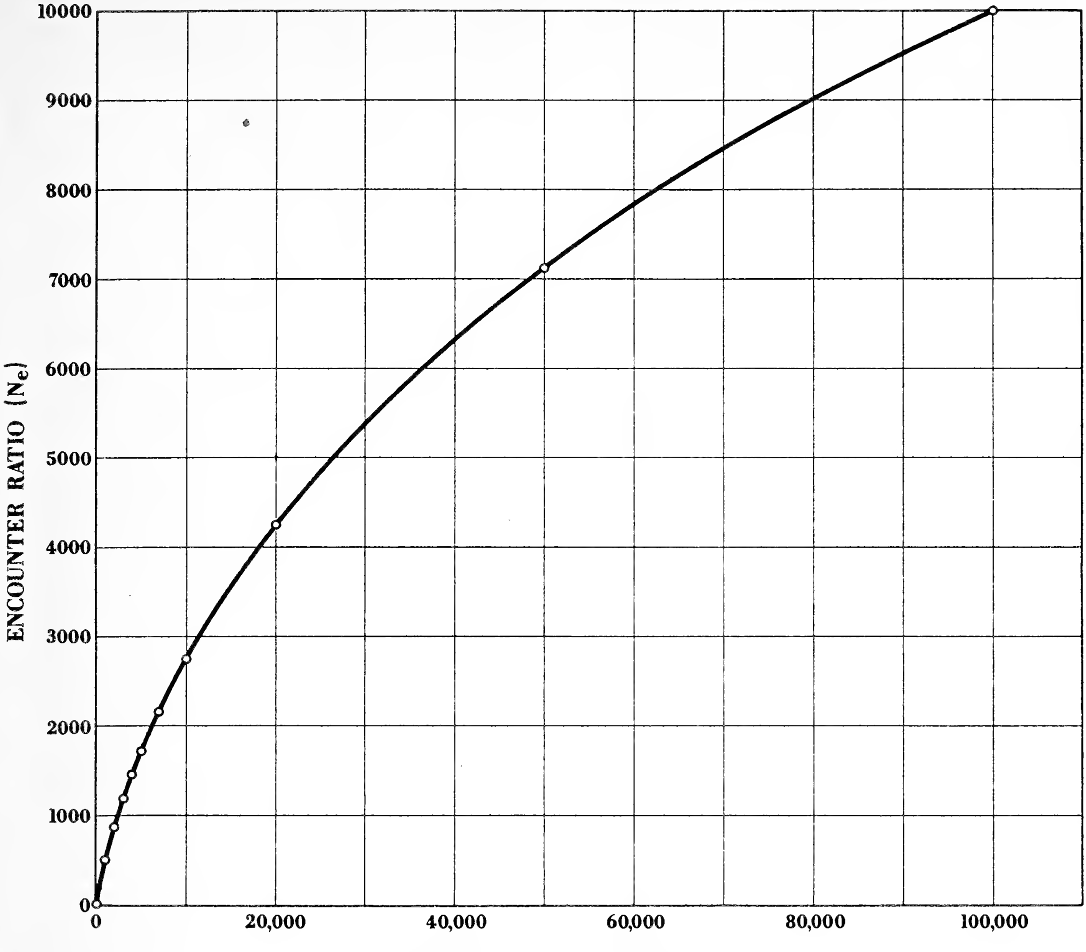

FIG. 3. Effect of increase in the number of fish in a school on the encounter ratio.

Figure 2 is a plot of the ratio N_e, the encounter ratio, against c, the distance among fish in the school. Visual range is assumed to be 25 meters and school size is taken at 5,000 fish. The increase of the encounter ratio with a reduction in the spacing (c) among fish in a school—as compared to an equal number of scattered fish—is apparent. This is to be expected, for the fish in a school approach the condition of scattered fish as a limit as the spacing among the schooled fish approaches the visual range. At this point, by definition, the school ceases to exist. If the spacing among schooled fish were a function of fish length, the relationship shown by the figure would suggest that schooling may be less effective for large fish than for smaller ones.

Figure 3 illustrates the effect on the encounter ratio of an increase in the number of fish in a school, assuming r equals 25 meters and c equals 1 meter. The encounter ratio is, of course, determined by the particular values assigned to r, c, and N_f, if the relationship postulated in equation (1) is valid. While the values selected are arbitrary, they are not unreasonable, except possibly in the magnitude of some of the bigger schools.

A school will scout a larger volume than that scouted by an individual fish, but less than that scouted by an equal number of scattered fish.

However, on the occasion of a school encountering a set of longline gear, a probability exists that if one fish should be captured from the school, additional fish will be captured thereafter. If the movement of the school is random and confined within a given depth, a likely situation in the tropics due to the rapid cooling of water with depth below the thermocline, the probability of hooking additional fish from the school may be roughly estimated in the following way.

If a fish should be taken on the jth hook of a set of longline gear, for the ith hook there will be a component of P of the form

$$P = \frac{\pi\,(r+r')^2 h_{1i-j1} K}{\pi\,(h_{1i-j1})^2 d}$$

and, summing for all i hooks and simplifying, we obtain

$$\sum_{i=1}^{n} P = \frac{(r+r')^2 K}{d} \sum_{i=1}^{n} \frac{1}{h_{1i-j1}} \qquad (2)$$

where h_i is the distance from the first hook taken to successive hooks (h_1, h_2, $h_3 \ldots h_n$), d the depth of water in which the fish may be expected to range, r the visual range, r′ the radius of the school, and K a factor with values between zero and one expressing the likelihood of a fish biting a baited hook.[2] An estimate of the probability of taking at least one additional fish was computed on the basis of a school of 2,000 fish with the values for equation (2) used in Figure 2, and a K value of one, a hook spacing of 54.86 meters (30 fathoms), and an isothermal layer, in which the fish occurred, 150 meters thick.

$P = .7382$ for 18 hooks, which would imply that additional fish may be hooked in three out of four sets of the gear where a school of the dimensions assumed here encounters a set of this number of hooks. Considering the possible high values of N_e, additional fish taken from schools may have relatively little effect toward increasing the catch from schooled as compared to scattered fish; from a school of 2,000, some 884 fish would have to be taken to cancel the effect of schooling on the basis of the school dimensions and visual range assumed in this example. Models with increased spacing among the schooled fish or with reduced visual ranges would reduce the effect of schooling; the assumed visual range is conservative for the areas where longline fishing is done. The example does imply, however, that runs of fish may be expected occasionally when a school encounters a set of longline gear, and that is the reason for presenting it.

It has been suggested that the number of fish in a school may be, on the average, an inverse function of the size of fish, with the largest fish occurring either in very small schools or not schooled at all. Accepting this assumption, it has been further hypothesized that the fishing efficiency of longline gear would be inversely related to the degree of schooling. If these are both true, then the longline catch should be composed of a disproportionate number of non-schooled fish or of fish from small schools. However, a probability exists for the capture of several fish from a school, and it is reasonable to assume that this probability is some function of school size.

If both the assumptions and the reasoning based on them are valid, it then follows that the mean size of fish taken by longline gear occurring in pairs or in larger groups on adjacent hooks should be less than that of the solitary hooked fish, and the greater the number of fish in a group the less their average size.

If such a size difference between grouped and solitary fish on longline gear does not exist, then, aside from the possibility of some artifact in the data, the hypothesis erected in this paper and briefly summarized above should be rejected. On the other hand, the existence of such a size difference would constitute evidence of the validity of the hypothesis, lacking alternate possible causes for this difference. It would also, thereby, constitute evidence for the validity of the fish schooling theory of Brock and Riffenburgh, since a pattern of size differences of this kind for longline gear is predicted by the theory.

Longline catch data obtained by the Bureau of Commercial Fisheries in the central Pacific

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[2] In the case where $(r+r')^2 > h_{1i-j1}d$, equation (2) cannot be interpreted as a simple probability.

for the past several years were examined for evidence of a difference in the size of fish taken on adjacent hooks as compared to those not so taken. The results are given in Table 1.

The significance of the mean difference in length between solitarily hooked fish and all the fish hooked may be estimated by the Bienaymé-Tchbycheff Inequality. While the use of this inequality does not require any assumption of normality of the distribution of fish lengths, it does assume that the mean and the variance of the population are known. Since the sample is large (4135), it was assumed that the mean and the variance of all fish measured would adequately approximate those of the population.

$$\Pr\left[|\bar{x}-\mu|>e\right] \leq \frac{\sigma^2}{Ne^2} \qquad (3)$$

If the probability of deciding that $\bar{x}$ is different from μ when it is in fact not so should be taken to be 0.01, then

$$\frac{\sigma^2}{Ne^2} = \frac{389.52}{3192e^2} = 0.01, \text{ from which}$$

$$e = 3.49$$

For these data, $\bar{x} = 138.1$ and substituting this in the left side of (3), we have: $\bar{x} - 130.7 = 7.4 > 3.49$.

The probability given in (3) is seen to be less than 0.01; hence the difference between the solitary fish and all fish is significant.

If an assumption of normality of the distributions of fish length for each of the four groups is made, both the analysis of variance and the *t*-test indicate a highly significant difference among the groups.

The assumption that runs or pairs were invariably associated with catches from schools and that solitary fish taken were not from schools is obviously not completely true; pairs or groupings of higher numbers can occur by chance and it is at least possible to catch only a single fish from a school. The effect of chance groups and of the capture of single fish from a school would be to reduce the differences in size between the solitary fish and pairs or runs of higher numbers.

Through the application of simple probabilities, the number of fish that might be expected to be hooked in groups or individually was computed on the basis of the following assumptions.

1. The fish were randomly distributed and not schooled.
2. Fish were not caught simultaneously.
3. The catch rate was uniform at 6 fish per 100 hooks, which is a higher average rate than that for the catches in Table 1, and the gear set had 100 hooks.
4. Only a single species, yellowfin tuna, was considered in the computation, because the inclusion of other species would reduce the number of pairs and larger groups as compared to solitary fish.
5. While the end hooks on the set of gear were regarded as being available for fish, the computation of groups based on their occupancy was not made; this would also reduce the proportion of groups as compared to solitary fish.
6. The likelihood of a fish taking a hook was assumed to be the same for all unoccupied hooks.

Obviously the first fish hooked is solitary; the next fish may make a pair by taking a hook on

TABLE 1

MEAN SIZE AND NUMBER OF FISH HOOKED SEPARATELY OR IN GROUPS ON LONGLINE GEAR

NO. YELLOWFIN HOOKED SEPARATELY OR ON ADJACENT HOOKS	SAMPLE SIZE	MEAN WEIGHT (pounds)	MEAN LENGTH (centimeters)	VARIANCE (length)
1	3197	113	138.1	411.70
2	712	102	133.6	363.87
3	169	86	126.4	346.49
4	57	83	124.7	443.48
	4135			

TABLE 2

COMPUTED DISTRIBUTION OF FISH HOOKED FROM RANDOMLY SCATTERED INDIVIDUALS AND AN OBSERVED DISTRIBUTION OF THE FISH HOOKED ON LONGLINE GEAR

NO. YELLOWFIN ON ADJACENT HOOKS	SAMPLE SIZE		DIFFERENCE BETWEEN COMPUTED AND OBSERVED
	Computed	Observed	
1	3919	3197	—722
2	125	712	587
3	58	169	111
4 and over	33	57	24
	4135	4135	

either side of the first fish or may take another hook elsewhere.

For each additional fish caught there are certain limited numbers of possibilities of forming pairs or larger groups. Some of these are mutually exclusive, depending upon the particular arrangement of hooked fish at that time; and the sum of the probabilities for each of these, together with the probability of taking a hook apart from those with fish, must equal one. However, by setting up all possible combinations until six fish were caught, the basis for the distribution given in Table 2 was computed. It is obvious that—on the assumption that the fish were all taken from a randomly distributed population—the agreement is very poor between the numbers of fish hooked solitarily or in groups and the numbers of fish actually caught solitarily or in groups.[3]

The comparison given in Table 2 would imply that fish in groups occurred more frequently than would be anticipated if the distribution of the fish was random. It would strengthen the inference that many of the fish taken in groups were from schools. This is in agreement with the conclusions of Murphy and Elliot (1954), who, by the examination of the frequency of "runs," found some evidence for schooling in yellowfin catches taken by longline gear.

While the comparison given in Table 2 may provide some measure of the proportion of solitary fish occurring in groups, and hence an estimate of the contamination of groups formed by schools by adjacent fortuitous captures of solitary fish, the information is not adequate to provide a basis for adjusting the mean lengths of each of the groups; the reverse contamination of the solitary fish category by captures of single fish from schools has not been estimated. I can see no practical way of making such an estimate.

DISCUSSION

The mechanism of size selection of yellowfin taken by longline gear suggested here, that of schooling by fish size, if valid, has some interesting implications in regard to the magnitude of yields that may be anticipated at various fishing intensities. The availability of fish for a longline fishery may, on this basis, depend primarily upon the magnitude of that fraction of the population which is not schooled or is in small schools. In contrast, the efficiency of some other fishing methods for tuna, such as purse seining and live-bait fishing, depends primarily on the occurrence of fish in schools near the surface and larger than some minimum size. These fishing methods presumably would take fish before they were available to longline gear.

The relative fraction of the population available to the methods effective for schooling fish, as compared to those effective for scattered fish, would depend upon the pattern of growth and mortality.

Since fish are initially available to those methods effective for schools, a heavy fishing mortality for schooling fish would certainly re-

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[3] The lack of agreement is sufficient between the "computed" and the "observed" to justify the assumption of a significant difference here without a formal statistical test.

duce the population available for longline fishing. This situation would be true regardless of the validity of the hypothesis proposed here regarding the mechanisms of catch selection by these fishing methods.

If mortality rates are uniform and high for the stock being fished, a high catch rate by longline gear suggests that fish of schooling sizes may be abundant enough to afford greater yields than those obtainable by longline fishing. This would be less true if mortality rates were much lower, especially for the medium-sized, rapidly growing fish than for the oldest fish.

To illustrate the relationship between longline catch and the population of fish whence the catch came, the distribution of the weight of a hypothetical population in terms of age is shown in Figure 4, together with the longline

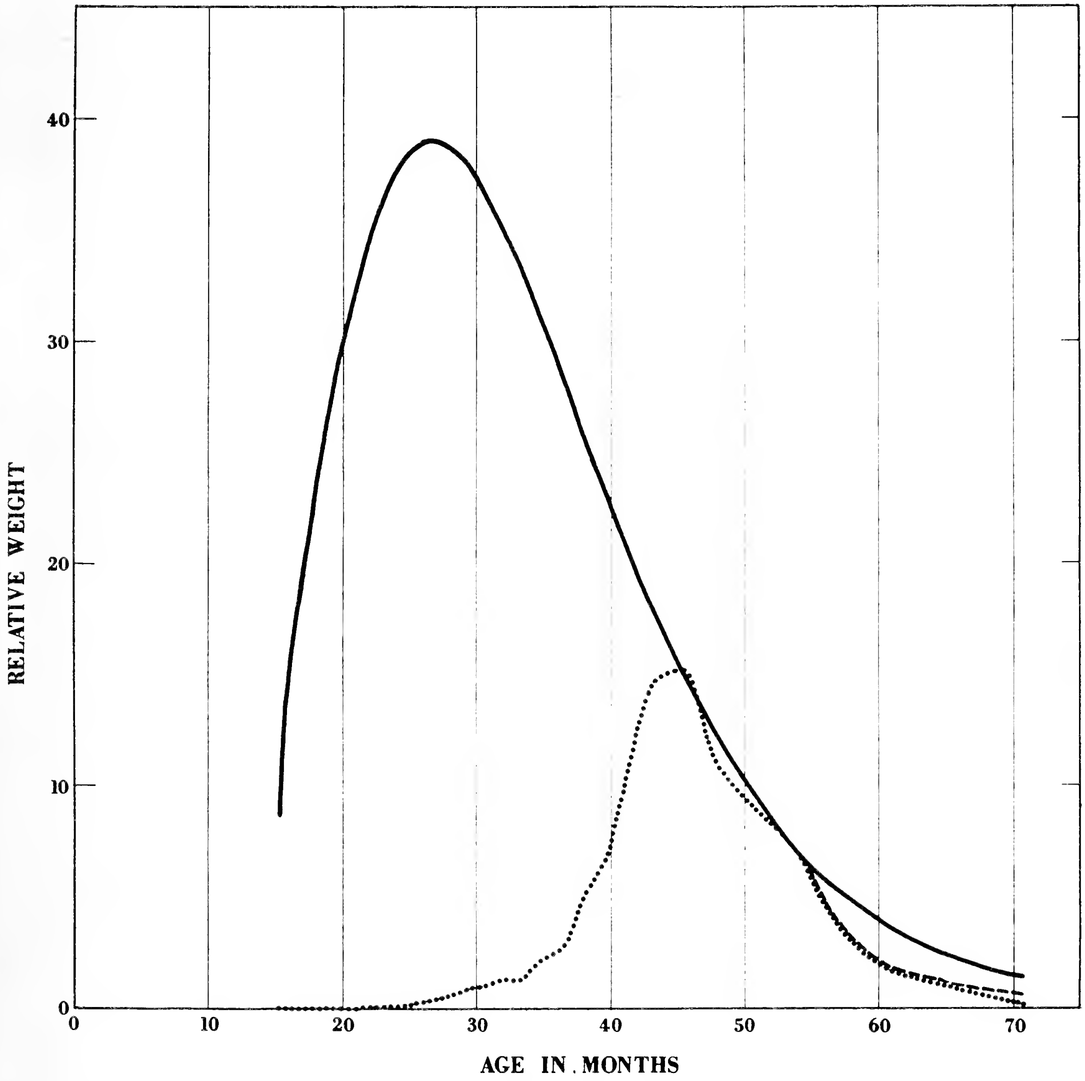

FIG. 4. Weight distribution for a hypothetical population and for fish taken by longline with identical mortality rates. The hypothetical population is shown by the solid line and by the dashed line (which is explained in the text). The dotted line is the age-weight distribution of yellowfin taken by longline gear in the central Pacific.

catch data shown in Figure 1*a*, also transformed into a plot of weight against age.

The weight–age relationship of the hypothetical population was computed as follows:

The longline catch data depicted in Figure 1*a* were transformed into a "catch curve" by converting length classes into age classes and plotting the age frequency curve on a semilogarithmic basis.

The transformation of length into ages was done by using the von Bertalanffy equation of growth in the form

$$t = t_o - \frac{1}{k} \ln \left(1 - \frac{L_t}{L_{oo}}\right)$$

where t is the age at length L_t, K a constant, and t_o a time constant. The values for K, L_{oo}, and t_o were estimated from the growth rates for yellowfin tuna given by Moore (1951).

Four of the age classes following the modal class approximated a straight line, the slope of which was taken as an estimate of the mortality rate of the exploited stock. The terminal age classes did not fit this line. Current work on the growth of bigeye tuna by Richard Shomura (personal communication) suggests that for this species a differential mortality by sex may occur for the largest sizes, with the females dying before the males. Assuming a differential mortality rate by sex for the largest yellowfin, an adjusted fit was made for the last four age classes on the basis that (1) the sex ratio was initially 1:1, (2) that half the remaining female fish died between ages of 54.15 months and 56.6 months, (3) that all were dead thereafter. This adjusted fit is shown as a dashed line in Figure 4. The fit is surprisingly good. The weight of fish in each age class was obtained from the length-weight relationship

$$\text{Log weight} = -7.3548 + 2.9959 \text{ Log Length}$$

where length is in millimeters and weight is in pounds. Fish approximately 15 months of age and older were included in the hypothetical population.

This estimate of instantaneous mortality for the longline catch was $e^{-1.404}$, equivalent to an annual rate of .754.

The area of the longline catch curve is about 21 percent of that for the hypothetical population; this figure is an estimate of the fraction of the population available to longline gear. At an annual mortality rate of .374 the mode of the longline weight distribution and that for the hypothetical population would be in approximate coincidence.

I have no means of estimating the degree of agreement between the population of fish from which the longline catches were taken and the hypothetical population depicted in Figure 4. If the agreement is good, this is likely to be fortuitous; data for longline catches are taken from survey fishing efforts for a span of years and over a large area of the equatorial Pacific south of Hawaii. They are those catches for which both the size and specific hook position on the set of gear were recorded for each tuna taken. In addition, the assumptions of uniform recruitment, a uniform mortality rate, the growth rate used here, and equal availability of the four age classes older than the modal age class, would have to be satisfied to obtain a good agreement.

However, the pattern of weight increase with age is such as to suggest that longline gear, selectively taking the largest fish, would be an inefficient harvesting method except for tuna stocks subject to modest rates of mortality. It may also be difficult to realize yields approaching the maximum sustainable yield for stocks of yellowfin tuna by longline gear, since increases in the catch of fish would increase mortality rates with a disproportionate reduction in catch rates. If the weight of the landings is proportional to the weight of fish of the sizes available to longline gear, the effect in changes in mortality rates on catch rates may follow a pattern like that given in Table 3.

The values of Table 3 are based on the growth

TABLE 3

CHANGES IN AVAILABILITY OF FISH TO LONGLINE GEAR WITH CHANGES IN MORTALITY RATES

MORTALITY RATE %	CATCH RATE %
45	100
60	37.7
75	7.2

rates for Hawaiian yellowfin tuna (Moore, 1951) and the pattern of size selection of fish by longline gear for the catches shown in Figure 1*a*.

The purse seine method for fishing tuna is rapidly developing at the present time, a situation which may lead to the development of profitable fisheries in areas where this gear is not presently used. It may be suggested, however, that for those portions of the ocean where the isothermal layer is usually deep, there is not now available any fishing gear suitable for schooling fish when the fish may not ordinarily be at the surface of the sea. This may apply with greater force to the bigeye tuna, which is only occasionally caught at the surface anywhere.

SUMMARY

The selective capture of large fish by longline gear is described and various causes for this are discussed. One cause suggested is that small tuna are more highly schooled than large ones and, according to the schooling theory of Brock and Riffenburgh, the likelihood of capture on a longline would be greatest for scattered fish.

The probability of taking more than one fish from a school on longline gear after the school encounters the longline is shown to be good, depending upon the diameter of the school and the visual range of the fish.

If there is an inverse relationship between the fish size and the number of fish in a school and if the probability of a number of fish occurring on adjacent hooks is proportional to the size of the school, then the mean size of the fish hooked in a group should be inversely proportional to the number of fish in the group. This is shown to be true for longline catches made by the Honolulu Laboratory in the central Pacific.

The relatively low availability of schooled fish to longline gear is discussed, together with the probable effect of high mortality rates on the longline catch rates.

It is suggested that there are no fishing methods effective for schooling yellowfin where the schools are not present at or near the surface of the sea, and that schools are apparently uncommon in surface waters for the greater portion of the tropical Atlantic and Pacific and for all of the Indian Ocean, where the isothermal layer is deep. The possibility of an analogous situation for bigeye tuna is suggested for all tropical oceans.

REFERENCES

BREDER, C. M., JR. 1959. Studies on social groupings in fishes. Bull. Am. Mus. Nat. Hist. 117(6): 393–482, 28 figs., 10 plates.

BROCK, VERNON E. 1959*a*. The tuna resource in relation to oceanographic features. U. S. Fish and Wildlife Service Circular 65: 1–11, 15 figs.

——— 1959*b*. Tuna fishing methods and their application. U. S. Fish and Wildlife Service Circular 65: 12–16, 4 figs.

——— and R. H. RIFFENBURGH. 1960. Fish schooling: a possible factor in reducing predation. Jour. du Cons., Cons. Internat. Expl. Mer 25(3): 307–317.

HENNEMUTH, RICHARD C. 1961. Size and year class composition of catch, age and growth of yellowfin tuna in the eastern tropical Pacific Ocean for the years 1954–1958. Inter-Am. Trop. Tuna Comm. Bull. 5(1).

MAIS, KENNETH F., and TOM JOW. 1960. Exploratory longline fishing for tunas in the eastern tropical Pacific, September 1955 to March 1956. Calif. Fish & Game 46(2): 117–150.

MIMURA, K. 1958. Study of the fishing conditions of the yellowfin in the Indian Ocean, especially on annual differences of the hooked-rate and size composition. Rept. Nankai Reg. Fish. Res. Lab. 7: 59–71.

MOORE, H. L. 1951. Estimation of age and growth of yellowfin tuna (*Neothunnus macropterus*) in Hawaiian waters by size frequencies. U. S. Fish and Wildlife Service, Fish. Bull. 65: 133–149, 14 figs.

MURPHY, G. I., and K. C. ELLIOT. 1954. Variability of longline catches of yellowfin tuna. U. S. Fish and Wildlife Service, Spec. Sci. Rept. Fish. 119.

——— and R. S. SHOMURA. 1955. Longline fishing for deep-swimming tunas in the Central Pacific, August–November 1952. U. S. Fish and Wildlife Service, Spec. Sci. Rept. Fish. 137.

SHOMURA, R. S., and G. I. MURPHY. 1955. Longline fishing for deep-swimming tunas in the Central Pacific, 1953. U. S. Fish and Wildlife Service, Spec. Sci. Rept. Fish. 157: 1–70, 19 figs.

WILSON, ROBERT C., and BELL M. SHIMADA. 1955. Tuna longlining: results of a cruise to the eastern tropical Pacific Ocean. Calif. Fish and Game 4(1): 91–97.

YABUTA, Y., and M. YUKINAWA. 1957. Age and growth of yellowfin tuna (*Neothunnus macropterus*) in Japanese waters by size frequencies. Nankai Reg. Fish. Res. Lab. Rept. 5: 127–133.

——— and ——— 1959. Growth and age of the yellowfin tuna (*Neothunnus macropterus*) in the equatorial Pacific. Study of length frequency distributions—1. Rept. Nankai Reg. Fish. Res. Lab. 11: 77–87, 7 figs.

On the Biology of Sexual Reproduction of Hydromedusae, Genus *Phialidium* Leuckhart[1]

EDWARD C. ROOSEN-RUNGE[2]

THE GENUS *Phialidium* is nearly ubiquitous in the coastal waters of the temperate zone. The medusae occur at Friday Harbor certainly from April through September and disappear rather suddenly in October, under circumstances which need investigation. Drifting with tides and currents, they occur in swarms which greatly vary in density. During the present investigation no swarms were seen in which individuals, on the average, were closer to each other than a few inches; usually they were many inches to several feet apart. Under these circumstances it would seem that fertilization becomes somewhat of a problem. In a population which, as a whole, is moving passively, and in which individuals appear to have no affinity to each other, ovulation and spermiation must be closely and appropriately timed and the properties of eggs and sperms evolved to insure a high rate of fertility, the results of which are seen in the wide distribution and in the tremendous numbers of colonies of the sessile stages of the species, the hydroid polyps. The present paper attempts to clarify some of the factors which insure the high reproductive capacity of hydromedusae under what, on first sight, appear to be difficult circumstances.

MATERIAL AND METHODS

Among the hydromedusae found at Friday Harbor there are apparently two species of *Phialidium.* One of these, used infrequently in the present investigation, is almost certainly *P. hemisphaericum* (L.). It conforms in all essentials to the description given by Russell (1953: 287). The second form of *Phialidium*[3] was found much more frequently at Friday Harbor in August 1959 and was used prevalently in the present work. It has usually been called *P. gregarium* (L. Agassiz). It could be clearly distinguished from *P. hemisphericum* by its size, maximum 20–22 mm., the number of tentacles, up to 60, the number of statocysts, 90–120, by a thicker umbrella, a more viscous jelly and more folded lips (Fig. 1). Recently, the species has been redefined by Kramp (1962) who has pointed out the reasons for designating it as *P. gregarium,* although its original description by Agassiz must be considered inadequate.

The animals used in this investigation were almost all caught during the month of August 1959 from the dock at the Friday Harbor Laboratories at various times of the day between 0800 and 2200 hours. In the evening hours a nightlight was used in the water. The animals were taken out in glass bowls, never by hand or by net, and throughout the investigations were transferred in water by means of plastic spoons or small bowls. As a consequence of the method of catching, only animals floating near the surface (not deeper than 1 ft.) were used. In the laboratory the animals were kept in dishes of 50–1200 cc. capacity. The dishes were maintained on a water table in running sea water which kept the temperature between 11° and 13° C. The animals themselves were not kept in running water but the water was usually renewed twice a day or more often. By using only new utensils which had been soaked for at least a few days in running sea water before use, chemical contamination was held at a minimum (the pipe lines at Friday Harbor are nonmetal).

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[3] The term "*Phialidium* species" used throughout this paper should be construed to mean *Phialidium gregarium.*

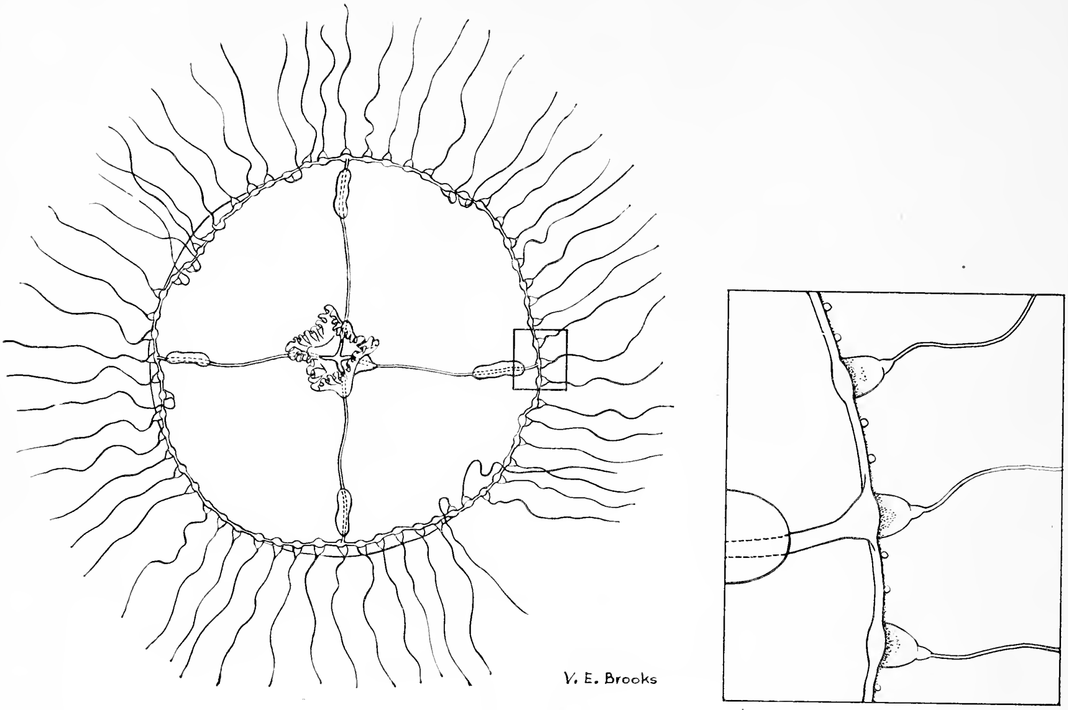


FIG. 1. *Phialidium* species. Semidiagrammatic drawing of subumbrellar view. Magnification approx. 3×.

Light conditions in the laboratory during the daytime were similar to those found in the upper layers of the sea outside. At night, for many hours after sunset, it often was much lighter in the laboratory than under natural conditions.

Moving the animals, and especially transferring them in spoons, often caused violent contractions of their bells and they frequently remained contracted for many seconds, but these rare shocks are not dissimilar to those which an animal may receive in nature by being thrown about in waves and tidal currents. A more unnatural condition was introduced by the lack of irritation during the long periods in which more or less isolated animals were kept in standing water. If a medusa lives under such conditions it usually becomes very quiet, pulsates only infrequently and may even turn upside down and lie almost motionless for a half-minute or longer at the bottom of the dish. When moved or touched it will immediately begin to pulsate again. It was not investigated whether the periods of enforced quiet had any influence on the reproductive behaviour.

No attempt was made to feed the animals in the laboratory. All animals were freshly caught a few hours before they were used and no animal was used in experiments for longer than 48 hr. Although microplankton was available in the dishes the animals rarely had any visible stomach contents at the end of the experiments, but neither did they show any effects of lack of food. Nearly all animals which were kept for days or weeks survived but after some days began to regress. The atrophy became visible first in the gonads but later in all structures of the medusa. After 7–10 days the animals showed a marked decrease in size and remained motionless unless stimulated.

Two simple techniques were used in experiments: (1) *Artificial periods of darkness* were introduced by a simple box which was put over the dishes. This box had an inlet and outlet under water through which circulation was maintained and the animals were thus kept at the same temperature as those outside the box. (2) *Sperm counts* were made of water in which males had been present. Hemocytometers (B & L) were used for counts. Preliminary studies to determine the reliability of the technique revealed that results were reasonably consistent, provided that the operator was able to identify the spermatozoa at a magnification of approximately 400×. They can be identified when either the flagellum is visible or when the size and shape of the refractile head, often together with a characteristic motion, can be recognized. In the final counts spermatozoa were counted only when these two sets of criteria were verified singly or in combination. Sperm were counted in the whole area of the chamber, 1 mm.[2] Usually no dilution of the water containing sperm was necessary. The water was stirred thoroughly, and sucked into a leucocyte pipette, and shaken briefly; the first two drops were discarded and the chamber was filled. Long shaking proved to be unnecessary because the spermatozoa of *Phialidium* show no tendency to congregate or coagulate. In fact, the relative ease and reliability of the method appeared to rest in great part on these characteristics.

Many observations were made with the dissecting microscope at magnifications between 25 and 50×. In addition, the gonads were often studied in anesthetized animals (chloretone-magnesium chloride was added until the animals remained quiet) with the phase microscope, usually under a magnification of 400× but occasionally up to 1,000×. Histological preparations were made of the gonads. A battery of fixatives, including acrolein at room temperature and chilled 1 per cent potassium permanganate, was tried. However, the more conventional methods—such as Bouin's solution in sea water or 10 per cent formalin for 1–2 hr. with after-fixation for 1–2 hr. in Helly's or Maximow's—gave better results. The preparations (3–6 μ thick) were stained with Heidenhain's Iron-Hematoxylin, Heidenhain's Azan, or with the PAS reaction.

RESULTS

Observations and Experiments on Ovulation

Every female *Phialidium* with intact gonads brought into the laboratory during August 1959 released eggs at least once within the next 24 hr. In several cases ovulation was observed directly, but usually the approximate time of ovulation was calculated from the age of the developmental stages of the eggs observed at varying times after ovulation. The data used were derived from many observations of developing eggs and are summarized in Table 1. After ovulation the outline of the ovary is smooth and the eggs appear compressed into the confines of the "linear" gonad. Several hours before ovulation the eggs to be ovulated can be recognized because they begin to bulge at the surface of the ovary. At first the ovary presents a slightly wavy surface but shortly before ovulation the eggs have completely protruded and appear to hang like grapes from a stalk. Ovulation usually takes place within 10–15 min. The majority of the eggs are released in less than 5 min. In a fully grown and well-fed specimen a total of 50–70 eggs may be released, in smaller animals only 10 to 20, but occasional ovulations of only 1 egg or of very few ova were also observed.

The eggs are very gently released from the ovary without any motion which would indicate that they are propelled. However, as soon as they become free in the subumbrellar cavity, they are rapidly dispersed by means of the pulsations of the animal. Usually, the females are very actively pulsating during the period of ovulation as though they were somewhat irri-

TABLE 1

TIME TABLE FOR CLEAVAGE STAGES OF *Phialidium* SPECIES AT 11°–13° C.

FROM OVULATION AND IMMEDIATE FERTILIZATION	
To Beginning of:	Average Times
1st cleavage	50 min.
2-cell stage	70–90 min.
2nd cleavage	95 min.
4-cell stage	110–120 min.
8-cell stage	150 min.
approx. 16-cell stage	180 min.
approx. 32-cell stage	210 min.

tated. Two females were observed in contraction during the height of ovulation, in the same way in which animals contract which have been violently touched. These females were lying upside down for about a minute, during which many eggs fell slowly from the ovary into the subumbrellar cavity. When the animals began to pulsate normally again they righted themselves and immediately scattered the eggs widely into the water.

In the majority of cases ovulation took place twice within 24 hr., once at night after sunset and once in the morning before sunrise. Nineteen dishes containing 2–6 females each were studied at various times through 24 hr., and the observed ovulations and eggs indicated that in every case at least 1 female, often all, had two ovulation periods. In 45 different cases, individual females were observed through at least 24, sometimes through 48 hr. Twenty-one had an evening and a morning ovulation and all 5 animals which were observed for another day showed another evening and morning ovulation. Twenty animals had only an evening ovulation. Of these, 5 were observed for 24 hr. longer and 3 continued in the same pattern with evening but no morning ovulation. The other 2 had an evening and a morning ovulation on the second day. Four females had only a morning ovulation on the first day and 1 of these, observed for another day, then had only an evening ovulation.

In 32 individual cases the ovulation time was determined (Fig. 2). It was found that ovulations occurred from 55 min. before to 4 hr. after sunset, with the majority of cases between 1 and 3 hr. after, and from 1¾ hours before to 2¾ hours after sunrise, with most ovulations occurring about 1 hr. before. Many other cases not recorded in detail appeared to fall within these limits—with a few notable exceptions. Two animals shed a few eggs around noon; in each case there had been several transfers immediately before ovulation. There were other occasional observations of single eggs being released at almost any time of the day.

In those cases in which both evening and morning ovulations were observed, the evening ovulation nearly always produced the greater number of eggs. Furthermore, eggs were almost 100 per cent fertilized in the evening but only 90 per cent or less in the morning.

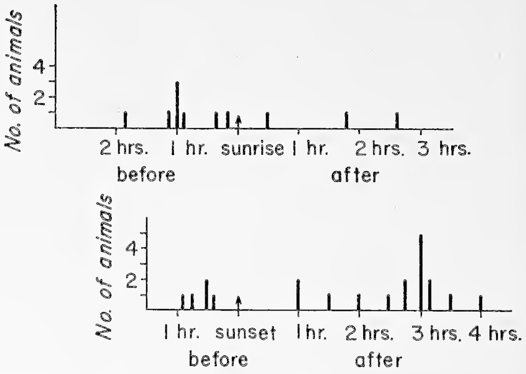


FIG. 2. Ovulation times of *Phialidium* species.

Only a few individuals of *P. hemisphaericum* were thoroughly investigated. It appeared that this species also usually ovulated after sunset and in the morning, but in 6 cases in which the morning ovulation was timed precisely it occurred 2–3 hr. later than in the animals of *P.* species observed on the same mornings.

Several series of experiments were performed to ascertain in a general way the effect of light on the times of ovulation. Of these six will be recounted as examples.

Experiments with Morning Ovulation

No. 1: Nine pairs of *P.* species were kept separate, darkened around the time of sunset (1915), until the dark box was removed at 0510, about 20 min. after sunrise. Five females had ovulated late at night, as did all of the 4 controls. Of these 5 only 3 ovulated again on the following morning, at 0555 and two at 0630. The 4 females which had not ovulated at night released eggs at 0515 and 0530. One female ovulated at 0400, the same time as all 4 controls. The dish containing this animal was found to receive some light through a drainage hole.

No. 2: Five pairs of *P.* species were kept separate, darkened around the time of sunset (1920), until the dark box was removed at 0600, 1¼ hr. after sunrise. All females laid eggs late at night, as did the 4 controls. All females had morning ovulations between 0700 and 0830; 3 of the controls ovulated between 0400 and 0530, 1 did not ovulate in the morning.

NO. 3: Three pairs of *P.* species were kept separately and darkened around the time of sunset (1910). The dark box was removed at 0735, about 3 hr. after sunrise. All 3 females laid eggs at 0900, 1 at 1000, and 1 had apparently released eggs over a protracted period from 0500 to 0630 while still in the dark. The 2 controls ovulated around 0400.

These experiments indicate an effect of light on morning ovulation. In 13 out of 17 cases, ovulation occurred much later than in the controls. Ovulation occurred 5 min. to 3 hr. after exposure to light, with 7 cases ovulating after 1½ to 2½ hr. Intervals were very short only in the experiment (No. 1) in which the difference between artificial exposure to light and sunrise was not great.

Experiments with Evening Ovulation

NO. 4: Six pairs of *P.* species, 2 pairs to a dish, were darkened from noon until 1645. One female ovulated at 1445, 2 at 1600, the other 3 between 2000 and 2200. Three controls ovulated between 2100 and 2200.

NO. 5: Four pairs of *P.* species, kept separate, were darkened at 1300, 4 were darkened at 1500. The experimental animals were kept in the dark until the dawn on the next morning, but were briefly subjected to light on four occasions during the evening. Four controls laid eggs at night, 2 at 2000, and 2 at 2150; only 1 control ovulated the next morning, at 0700. One control which had laid a few eggs at noon immediately after having been caught from the sea, shed 2 eggs at 1500 and 3 eggs around 1700. All of these developed normally. The experimental animals which were darkened at 1300 behaved essentially like the controls; 2 laid eggs around 2200, 2 between 2300 and midnight. Three of the animals put in the dark at 1500 ovulated around 1830 and again in the morning between 0330 and 0500, 1 ovulated at 2230 and had no morning ovulation. Fertilization and development of the eggs appeared normal in all cases.

NO. 6: Series A consisted of 4 pairs, kept separate, which were put into the darkbox at 1600. Series B, also 4 pairs, were treated in the same way as Series A; these were animals used in experiment No. 5, which had been darkened at 1500 on the previous day. Four controls were kept, of which 2 had been used as controls on the day before. The last ovulated between 2230 and 2300 but not on the following morning; of the other controls, 1 ovulated at 2300 and 0830 the other at 1800 and around 0500.

All animals of Series A laid eggs between 1930 and 2000 and 1 female ovulated in the morning around 0830. Those of Series B ovulated at 2030, 2100, and 2115, and 1 had no evening ovulation but shed eggs at 0430.

These experiments, and others not reported in detail, indicate an effect of darkening on evening ovulation depending on the time of day at which the animals are put in the dark. Of 10 animals darkened at noon or 1300, 2 ovulated after 2½ to 4 hr. Of 4 animals darkened at 1500, 3 ovulated 3½ hr. later. All 4 animals darkened at 1600 ovulated 3½–4 hr. later. Animals which appeared to respond to darkening at 1500 on one day seemed to respond more slowly to darkening at 1600 on the next day: 3 out of 4 shed eggs 4½ to 5¼ hr. after darkening. There was no indication that brief exposure to light, which in some experiments took place after the period of dark, had any influence on ovulation.

Observations and Experiments on Sperm Production

Spermiation (sperm release) involving small numbers of spermatozoa was repeatedly observed. When males were closely scrutinized around the usual ovulation times of the females, the surface of the testes was sometimes seen to be uneven in places. Under the phase microscope at magnifications around 400 × it was observed that the surface cells in such areas appeared thickened and bulging. Spermatozoa in small numbers appeared to move slowly in a smooth and almost continuous stream through breaks in the surface. Within the testis the flagella of the sperm cells showed a low degree of motility but the flagellar motion increased as the spermatozoa became free of the gonad. Immediately after the release the flagellar beat of the epithelial cells of the gonadal surface swept the spermatozoa away. Whenever males were closely observed, some living spermatozoa were found moving about in the vicinity of the gonad even though actual spermiation was not always seen.

TABLE 2

AVERAGE TOTAL SPERM COUNTS PER MALE FOR VARIOUS INTERVALS OF TIME, BEGINNING AT 1600 OR 1700

EXPERIMENT	NO. OF MALES	INTERVAL (hours)	TOTAL COUNT PER MALE IN 10^6
1	8	2½	1.2
	8	19	2.5
2	8	17	2.4
	8	26	1.2*
3	4	14	3.6
	4	16	3.6
4	4	18	2.9
5	4	1	0.4
	4	19	2.9
6	2	1	0.4
7	1	1	0.5
	1	2½	1.1
8†	1	16	2.2

* Many dead spermatozoa seen.

† Data from animal *A* of Fig. 3, to show comparability.

Some years ago a major sperm release was once accidentally observed in which dense clouds of spermatozoa issued from the gonads of an animal about the time of sunrise. In the present investigation many attempts were made to observe a major sperm release in the late evening and early morning hours but all were unsuccessful. The number of spermatozoa observed to leave through small breaks in the gonadal surface never exceeded one or two hundred.

It was observed that sperm cells dispersed rapidly. Their motility was extremely vigorous in fresh preparations. When the spermatozoa were confronted with small obstacles the speed and excursion of flagellar activity was remarkable. Even hours after spermiation spermatozoa were often seen to move energetically in the counting chamber.

Results of sperm counts are demonstrated in Table 2 and Figure 3. In studying the data it should be kept in mind that every 10,000 spermatozoa in the total counts correspond to 1 single spermatozoon actually counted. The accuracy of the individual counts is, therefore, not high, particularly in the lower range. However, the data in Table 2 are fairly consistent throughout and indicate an approximate rate of production of at least 3,000,000 sperm per day on the average.

The data presented in Figure 3 appear to confirm what direct observations indicated, that sperm release may occur in small amounts at almost any time of day or night but that there are major periods of release in the late evening and early morning hours. There appear to be great individual variations in this phenomenon. In all probability major periods of spermiation are brief.

Sperm Concentrations and Fertile Age of Eggs and Sperms

A number of experiments were performed which indicated that spermatozoa survived and were fertile in considerable dilution. Females were transferred through several changes of filtered sea water and kept in filtered sea water in order to exclude the accidental presence of spermatozoa. Sperm was added in various dilutions and at various times before and after ovulation. For instance, approximately 4 cc. out of 250 cc. of sea water in which one male had been swimming from 1720 on were added at 2200 to a bowl containing freshly laid eggs in 250 cc. of water. On the next morning at 0600 about 50 eggs were found in normal development. Four similar experiments were performed on various days with essentially the same re-

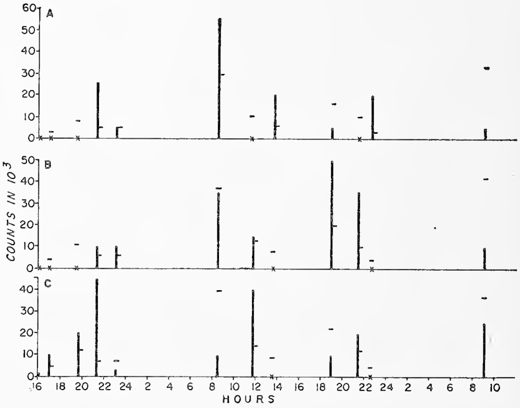


FIG. 3. Sperm counts of 3 different males of *Phialidium* species. Each column represents the amount of spermatozoa shed since the last count (after each count there was a thorough change of water).

x = count 0.

– = theoretical count if sperm had been shed continuously and in equal amounts over the whole period of observation for the respective male .

sults. In the absence of sperm counts it may be assumed that the water in which the male had been swimming for 4 hr. and 40 min. contained at least 1.5 million spermatozoa or 6,000/cc. This means that at least 24,000 sperm were added to the 250 cc. of water containing the eggs. Fertilization presumably took place at an average sperm concentration of about 100/cc. This concentration appeared ample as failures were not recorded in these 5 experiments. Concentrations of approximately 2 spermatozoa/cc. were always unsuccessful, while concentrations between 5 and 80/cc. were successful in varying degrees. For instance, in one experiment a drop (about 0.05 cc.) out of 250 cc. of water in which 8 males had been placed for 12 hr. was added to 88 eggs in 130 cc. of water. Eight of the eggs were fertilized and developed normally. If it is assumed that 8 males produced about 16 million spermatozoa in 12 hr. (Table 2) then approximately 30,000 sperm were added to the eggs and acted in a concentration of 32/cc.

At all concentrations of less than 100 spermatozoa/cc. fertilization occurred over a period of time which extended over 2½ to 3 hr. (as estimated by the appearance of the first furrow). In these cases the eggs which began development last often developed abnormally. It was possible, however, in some cases to fertilize eggs with higher concentrations of sperm until 4½ hr. after ovulation; these eggs showed a high proportion of normal embryos.

When sperm which was 10 hr. old was used in high concentration to fertilize fresh eggs, less than 50 per cent of the eggs developed and these began development slowly, ½ hr. after ovulation. The age of the sperm below 10 hr. did not appear to make an appreciable difference in the rate of fertilization. In one case a few eggs developed normally after having been fertilized with spermatozoa nearly 12 hr. old.

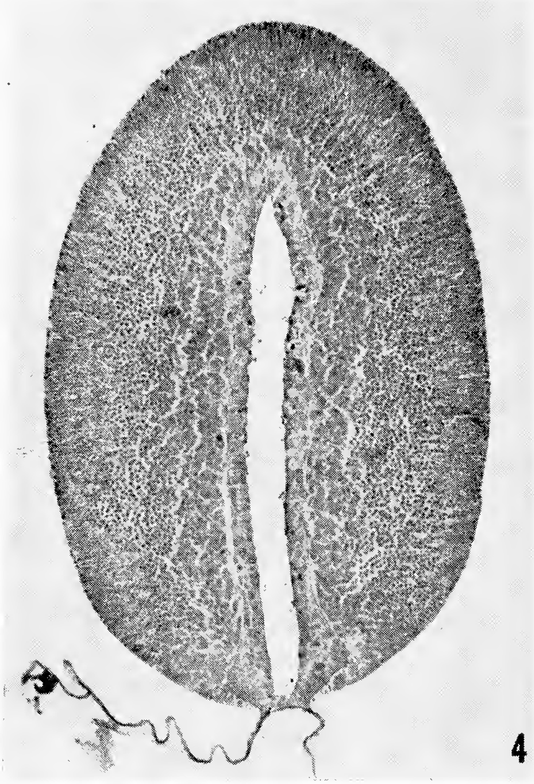
Some Notes on the Histology of the Gonads

There are very few observations on the internal structure of the gonads of hydromedusae in the literature. The most extensive observations were made by O. and R. Hertwig (1878: 27), whose figures depict many of the features found in the present investigation. Brooks (1888) and Mayer (1910: 271) have described the process by which, in *P. McCradyi,* hydroid blastostyles develop in the region of the gonads, and they have given casual descriptions of the normal structures. As a consequence of the small amount of research done on the subject, the prevailing view today is that "the gonads in hydromedusae can scarcely be designated organs, being merely accumulations of sex cells in definite sites" (Hyman, 1940: 431). The following brief account of the histology of the gonads of *Phialidium* is a preliminary survey and is appended here only because a basic knowledge of the structure of the ovary and particularly of the testis is helpful in discussing the biology of reproduction. In a future publication a detailed and more quantitative account of gametogenesis in *Phialidium* will be given.

The gonads in *Phialidium* (Figs. 4, 5) are situated at the subumbrellar side around the radial canals. The canals not only widen inside the gonad but their gastrodermal lining takes on a special character. It is much taller and more complex in structure throughout the extent of the gonad. This specialized epithelium is most developed in the most active gonads and regresses in correlation with regression of the gametogenic tissues.

In the male, the gastroderm is delimited toward the gonad by a conspicuous basement membrane which is PAS positive and stains strongly with aniline blue. The membrane appears somewhat scalloped, with fine processes pointing at regular intervals toward the surface of the testis (Fig. 4). In the female the gastrodermal cells often extend among the gametes, surrounding them in places and even appearing to attach themselves to their surface.

In both sexes the gonads are covered with a pigmented epithelium composed of fairly large cells. The degree of pigmentation varies; it is greater in *P. hemisphaericum* than in *P.* species, and the pigment granules appear larger and more frequent in males than in females. In the ovary this epithelium is clearly demarcated in most areas by a PAS positive basement membrane. In the testis the morphology of the surface cells is complex and has not been elucidated in full detail. It was observed, however, that the nuclei often lie considerably below the surface



FIGS. 4, 5. Cross-section through testis of *Phialidium* species, with a small piece of subumbrellar epithelium attached; PAS stain, 6 μ thick; magnification 115×. 5, Cross-section through ovary of *Phialidium* species; PAS stain, 6 μ thick; magnification 115×.

and that columns of cytoplasm appear at intervals to extend from the surface and in some cases, perhaps in all, reach the basement membrane of the gastroderm with more or less tenuous processes. Along these processes of the surface epithelium the spermatids appear ordered. The flagella generally point in bundles toward the basement membrane. In the testis the gametes are arranged in definite layers within which the germ cells are often in the same stage of development over large areas. A generation of large spermatogonia is situated near the basement membrane; next in the direction toward the surface is another layer of smaller spermatogonia, then follows a layer of spermatocytes and one of spermatids. The thickness of the last layer varies greatly. In the ovary (Fig. 5) the gametes are not aligned in definite order. The largest oocytes usually bulge on the surface and stretch the surface epithelium to a very thin layer.

DISCUSSION

Apparently it has not been reported before that *Phialidium* (or any other species of Hydromedusae) may regularly ovulate twice within 24 hr. Metschnikoff (1886 :25) stated that "*Clytia flavidula*" spawned at Naples between 8 and 9 A.M. in March and April while "*Clytia viridicans*" spawned at 8 P.M. *Clytia flavidula* is now generally regarded as identical with *P. hemisphaericum* (Mayer, 1910 :267; Russel, 1953 :293), and *Clytia viridicans* is considered to be identical with *P. buskianum,* which is possibly only a variety of *P. hemisphaericum* (Mayer, 1910 :267, 270). In any case, the two species of Metschnikoff are very closely related to each other and to the species described in the present paper. It is difficult to understand—even if it is conceivable—that Metschnikoff did not recognize two daily periods of spawning if they occurred. The possibility must be considered that the Mediterranean forms behave differently from those observed at Friday Harbor.

Ovulation appears to be regulated within certain limits by a change in light. Metschnikoff reported Merejkowsky as the first to suggest that ovulation in *Obelia* might be stimulated by light, but Metschnikoff rejected the suggestion because of the occurrence of evening ovulation in many other species. The experiments reported in the present paper indicate that eggs will be released not only at exposure to light but whenever there is a drastic change in the lighting intensity after lighting conditions have been more or less constant for several hours. Artificial darkness, if applied after noon, will produce ovulation in the course of several hours. The later the animals are subjected to darkness the more certain ovulation will take place as a result of it. In the morning an artificial prolongation of darkness of the night will delay ovulation in most cases. There are indications that ovulation cannot be delayed indefinitely by these means, but no experiments to elucidate this point were performed.

There is as yet no direct evidence that sperm release is affected by changes in illumination. There is some evidence that major sperm releases take place at approximately the same times as ovulations. It appears, therefore, reasonable to assume that spermiation is also sensitive to photostimuli. Although the periods of spermiation have been less precisely determined, and may in fact vary more than the ovulation periods, the sequence of generations as seen in sections of the testis (Fig. 4) is remarkably orderly. In the ovary, also, several generations can be distinguished even on superficial examination, although they are not ordered in strata.

At present it is not apparent how the regular periodic sequence of generations is accelerated or delayed by light changes. Observations on animals under normal as well as experimental conditions suggest that in many cases there is a latent period between light stimulus and ovulation which may be as long as 3 hr. or more. This interval may be long enough to permit changes in growth rate to become apparent. There are some cases, however, which show a fast response within 20 min. to 1 hr., and in these cases it must be assumed that the eggs were nearly mature and ready to be ovulated when the stimulus acted. Would they have ovulated at the same time without the stimulus?

A mechanism by which light might act on the actual release of gametes may be found in the epithelial cells covering the gonads. These contain appreciable amounts of pigment and have been observed to be contractile. It is, therefore, plausible to think of the release as initiated by metabolic changes in the surface cells which in turn bring about contraction. In the testis, contraction of the surface cells may act in two ways: the surface may become discontinuous and the contraction of the cellular processes (or some surface change along them) may release the spermatids. Live observations are in good agreement with this concept. In the ovary the surface cells have not yet been investigated in detail, but they appear to have no processes in association with the oocytes. It is certain, however, that eggs are ovulated through breaks in the epithelium.

It appears probable that light affects the rate of growth of the gametes as well as their release. Living ovaries were observed often after experimental light stimulus and were compared with controls. In general, the eggs grew faster with the stimulus than without. While the surface epithelium of the ovary has no conspicuous connections with the oocytes, the gastroderm underlying the gonad is a highly differentiated, specialized tissue containing a yellow or orange pigment which is dissolved by fat solvents. The possibility should be entertained that the nutrition of the oocytes may be changed through metabolic changes in the entoderm cells initiated by a reaction of the pigment.

The quantitative data on sperm production, crude as they are, enable us to arrive at a rough estimate of the relationship of density to fertility in swarms of *Phialidium*. If we assume that eggs are fertilized with 100 per cent probability at a concentration of 100 sperm/cc, that practically none are fertilized at 2 sperm/cc, and that a male releases about 1 million spermatozoa at a major spermiation; if we further stipulate a random 3-dimensional distribution of a population composed equally of males and females, then a swarm with average distance between individuals of 18 cm. will fertilize all its eggs, while one with an average distance of 69 cm. will have practically no offspring. The average distances in swarms observed at Friday Harbor were rarely less than 25 cm. and often much greater. Mayer (1910: 270) reported that *P. languidum* crowded the harbor of Eastport, Maine, during July and September "to such an extent that their bells nearly touch as they swim at the surface of the water." In such concentrations there must be an excess of spermatozoa present if the sexes are represented equally (there is evidence that this may not be the case: at Friday Harbor occasional swarms had very unequal sex proportions). On the other hand, the prevalent density of swarms at Friday Harbor in August 1959 was such that sexual reproduction was probably very low despite the fact that huge numbers of animals were present in the waters. Wherever a meeting of gametes was successfully accomplished it was due to the combined action of the following factors favoring fertilization: survival and action of spermatozoa in great dilution, fertilizability of the ova for many hours after ovulation, and the presence of a "trigger"—light—which regulates ovulation and spermiation alike and thus brings them about at approximately the same times of day.

SUMMARY

Observations on living and histological material, simple experiments with photostimulus, and sperm counts provided the following data concerning the biology of reproduction in *Phialidium* species. and *P. hemisphaericum:*

1. Females have two ovulation periods per day, in the majority of cases: one at night some hours after sunset, one in the morning before sunrise.
2. Males release some sperm almost continually, but major periods of spermiation occur at about the times of ovulation.
3. The total number of eggs released by mature females in 24 hr. is 50–100; the total number of sperms per male is in the order of 3 million in 24 hr.
4. Spermatozoa act in great dilution and retain their vitality in dispersion. At a concentration of 100 spermatozoa per cc., 100 per cent normal fertilization was obtained.
5. Spermatozoa remain fertile for 11–12 hr. under laboratory conditions, eggs for at least 3–4 hr.
6. Artificial darkness before sunset will cause ovulation earlier than normal; artificial extension of darkness beyond sunrise will delay ovulation.
7. The gonads, particularly the testes, are organs of some complexity. In them the gametes ripen in fairly rigid succession of generations. There is an unexplained, apparently inherent rhythm underlying the twice daily sperm and egg release, even though the exact timing of these events is influenced by the rising and setting of the sun.

REFERENCES

BROOKS, W. K. 1888. The life history of *Epenthesis McCradyi* (n. sp.). Stud. Biol. Lab. Johns Hopkins Univ. 4: 147–162.

FOERSTER, R. E. 1923. The Hydromedusae of the West Coast of North America with special reference to those of the Vancouver Island region. Contr. Canad. Biol. 1: 219–278.

HAECKEL, E. 1879. Das System der Medusen. Jena. Vol. 1.

HERTWIG, O., and H. 1878. Der Organismus der Medusen. Jena.

HYMAN, L. H. 1940. The Invertebrates. New York and London. Vol. 1.

KRAMP, P. L. 1962. Notes on Some Eastern Pacific Species of *Phialidium* (Leptomedusae). Pacif. Sci. 16(1).

MAYER, A. G. 1910. Medusae of the World. Carnegie Inst. of Wash. Publ. 109. Vol. 2.

METSCHNIKOFF, E. 1886. Embryologische Studien an Medusen. Wien.

RUSSELL, F. S. 1953. The Medusae of the British Isles. Cambridge.

Notes on Some Eastern Pacific Species of *Phialidium* (Leptomedusae)

P. L. KRAMP[1]

A COLLECTION OF *Phialidium* was sent to me by Dr. E. C. Roosen-Runge, University of Washington, Seattle, who wanted my opinion on their specific affinity. They were collected at Friday Harbor in Puget Sound, some few in August 1959, a great number in June 1960. They all belong to one species and agree perfectly with the species which was described by Murbach and Shearer (1903) under the name *Phialidium gregarium* (A. Agassiz). It is questionable, however, whether the medusa observed and carefully described by Murbach and Shearer really belonged to the same species, which was briefly described by Agassiz as *Oceania gregaria.*

According to the first description by A. Agassiz (in L. Agassiz, 1862: 353), *Oceania gregaria* had "four pale-yellow, linear ovaries, extending from the circular tube along half the length of the chymiferous tubes. Thirty-six short tentacles, not capable of great expansion. Lips of actinostome very thin, convoluted. Three quarters of an inch in diameter." It was found in the Gulf of Georgia, from May to September. A. Agassiz (1865: 74, fig. 103) did not repeat the description, but emphasized "the great length of the slender lips" in contradistinction to the eastern American species *Oceania languida,* from which it also differed in the colour of the gonads and tentacle bulbs, which were "a beautiful pale yellow, in strong contrast to the dark coloring of our species" (i.e., *O. languida*). "The whole surface of the water for several miles was often thickly covered with these Medusae." *O. languida* was said to have 32–40 tentacles, and "the ovaries and the base of the digestive cavity are light brown; the base of the tentacles is somewhat darker." Haeckel (1879: 188) quoted Agassiz's description of *O. gregaria,* but as to the position of the gonads he used the somewhat stronger expression "den Schirmrand unmittelbar berührend."

Murbach and Shearer (1903: 179, pl. 20, fig. 1, 1a) thought they saw two species in Victoria Harbor, *Phialidium languidum* and *P. gregarium,* but the descriptions of both are almost completely alike, except that in *P. languidum* there are two marginal vesicles between successive tentacles, in *gregarium* one, occasionally two; both were 12 mm. in diameter; in *P. languidum* there were 60 tentacles, in *P. gregarium* the number of tentacles and "buds destined to develop" likewise 60. The short diagnosis of *P. gregarium* in Mayer (1910: 272) is derived from Murbach and Shearer, and he doubts the occurrence of *P. languidum* in Puget Sound. Since then, *P. gregarium* has repeatedly been recorded from Puget Sound; the hydroid was reared by Strong (1925: 384, figs. 1–6), and physiological experiments were carried out by Hyman (1940: 282ff) and Bonner (1955: 18–20, fig. 1, A–E).

An important account is given by Foerster (1923: 259), who examined Atlantic specimens of *P. languidum* in comparison with the Pacific forms; he found that "there seem to be differences between the common Atlantic form, *P. languidum,* and the common Pacific form. Yet there are intergrading forms, such as *P. languidum* Murbach and Shearer and *P. lomae* Torrey, which have characteristics common to both species and thus are united to the older species." Foerster, therefore, found it "advisable to consider the Pacific form of *Phialidium* a variety of the Atlantic form, *P. languidum.*" His comparison, however, seems to me to reveal such considerable differences that the two species cannot possibly be identified, which is confirmed by my own examination of specimens from both areas. (As to *P. lomae,* see below.)

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[1] Zoological Museum, Copenhagen, Denmark. Manuscript received January 9, 1961.

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The specimens are up to 21 mm. in diameter, most of them between 15 and 20 mm.; unfortunately there are very few younger specimens. The umbrella is watchglass-shaped, the stomach is small, its perradial diameter less than 3 mm., its base distinctly cruciform. The mouth lips are fairly long and narrow, spread outward, tapering, but not sharply pointed, the margins densely and regularly crenulated throughout the entire length, without any difference between the various portions of the margin.

The gonads are laterally compressed bands, up to 1 mm. in height, more or less wavy with up to three bendings to either side; in good-size specimens the gonads occupy the distal half of the radial canals or slightly more, reaching almost, but usually not quite to the ring canal; male and female gonads are of the same length and shape. The sample contains slightly more female than male individuals. Dr. Roosen-Runge tells me (in a letter) that he has observed sex reversal from male to female; in the sample examined by me no hermaphroditic specimens were found.

The tentacle bulbs are almost globular, as broad as long; the extended tentacles are almost equally thin throughout their length and uniformly armed with nematocysts. The velum is thin, up to 1 mm. broad. In specimens 16–20 mm. wide the number of fully developed tentacles varies between 48 and 65, and averages 56. There are always a few young bulbs not yet developed into tentacles; in specimens 16–20 mm. wide the average total number of tentacles plus young bulbs is 60, varying between 51 and 67, and in the somewhat younger specimens, 13–15 mm. wide, the average number is very nearly the same, 59.

As opposed to the comparatively slight variation in number of tentacles, the number of marginal vesicles is very variable. There may be one or two, exceptionally three, marginal vesicles in the spaces between successive tentacles (including young bulbs). Usually it has not been possible to count the marginal vesicles in the entire margin of the specimens, but in a great number I have been able to calculate the percentage number of spaces with two and with only one marginal vesicle. The results are seen in the following table.

NO. OF TENTACLES + YOUNG BULBS	PER CENT OF SPACES WITH ONLY ONE MARGINAL VESICLE	
	Average	Variation
51–55	63	43–78
56–60	71	43–88
61–65	63	41–80
(66–71	64	62–69)
51–60	66	43–88
61–71	66.5	44–80

It appears from these figures that in most of the specimens examined there are more spaces with one than with two marginal vesicles, but in some specimens the opposite is the case, and the percentages are independent of the number of tentacles in the individuals. Examination of young specimens might have revealed a certain regularity in the succession of the development of the marginal vesicles (see below on *Phialidium lomae*).

A feature which apparently has escaped the attention of previous observers is the pigmentation, which consists of fine, black granules. They are present everywhere in the walls of the stomach, and are especially dense along the lines of attachment to the subumbrella; the lips are very faintly pigmented except along the free, crenulated margins, where the granules are densely set; the radial canals have no black pigment, but granules are evenly distributed on the gonads, mainly on their adoral margin; the tentacle bulbs are evenly and rather densely pigmented, but not so densely that they are conspicuously dark; on the umbrella margin, on the other hand, the pigmentation is so concentrated that the margin appears as a sharp, jet-black rim, very conspicuous when seen on a white background; the marginal vesicles are destitute of pigment. In no other species of *Phialidium* have I seen a similar pigmentation.

Comparison with Other Species

The delimitation of the numerous species of *Phialidium* is very difficult, and the genus certainly needs revision. Among the species which have been described from Pacific waters, we may at once exclude the small medusae with only 16 tentacles: *ambiguum* (Agassiz & Mayer) from the Fiji Islands, *pacificum* (Agassiz & Mayer) likewise from the Fiji Islands, *rangiroae* (Agassiz & Mayer) from the South Pacific; likewise *simplex* Uchida from the Palau Islands, with up to 28 tentacles, and *pacificum* Maas from the Malayan Archipelago, Torres Strait, and China, with up to 32 tentacles. (The two latter species shortly will be provided with new names.) There are, however, a few Pacific species, which may have a size and a number of tentacles similar to the common Puget Sound species generally named *Phialidium gregarium.* One of them is *P. simplex* Browne; it is up to 22 mm. wide, with 60–85 tentacles and a few young bulbs; it differs from our species in having somewhat longer gonads, only one marginal vesicle between successive tentacles, and a complete lack of black pigmentation; moreover its occurrence is far removed from the Pacific coast of North America: Falkland Islands, Brazil, South Africa and northeastern Australia.

Phialidium lomae was described by Torrey (1909: 22, fig. 8) from San Diego in California. It was 9–12 mm., rarely 14 mm., in diameter, with 28–34 tentacles, rarely more, though one specimen had as many as 66; rarely did it have more than one marginal vesicle between successive tentacles; it had gonads along the distal half of the radial canals; and the lips were short. I have seen a few specimens of this species from the coast of Chile (Kramp, 1952: 7, figs. 3–5), and numerous others from San Juan Island, Wash., collected in August 1954 by H. H. Osborn. They are up to 18 mm. in diameter, and none of them have more than 36 tentacles. The collection is particularly interesting, because it contains specimens of all sizes between 6 and 18 mm. in diameter, so that it represents a valuable developmental series. The mouth lips are generally short and blunt, but during growth they become more folded and pointed, though not as much as in the medusa from Puget Sound. In young specimens the gonads first appear in the middle of the radial canals, whence they are gradually prolonged outwards; in specimens more than 8 mm. wide the gonads occupy the distal half of the radial canals, or slightly less, though they do not quite reach to the ring canal; they are of equal shape in both sexes.

The number of fully developed tentacles increases gradually from 22 in the smallest specimens to 36 in specimens more than 14 mm. wide, but there is a corresponding decrease in the number of young bulbs, from 14 in the youngest to 2 or 3 in the largest, so that the total number of tentacles and young bulbs remains unaltered, between 32 and 40, independent of the age within the sizes observed, and with remarkably slight variation.

Of particular interest is the number of marginal vesicles, which increases considerably during the growth of the individuals. The number of marginal vesicles between successive tentacles is generally considered an important character for distinction of species within the genus *Phialidium,* but the present collection makes this distinguishing character less reliable. In specimens up to 9 mm. wide the number of marginal vesicles is very nearly the same as the number of tentacles plus young bulbs, but in specimens more than 9 mm. wide the number increases, in the largest specimen observed, 18 mm. wide, even to somewhat more than twice the number of tentacles plus bulbs; in the larger specimens there are two vesicles in most of the spaces, but occasionally one or three.

It must still be mentioned that no black pigmentation like that in the medusae from Puget Sound is found in *P. lomae.*

Mayer (1910: 495) could "not distinguish this California medusa from the common *Phialidium languidum* of the Atlantic coast of North America." A direct comparison between the two species, however, strongly contradicts the supposition that they should be identical; and, as will appear from the above statements, it is also excluded that the medusa from Puget Sound may belong to *P. lomae* Torrey.

On a previous occasion (Kramp, 1933: 239) I have examined a collection of *Phialidium languidum* from the Gulf of Maine, where this eastern-American medusa is very abundant. It is well described by Mayer (1910: 269, pl. 33, figs. 4–8, pl. 34, fig. 5). *P. languidum* is usually 15–20 mm. in diameter; the walls of the umbrella are fairly thin and flexible; the manubrium is small and tubular; the mouth has four small, slightly recurved and simple lips; the gonads are linear along the outer 1/2–2/5 of the radial canals. In specimens from the New England coast there are usually 32 tentacles, but according to Mayer specimens from Florida may have a somewhat larger number of tentacles; the number of marginal vesicles between successive tentacles is usually two, though sometimes one or three. I have re-examined the collection previously dealt with by me and compared it with the collection from Puget Sound, and I find the two species entirely different. Nothing like the long, pointed, crenulated lips in the Puget Sound medusa are found in *P. languidum,* the medusa from Puget Sound has a larger number of tentacles, and in most of the spaces between the tentacles there is only one marginal vesicle. Moreover *P. languidum* is entirely destitute of the characteristic black pigmentation mentioned above.

My previous examination of *P. languidum* was made in order to compare it with the common European *P. hemisphaericum;* I found the medusae of the two species indistinguishable, their range of variation being overlapping, but I hesitated to unite them owing to the available accounts of their hydroids.

Dr. Roosen-Runge, in a letter to me, is inclined to think that some of the specimens collected in Puget Sound in June 1960 belonged to *P. hemisphaericum;* this species, however, has never been recorded in literature from the eastern Pacific, and none of the specimens sent to me can be referred to it. *P. hemisphaericum,* it is true, seems to have a much more extensive distribution than was known up to now. I have recently examined a great number of *Phialidium* specimens from the southwestern Pacific and the Malayan Archipelago, which I cannot distinguish from our common European species; but I dare say that the western-American medusa commonly called *P. gregarium* is very different from *P. hemisphaericum.*

We then return to the question, whether the medusa described by Murbach and Shearer (1903) was identical with *Oceania gregaria* Agassiz. The statements that both forms may occur in enormous quantities in the same waters and at the same season suggest that they belong to the same species. The characteristic shape of the mouth lips likewise points towards a unification of the two forms. The great obstacle is that in *Oceania gregaria* Agassiz the number of tentacles was only 36, even in specimens ¾ in. (20 mm.) in diameter, whereas there were many more tentacles in specimens of corresponding sizes observed by Murbach and Shearer. We may presume, perhaps, that Agassiz overestimated the size of his specimens; or that young bulbs and developing tentacles, were present between the fully developed tentacles, increasing the total number towards a number similar to that stated by Murbach and Shearer.

CONCLUSIONS

The results of the present investigations may be summarized as follows: (1) The medusae, which every summer abound in Puget Sound, belong to the same species which was described by Murbach and Shearer (1903). (2) The description of *Oceania gregaria* as given by Agassiz is insufficient for a reliable determination. (3) Accordingly, we cannot with certainty identify *Phialidium gregarium* Murbach and Shearer with *Oceania gregaria* Agassiz. (4) From the comparative studies reported in this paper it is evident that none of these can be referred to any other known species of *Phialidium.*

It seems highly deplorable, however, to add a new name to the long list of species of *Phialidium* and to do away with the specific name *gregarium,* which since 1903 has been generally applied to the common species of the Vancouver Island region on the Pacific coast of North America. In the present situation, where the original material of Agassiz has disappeared, it seems to me that we may reason as follows:

Agassiz described an extremely common species from the vicinity of Puget Sound, and if that species is not the same one as the admittedly extremely common species more thoroughly described by Murbach and Shearer, then Agassiz's species seems to have been unobserved ever since his time. This is so highly improbable that we are forced to accept the description given by Murbach and Shearer as covering the same species as described by Agassiz. So, I propose to call the species *Phialidium gregarium* (Agassiz), with a note that this name is taken in the sense as defined by Murbach and Shearer.

The specimens examined by me, and now deposited in the Zoological Museum of Copenhagen, may be designated as neotypes of *Phialidium gregarium* (Agassiz).

REFERENCES

AGASSIZ, A. 1862. In L. Agassiz, Contributions to the Natural History of the United States of America, vol. 4.

——— North American Acalephae. Illustr. Catal. Mus. Comp. Zoöl. Harvard Coll., no. 2.

BONNER, J. T. 1955. A note concerning the distribution of polysaccharides in the early development of the hydromedusan *Phialidium gregarium*. Biol. Bull. Woods Hole, vol. 108.

FOERSTER, R. E. 1923. The Hydromedusae of the west coast of North America, with special reference to those of the Vancouver Island Region. Contrib. Canad. Biol., N. S., vol. 1.

HAECKEL, E. 1879. Das System der Medusen, I.

HYMAN, L. H. 1940. Observations and experiments on the physiology of medusae. Biol. Bull. Woods Hole, vol. 79.

KRAMP, P. L. 1933. Occasional notes on Coelenterata, II. Vidensk. Medd. dansk naturhist. Foren., Bd. 94.

——— Medusae collected by the Lund University Chile Expedition 1948–49. Acta Univ. Lund, N. F., Avd. 2, Bd. 47.

MAYER, A. G. 1910. Medusae of the World.

MURBACH, L., and C. SHEARER. 1903. On Medusae from the coast of British Columbia and Alaska. Proc. Zool. Soc. London, 1903.

STRONG, L. H. 1925. Development of certain Puget Sound hydroids and medusae. Publ. Puget Sound mar. biol. Stat., vol. 3.

TORREY, H. B. 1909. The Leptomedusae of the San Diego Region. Univ. Calif. Publ. Zool., vol. 6.

Species of *Cryptochirus* of Edmondson 1933 (Hapalocarcinidae)

R. SERENE[1]

EDMONDSON (1933) describes four new species of *Cryptochirus: C. rugosus, C. pyriformis, C. minutus,* and *C. pacificus.*

Utinomi (1944) considers these four species as synonyms of *C. coralliodytes.* Fize and Serene (1955, 1957), in their studies on the NhaTrang species, point out that they belong to *C. rugosus,* and that this one is a true species, but that it must be referred to the genus *Troglocarcinus.* The question was to know whether three others of Edmondson's species were valid: *C. pyriformis, C. minutus,* and *C. pacificus.*

Professor Edmondson very kindly sent me a small collection of Hapalocarcinidae consisting of specimens of those species identified by him. The collection consists of six tubes:

Tube 1, labelled "*Cryptochirus pyriformis* Ed., Washington, August 1924"; with 7 specimens.
Tube 2, labelled "*Cryptochirus minutus* Ed., January 18, 1937; Oahu, Hanauma"; with 13 specimens.
Tube 3, labelled "*Cryptochirus crescentus* Ed., Johnston 1923"; with 2 specimens.
Tube 4, labelled "*Cryptochirus rugosus* Ed., Palmyra Isl., 1923"; with 1 specimen.
Tube 5, labelled "*Cryptochirus* sp. Ed., Raratonga, 1929; Wilder and Parks"; with 5 specimens.
Tube 6, labelled "*Cryptochirus pacificus* Ed., type"; with 2 specimens.

Tube 6, containing the type (?) of *C. pacificus,* has been given back to Dr. Edmondson. In order to make their study easier, the specimens of the other tubes have been registered under the following numbers:

C. pyriformis Ed.	1 to 6
C. minutus Ed.	7 to 19
C. crescentus Ed.	20 to 21
C. rugosus Ed.	22
C. sp. Ed.	23 to 27

The 27 specimens mentioned above have been referred to species according to this distribution:

Ed. 23, 24, 25, 27: *Cryptochirus coralliodytes* ? (Heller)
Ed. 20, 21: *Troglocarcinus* (*Troglocarcinus*) *crescentus* (Edmondson)
Ed. 22, 26: *Troglocarcinus* (*Favicola*) *rugosus* (Edmondson)
Ed. 1, 2: *Troglocarcinus* (*Favicola*) *helleri* (Fize & Serene)
Ed. 3–6: *Troglocarcinus* (*Favicola*) *pyriformis* (Edmondson)
Ed. 7–19: *Troglocarcinus* (*Favicola*) *minutus* (Edmondson)

Study of the specimens (1) confirms the attachment of *C. rugosus* to the genus *Troglocarcinus* by Fize and Serene (1955); (2) allows the attachment to the same genus of *C. pyriformis* and *C. minutus* also; (3) shows the existence of two distinct species under the name *C. pyriformis,* the other being *T. (F.) helleri* Fize & Serene (1957); (4) does not permit a precise determination of the position of *C. pacificus.*

I recall that, according to Utinomi (1944), the genus *Troglocarcinus* is separated from the genus *Cryptochirus* chiefly by the biramous character of the pleopods on the first pair of the female, while on *Cryptochirus* all of the pleopods of the female are uniramous. In all three species, *C. rugosus, C. pyriformis,* and *C. minutus,* those pleopods are biramous, and the attachment of the species to the genus *Troglocarcinus* abolishes any thought of putting them into synonymy with *C. coralliodytes,* according to Utinomi's opinion (1944).

In the same manner Utinomi (1944) had already attached Edmondson's *C. crescentus* to the genus *Troglocarcinus,*[2] which also has the first pleopod biramous in the female. The bi-

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[1] Oceanographic Institute of NhaTrang, ViêtNam. Manuscript received June 28, 1957.

[2] Utinomi uses *Pseudocryptochirus* as the name of the genus, but *Troglocarcinus* has priority.

ramous character of the first pleopod of the female is found in two other genera: *Hapalocarcinus* Stimpson and *Pseudohapalocarcinus* Fize & Serene; but those two genera have other specific morphologic characters, and live chiefly in the galls that they form between the branches of corals and not in the galleries hollowed in the coral, as is the case with *Cryptochirus* and *Troglocarcinus*.

In their study of the Hapalocarcinidae of ViêtNam, which distinguishes 22 species, Fize & Serene (1957) define the genus *Troglocarcinus* and separate it from a new genus, *Neotroglocarcinus,* which is characterized by the two first pairs of biramous pleopods on the female. Although all species of *Troglocarcinus* are characterized by the presence of biramous pleopods on the first pair, they are often of various shapes: some have a carapace with a morphology very close to that of *Cryptochirus,* whereas other species have a carapace with a very different morphology. The classification of the genus is reviewed; and the authors divide the genus *Troglocarcinus* into four subgenera, of which the subgenus *Troglocarcinus* (*Favicola*) is used for species which live in hosts belonging to several genera in the subfamilies Faviinae and Montastreinae. The species *T.* (*F.*) *minutus, T.* (*F.*) *pyriformis,* and *T.* (*F.*) *helleri,* identified in the present collection, belong in that subgenus. The species of the subgenus *Favicola,* by the morphology of their carapace and of their pereiopods, are generally very nearly related to the species of *Cryptochirus* and especially to *C. coralliodytes.* The uniramous or biramous character of the first pleopod of the female is the better character, and provides the clearest, sometimes the only reliable criterion for the differentiation of the genus.

The species *Troglocarcinus* (*Troglocarcinus*) *crescentus, T.* (*F.*) *rugosus, T.* (*F.*) *helleri,* and *T.* (*F.*) *minutus* are described in detail by Fize and Serene (1957), and it is not necessary to repeat the information on those species. But the carapaces, chelipeds, and pleopods of the first pair, and the third maxillipeds of three last, are illustrated on account of their close relationship with the two parent species and especially with *T.* (*F.*) *pyriformis.*

Utinomi (1944) has considered the third maxillipeds as being a valuable distinctive generic character between *Cryptochirus* and *Troglocarcinus.* He has pointed out that in *C. coralliodytes* the anteroexternal distal border of the merus of the third maxilliped is extended, while it is not extended in *Troglocarcinus crescentus* and *T. viridis.* That character has no value for generic differentiation, since it has been shown that some of the species of *Troglocarcinus* are similarly extended. In fact, the degree of development of that extension is difficult to appreciate on some specimens of *C. coralliodytes.* Therefore this character is not used in descriptions of new species of *Cryptochirus* discussed since Utinomi's work (1944).

The labels on the specimens of the Edmondson collection do not give any references to the host-species of *Hexacorallia* on which the specimens were collected. Therefore the questions of hosts can not be considered in this study, but the importance of hosts will be indicated where it is pertinent.

Cryptochirus coralliodytes, Heller 1862

Figs. 1*f*, 2*f*, 3*a–f*, 4*a–c*, 5*H*, *h*, *L*

Cryptochirus coralliodytes, Heller 1862, Akad. Wiss. Math. Nat. Class. Wien. vol. 43, abt. I: 370–371, pl. II, figs. 33–35.

C. coralliodytes, Fize & Serene 1957, Mém. Mus. Nat. Hist. Nat. Paris 7è Ser. V (synonymes): 31, fig. 4 A–D, 52 B–E, pl. I B, 3–6, II A, 1–3, X A, XIV A–H.

Tube 5 of Edmondson's collection contained five specimens under the name of *Cryptochirus* spp. Of these, one (Ed. 26) is reported to be *T.* (*F.*) *rugosus.* Two others (Ed. 23 and 24) are very small and will not be studied. Ed. 25 is a female, 5.65 mm. in length, and Ed. 27 is a female, 5.55 mm. in length; both are somewhat similar and are characterized by the greater width of the carapace as compared with its length: the ratio is 1.38 to 1.31. They are very strongly convex from front to back, the meeting of two sloping planes, the anterior forward and the posterior backward, making a round angle. On those two specimens, there is a slanting groove separating on each side the median gastric elevation from the epigastric elevations; there are also three pits, or hollows, in lines on each of the grooves limiting the gastric elevation anterolaterally; and, last, a clearly marked groove delimits anterolaterally the cardio-intestinal elevation. Those details confirm the necessity of a study of the variations of *C. coralliodytes,* because they ally the present specimens to *C. bani,* Fize & Serene 1957. In order to differentiate between *T.* (*F.*) *pyriformis* and *C. coralliodytes,* I prefer to refer to another specimen of *C. coralliodytes* (E. 38.795) of the same size of *T.* (*F.*) *pyriformis* and borrowed from the collections of the Oceanographic Institute of NhaTrang, rather than use the two specimens of Edmondson (Ed. 25 ad Ed. 27).

Troglocarcinus (*Troglocarcinus*) *crescentus* (Edmondson 1925)

Cryptochirus crescentus, Edmondson 1925, Bernice P. Bishop Mus. Bull. 27: 33–35, fig. 6–A 1, pl. B, C.

C. crescentus, Edmondson 1933, Bernice P. Bishop Mus. Occ. Papers 10(5): 16, pl. IV, c–d, Shen 1936, The Hong Kong Natur. Supp. no. 5: p. 21, pl. 2. Hiro 1937, Palao Trop. Biol. Stat. Studies, no. 1: p. 142. Hiro 1938, Zool. Mag. 50(3): 149.

Pseudocryptochirus crescentus, Utinomi 1944, Palao Trop. Biol. Stat. Studies 2(4): 687–730; figs. 5–6 (D), 7 (C, F), 10, 11 (H), 12 (C); pl. IV, figs. 7–10, pl. V, fig. 3.

Troglocarcinus (*Troglocarcinus*) *crescentus,* Fize & Serene 1957, Mém. Mus. Hist. Nat. Paris, 7è Ser. I: 62, figs. 10–11, C, D, 12 B, pls. III B, 4, 7, V, 2, XI B.

The two specimens of the collection which are reported to this species are two females (Ed. 20 and Ed. 21) each 2.5 mm. in length. The species is well described and illustrated by Edmondson (1925, 1933), Utinomi (1944), and Fize & Serene (1957).

It is well characterized both by its habitat (on *Pavona* in holes with lunular apertures) and by its morphology; but its relationship with certain species of *Troglocarcinus,* its great difference from other species of the same genus, and chiefly its relationship with certain species of *Cryptochirus* (such as *C. edmondsoni*), which also lodge on *Pavona* in holes with lunular apertures, call for further observation.

Troglocarcinus (*Favicola*) *rugosus* (Edmondson 1933)

Figs. 1*c,* 2*c,* 5*A, a*

Cryptochirus rugosus Edmondson 1933, Bernice P. Bishop Mus. Occ. Paper 10(5): 6–8, fig. I a–h, pl. I A–F.

Troglocarcinus rugosus, Fize & Serene 1955, Bull. Soc. Zool. France T. 80, Fasc. 5–6: 381–382.

T. (*Favicola*) *rugosus,* Fize & Serene 1951, Mém. Mus. Hist. Nat. Paris 7è ser. V: 85, figs. 21–22 A, B, 23 A, 25 A, 27 A–C, pl. V 7, pls. VI A, 1–3, X D, E.

The two specimens of the collection which are reported to this species are Ed. 22, a female 5 mm. in length, and Ed. 26, a female 6 mm. in length. This later specimen came from the tube containing "*Cryptochirus* sp."

The two specimens have these features on the dorsal surface of the carapace: the gastric area, which is swollen, circular, higher, and covered with tubercules; on each side a small higher (epigastric) posterolateral lobe is also covered with tubercules; the transversal groove separating the gastric area from the cardio-intestinal area is marked, but much less so than the grooves which, on each side, separate the posterior part of the gastric elevation and the anterior part of cardio-intestinal elevation from the posterolateral epigastric elevation. Those characters, which are among the most distinct of those of Edmondson's description (1933), are sufficient to define the species, but they can be supplemented with others. In fact, certain specimens of *C. coralliodytes* show some related characters which are almost similar; that explains why Utinomi (1944) puts the species in synonymy with *C. coralliodytes.* Considering that the species is liable to important variations, just as is *C. coralliodytes,* it is therefore convenient to extend the list of characters given by Edmondson (1933) by adding these: (a) the pleopods of the first pair of the female are biramous (Fig. 1*c*); (b) the anterolateral grooves of the gastric elevation are marked and pigmented in black in the bottom; this is never the case with *C. coralliodytes;* (c) the chelipeds are without any mark of longitudinal pigmented

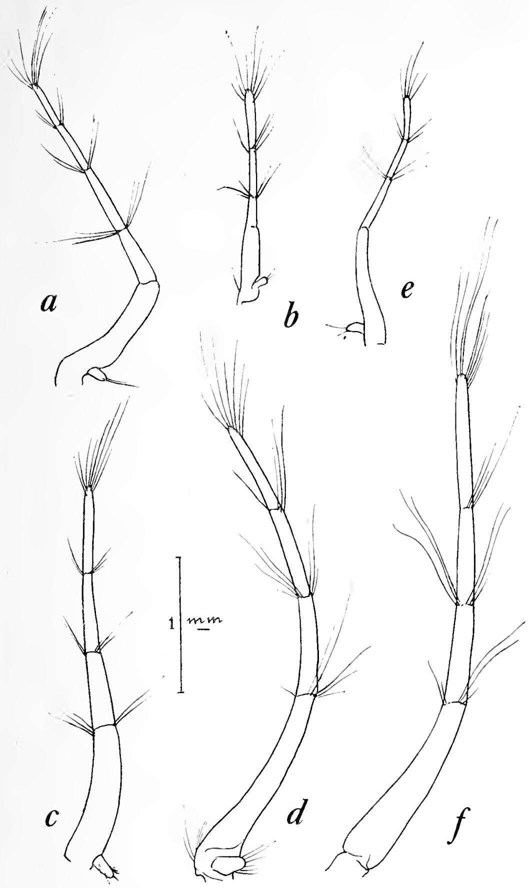


FIG. 1. Pleopods of the first pair on female: *a, Troglocarcinus* (*Favicola*) *pyriformis*, Ed. 4. *b, Troglocarcinus* (*Favicola*) *minutus*, Ed. 15. *c, Troglocarcinus* (*Favicola*) *rugosus*, Ed. 22. *d, Troglocarcinus* (*Favicola*) *rugosus*, Ed. 26. *e, Troglocarcinus* (*Favicola*) *helleri*, Ed. 1. *f, Cryptochirus coralliodytes*, Ed. 25.

lines which exist generally on *C. coralliodytes*, at least in specimens of the same size; the palms of the chelipeds are elongated, somewhat like those on *C. coralliodytes* (Fig. 5*a*); (d) the external distal end of the merus of the 3rd maxilliped is without a salient extension (Fig. 2*c, d*).

The two specimens of the collection are somewhat similar. Ed. 26 offers a very weak spinulation of the anterior part; the spines of the anterolateral borders of the carapace and of the external borders of the antennular basal article especially are very short. On the carapace the tubercles of the dorsal surface are lightly spinulous and very short; the flatness of the anterior part takes up almost half the length of the carapace; the posterior half of this is very convex in two ways and is obviously widened and swollen in proportion to the anterior and posterior border. The end of anterolateral gastric and epigastric grooves is marked with small chestnut clear spots.

Edmondson (1933) reports the species on *Favia speciosa;* in NhaTrang, it was found chiefly on specimens of the genus *Platygyra.* Fize & Serene (1957) have made a detailed study of it.

Troglocarcinus (*Favicola*) *helleri*, Fize & Serene 1957

Figs. 1*e*, 2*e*, 5*B*, *b*

Troglocarcinus (*Favicola*) *helleri*, Fize & Serene 1957, Mém. Mus. Hist. Nat. Paris 7è ser. V: 93, figs. 23 B, 24, 25 B, 27 D, E, 28 A, pls. V 8, 9, VI B, 4–9, X F, XVI E–G.

The two specimens (Ed. 1 and Ed. 2) of the collection which are reported to this species are both females, both 4 mm. in length.

The species, as described by Fize & Serene (1957), is characterized chiefly by: (1) the strong anterolateral grooves of the gastric elevation, very oblique towards the sides of the carapace (Fig. 5*B*); (2) the chelipeds with short palms, as high as long (Fig. 5*b*); (3) a strong spinulation; (4) a gastric elevation, egg-shaped, elongated, very spinuous, and surrounded on each side by epigastric anterolateral and posterolateral lobes, which are very infolded; (5) the posterolateral epigastric lobes of each side which are united behind the gastric elevation and separate this from the cardio-intestinal elevation.

This species, very close to *T.* (*F.*) *rugosus*, is distinguished from it chiefly by the height and the colour of the palm of its chelipeds and by the disposition of its gastric and epigastric elevations.

Edmondson has not separated it from *C. pyriformis*, in all probability because of the size of its chelipeds: the short, wide palm is a character common to those two species, but it separates both of them from *T.* (*F.*) *rugosus* as well as from *C. coralliodytes.*

In contrast, the development of the relief and of the spinulation of the dorsal surface of the carapace is very much stronger on *T.* (*F.*) *helleri* than on *T.* (*F.*) *pyriformis*, and affords sufficient evidence to separate the two species easily.

The two specimens of the present collection are of the same size and are similar, with a very strong spinulation and a very accentuated relief. They have somewhat the size of the type of the species (4 mm.), but some specimens can reach a length of 6 mm. In NhaTrang, it chiefly frequents *Favites abdita.*

Troglocarcinus (*Favicola*) *minutus* (Edmondson 1933)

Figs. 1*b*, 2*b*, 5*D*, *d*

Cryptochirus minutus, Edmondson 1933, Bernice P. Bishop Mus. Occ. Pap. 10 (5): 12–14, fig. 4, pl. 3 E, F.

Troglocarcinus (*Favicola*) *minutus,* Fize & Serene 1957, Mém. Hist. Nat. Paris 7è, ser. V: 106, figs. 27 F, 28 C, pls. V ii, XVI H, I, K, L.

The collection contains 13 specimens (Ed. 7 to Ed. 19) of which 11 are males and 3 are females.

The species, also found in NhaTrang, is well characterized by: (1) its small size; (2) two deep post-frontal grooves which mark, on the anterior dorsal surface of the carapace, the anterolateral angles of the carapace and the anterolateral angles of the forepart of the gastric elevation (Edmondson, 1933: fig. E, pl. 3); (3) the short and strongly spinous chelipeds (Edmondson, 1933: fig. 4).

On the females, the pleopods of the first pair are biramous (Fig. 1*b*), placing the species in the genus *Troglocarcinus.* The number of eggs is much smaller than that of other species, being usually 20 to 30 instead of 100 to 150, as in other species.

Edmondson (1933) reports finding the species on *Cyphastrea.* It is found on the same host in NhaTrang. The species, together with *C. coralliodytes,* lives on corals of that genus, but in a form of small size that Fize & Serene (1957) consider as a variety, *C. coralliodytes* var. *parvulus.*

Troglocarcinus (*Favicola*) *pyriformis* (Edmondson 1933)

Figs. 1*a*, 2*a*, 4*d–f*, 5*E*, *e–G*, *g*

Cryptochirus pyriformis Edmondson 1933, Bernice P. Bishop Mus. Occ. Paper, 10 (3): 10–12, fig. 3, pls. 3, 3 A.

The collection contains four specimens: Ed. 3, a female 3.5 mm. in length; Ed. 4, a female 4.1 mm.; Ed. 5, a damaged specimen (female); Ed. 6, a female 3.25 mm. The type specimen, a female of 4 mm., collected from *Favites abdita* on Washington Island by Edmondson (1933), is in the Bishop Museum, in Honolulu. The spe-

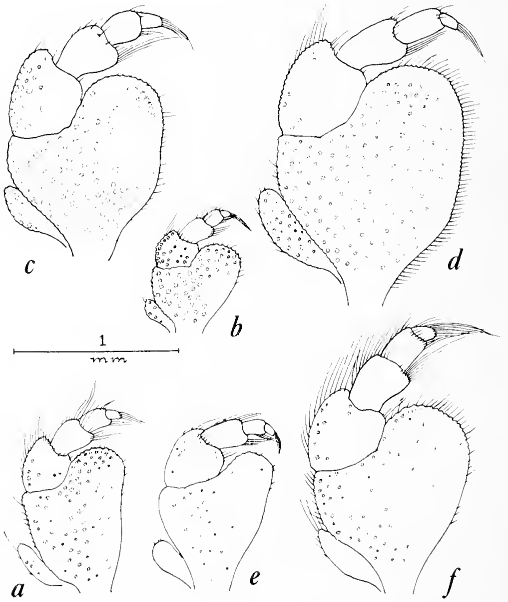


FIG. 2. The third maxillipeds of: *a, Troglocarcinus* (*Favicola*) *pyriformis,* Ed. 4. *b, Troglocarcinus* (*Favicola*) *minutus,* Ed. 15. *c, Troglocarcinus* (*Favicola*) *rugosus,* Ed. 22. *d, Troglocarcinus* (*Favicola*) *rugosus,* Ed. 26. *e, Troglocarcinus* (*Favicola*) *helleri,* Ed. 1. *f, Cryptochirus coralliodytes,* Ed. 26.

cies is also reported by Edmondson (1933) on *Orbicella curta* and *Hydnophora* sp.

The present specimens are similar to the Edmondson figures and description (1933). However, the tubercules of Ed. 3 are slightly more spinulous than are those of two other specimens. The largest (Ed. 4) is comparatively only slightly larger than two others, with its posterior part more swollen. Without insisting either on the description of present specimens, or their comparison with the Edmondson description and figures (1933), I shall use them to define the situation of the species with regard to species of *Cryptochirus* as well as to related species of *Troglocarcinus* (*Favicola*).

Edmondson (1933) characterizes the species chiefly with regard to *C. rugosus* and *C. pacificus.* He writes: "(1) the chelipeds are relatively larger than on *C. rugosus* and *C. pacificus* and the height of the merus in comparison with its length is larger than on those species. (2) The blunted teeth of the 4th walking legs separate that species from others, too."

In my opinion, the size of *Troglocarcinus* (*F.*) *pyriformis* does not seem to exceed 4 mm., and its small size affords another character, which separates it from those two species which are 6 mm. long. I should mention, further, my doubts about *Cryptochirus pacificus*; that species is not sufficiently defined, as I myself especially know, for I can define the situation of *T.* (*F.*) *pyriformis* with regard to it. On the contrary, the separation of *T.* (*F.*) *pyriformis* from *T.* (*F.*) *rugosus* does not present difficulties. I shall discuss the position of *T.* (*F.*) *pyriformis* first with regard to species of *Cryptochirus,* then to species of *Troglocarcinus* (*Favicola*).

SPECIES OF *Cryptochirus*

The biramous character of the first pair of pleopods separates *T.* (*F.*) *pyriformis* from all of the other species of *Cryptochirus*; the bigger size of the palm of its chelipeds separates it from *C. coralliodytes,* with which Utinomi (1944) puts it in synonymy. But some other characters in the description by Edmondson (1933) of *C. pyriformis,* and which are found on specimens of the present collection, are not much different from those of certain specimens of *C. coralliodytes.* In fact, that last species is liable to very many variations, which unfortunately are not yet the object of sufficient studies. In the present state of my observations, those variations would be related to various factors, among them the species of *Hexacorallia* hosts and the age (size) of specimens. Those factors do not have absolute value because there exist, if not the species, at least the varieties or the dwarf races of *C. coralliodytes,* and the species *sensu largo* inhabits numerous species of the various genera of *Hexacorallia.*

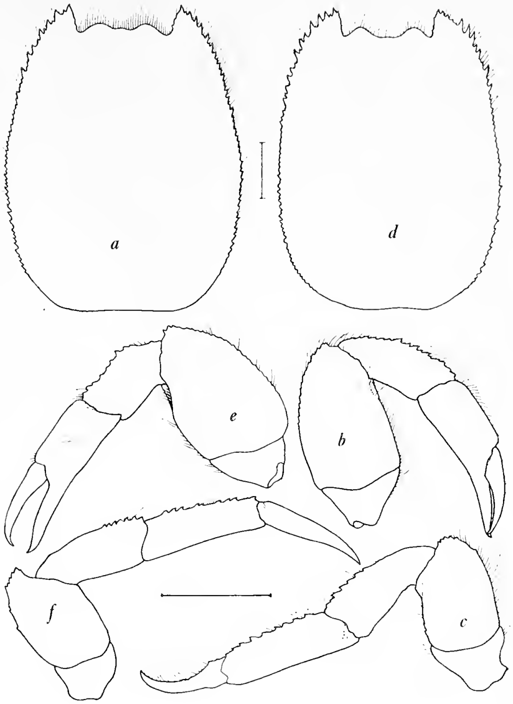


FIG. 3. *Cryptochirus coralliodytes:* (Ed. 25) 5.6 mm: *a,* Carapace; *b,* left cheliped, internal face; *c,* pereiopod 5 left, external face; (Ed. 27) 5.6 mm.: *d,* Carapace; *e,* cheliped right, internal face; *f,* pereiopod 5 right, external face.

The specimen Ed. 4 (4 mm. long) of *T.* (*F.*) *pyriformis* is compared (Fig. 4, *a–f*) with a specimen of *C. coralliodytes* (E. 38.795) of exactly the same size, taken from NhaTrang bay, and now in the collection of the Oceanographic Institute of NhaTrang.

The carapace of the second specimen is comparatively: (1) more spinulous; especially, the teeth of the anterolateral borders are much longer and sharper; (2) narrower, (that of *T.* (*F.*) *pyriformis* being wider at the posterior third). In dorsal view the outline of the carapace of the two species is different: the lateral borders are more convex on *T.* (*F.*) *pyriformis,* straighter on *C. coralliodytes.* The anterior border is narrower on *T.* (*F.*) *pyriformis*; it is chiefly the frontal margin (properly so called) which is shorter. That character of the outline of the carapace agrees with the meaning of the name *"pyriformis"* given to the species; but this does not mean that the carapace can not be capable of showing variations in a series of individuals. Moreover, perhaps certain specimens of *C. coralliodytes* can show similar variations in shape.

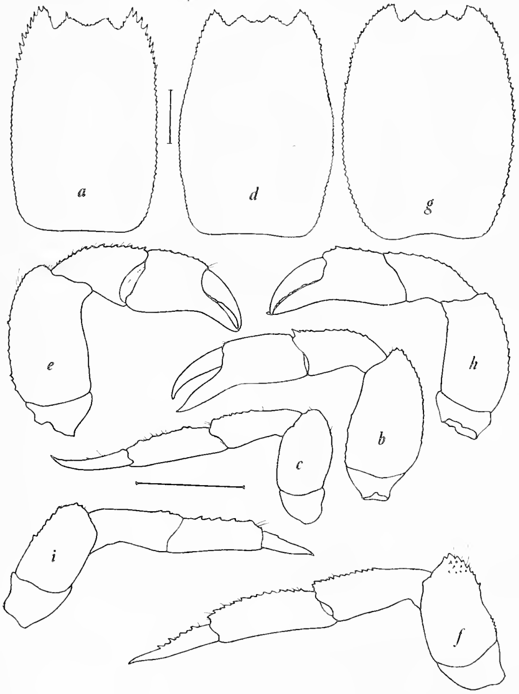


FIG. 4. *Cryptochirus coralliodytes* (E. 38.795) 4.1 mm.: *a,* Carapace; *b,* right cheliped, internal face; *c,* pereiopod 5 left, external face. *Troglocarcinus* (*Favicola*) *pyriformis* (Ed. 4) 4.1 mm.: *d,* Carapace; *e,* left cheliped, internal face; *f,* pereiopod 5 left, external face. *Troglocarcinus* (*Favicola*) *verrilli* (E. 39.000) 4.2 mm.: *g,* Carapace; *h,* right cheliped, internal face; *i,* pereiopod 5 right, external face.

Comparisons of the chelipeds and the 5th pereiopods are presented in Table 1. Measurements of length were taken on the upper margin in a straight line between the two extremities; the figures given for height are those obtained at the largest place on the structure being measured.

These measurements show that, as far as the chelipeds are concerned, the wrist is higher and the propodus is shorter and higher on *T.* (*F.*) *pyriformis.* One knows that the prolongation of the wrist, propodus, and dactylus of the cheliped shows some individual variations in *C. coralliodytes,* but in that species the prolongation is always much more accentuated than it is in *T.* (*F.*) *pyriformis.* The short and squat shape of the wrist and propodus of *T.* (*F.*) *pyriformis* affords a good character for distinguishing it from *C. coralliodytes,* at least in the present state of our knowledge of the variations exhibited by the latter species. Therefore, observations upon the sizes of the articles of chelipeds require more precision. Edmondson (1933) in describing *T.* (*F.*) *pyriformis* said only this: "fingers as long as palm, which is about one half the length of the carpus." On the specimens of the present collection, the palm is shorter than the finger, the length of the wrist being nearly twice the length of the palm, but less than twice the length of the dactyle. Edmondson (1933) also noted that, on *T.* (*F.*) *pyriformis,* the height of the merus in comparison with its length is larger than on *T.* (*F.*) *rugosus* and *C. pacificus.* On *C. pyriformis* that measurement is similar to the measurement of *C. coralliodytes.* In summary, on *C. pyriformis* the merus is similar, the wrist higher, the propodus shorter and higher, than on *C. coralliodytes.*

Edmondson (1933) also characterized *T.* (*F.*) *pyriformis* by the blunted teeth which garnish its 5th pereiopod. This character is very clear on the specimen (Ed. 4), especially with the presence of spinules on the dactylus which are missing on the *C. coralliodytes* of the same size. But the measurements show another differential character between the two species: The entire 5th pereiopod is longer on *T.* (*F.*) *pyriformis* than it is on *C. coralliodytes* (3.92 mm. com-

TABLE 1

COMPARISON OF THE CHELIPEDS AND OF THE FIFTH PEREIOPODS IN *C. pyriformis* AND *C. coralliodytes*

(All measurements are in mm. L = length; H = height.)

	C. pyriformis		*C. coralliodytes*		
	Ed. 4	Ed. 3	E. 38.795	Ed. 27	Ed. 25
Carapace:					
length	4.10	3.25	4.10	5.55	5.65
width	2.85	2.07	2.70	4.00	4.30
Cheliped:					
merus L.	1.30	1.10	1.30	1.42	1.37
merus H.	0.70	0.60	0.70	0.92	0.82
carpus L.	0.90	0.77	0.90	0.92	1.10
carpus H.	0.55	0.40	0.45	0.50	0.45
propodus L.	0.55	0.40	0.60	0.70	0.70
propodus H.	0.62	0.42	0.45	0.45	0.45
dactylus L.	0.67	0.55	0.65	0.80	0.80
dactylus H.	0.16	0.15	0.20	0.22	0.15
5th Pereiopod:					
merus L.	1.00	0.80	0.82	0.95	1.15
merus H.	0.64	0.47	0.40	0.70	0.70
carpus L.	1.10	0.90	0.85	1.17	1.15
carpus H.	0.45	0.30	0.32	0.45	0.47
propodus L.	1.00	0.70	0.80	1.00	1.05
propodus H.	0.40	0.30	0.30	0.40	0.45
dactylus L.	0.82	0.65	0.70	1.00	0.77
dactylus H.	0.20	0.17	0.17	0.20	0.25

pared with 3.17 mm.), each of the articles—merus, carpus, propodus, dactylus—is longer on the first species. These two characters of the 5th pereiopod of *T.* (*F.*) *pyriformis*—its being longer and more spinulous than *C. coralliodytes*—are very distinct with regard to our specimen (E. 38.795) of the same size.

Therefore, one can conclude from the comparison of Ed. 4 with E. 38.795, that *T.* (*F.*) *pyriformis* is separated from *C. coralliodytes* by: (1) the carapace of different shape, more elongated at the posterior one third, narrower on the anterior border, with a smaller development of the spinulation of the anterolateral borders; (2) the chelipeds with higher wrist and propodus; (3) the 5th pereiopods being longer and more spinulous, with spinules on the dactylus.

The *T.* (*F.*) *pyriformis* (Ed. 4) is compared with two much larger specimens of *C. coralliodytes* of the present collection (Ed. 26 and Ed. 27). The ratio of the width to the length of the carapace does not afford a distinct character of difference:

1.43 mm. on Ed. 4, *T.* (*F.*) *pyriformis,* (4 mm. in length)
1.51 mm. on E. 38.795, *C. coralliodytes,* (4 mm. in length)
1.38 mm. on Ed. 27, *C. coralliodytes,* (5.55 mm. in length)
1.31 mm. on Ed. 25, *C. coralliodytes,* (5.65 mm. in length)

But on the chelipeds, the height of the wrist and the propodus is always less than it is on *T.* (*F.*) *pyriformis*; on this species, the length of the 5th pereiopod is always relatively shorter, the whole length of the carpus, propodus, dactylus, measured from the upper margin of the carpo-meral articulation to the distal end of the dactylus, is 2.9 mm. on Ed. 4 and 2.2 mm. on E. 38.795 of the same size; but only 2.9 mm. on Ed. 26 and Ed. 27 which are much larger in size. And finally, the spinulation is much smaller on the three specimens of *C. coralliodytes* than on Ed. 4.

T. (*F.*) *pyriformis* is also separated by the wide palm of its cheliped from *C. nami* and *C.*

bani, two species of *Cryptochirus* related to *C. coralliodytes* (which inhabits the Astreidae hosts). *T. pyriformis* is separated without difficulty from *C. tri* and *C. edmonsoni,* which inhabit Hexacorallia of different families, the first on hosts of the genus *Echinopora,* the latter on hosts of *Pavona* and *Psammocora.*

SPECIES OF *Troglocarcinus*

The inclusion of *C. pyriformis* in the subgenus *Troglocarcinus* (*Favicola*) has been mentioned above. That subgenus now contains *T.* (*F.*) *rugosus, helleri, verrilli, pyriformis,* and *minutus.* The first species reaches a size of 9 mm., the second of 6 mm.; the three others are smaller and do not exceed 5 mm. in length. All inhabit hosts in the subfamilies Faviinae and Montastreinae.

T. (*F.*) *pyriformis* is separated from *T.* (*F.*) *rugosus* by: (1) the different shape of the outline of the carapace; (2) the relief of the carapace with its very deep grooves and spinulation; (3) the wrist and the propodus of the chelipeds, which are shorter and higher.

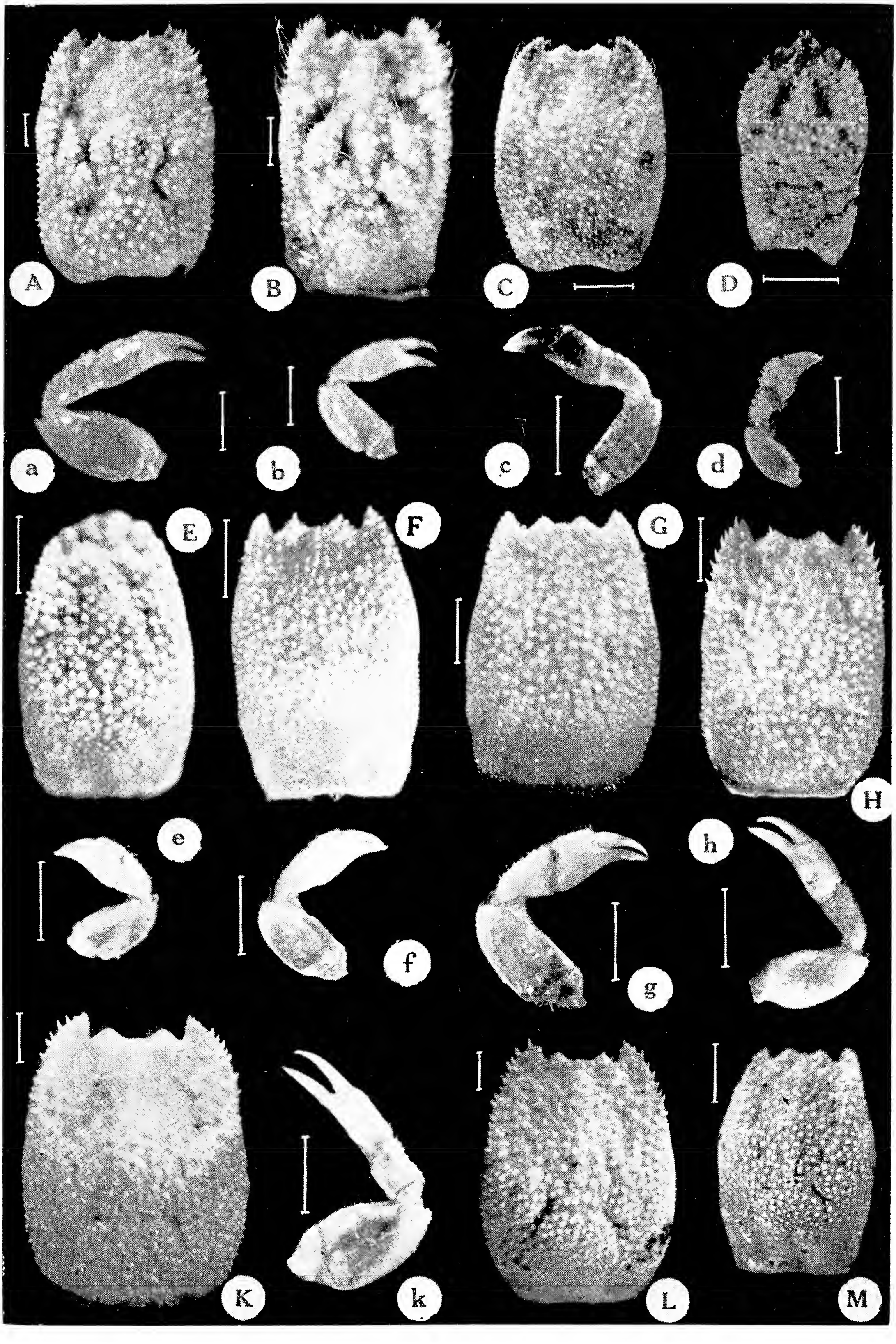
T. (*F.*) *pyriformis* is separated from *T.* (*F.*) *helleri* as well as from *T.* (*F.*) *rugosus* by the first two characters just mentioned, but it shares the third character with *T.* (*F.*) *helleri.* Perhaps, this is the reason why Edmondson, in the present collection, has not separated the two species. Given the difference in size of the specimens of the two species, one could think that *T.* (*F.*) *pyriformis* is a young form of *T.* (*F.*) *helleri,* considering as a character of youth the smaller relief and the weaker spinulation of the carapace. The specimens of *T.* (*F.*) *helleri* of the present collection (Ed. 1 and Ed. 2) have precisely the same size (4 mm.) as do the specimens of *T.* (*F.*) *pyriformis,* and no confusion is possible between them.

T. (*F.*) *pyriformis* is separated from *T.* (*F.*) *minutus* by the shape and weak spinulation of carapace and chiefly by its relief, which is not much marked, whereas *T.* (*F.*) *minutus* is well characterized by its gastric anterolateral grooves, which are wide and deep.

It is with *T.* (*F.*) *verrilli* that *T.* (*F.*) *pyriformis* is most closely related, generally having in common with it (1) a small size; (2) the weak relief and spinulation of its carapace; (3) the height of the propodi of the chelipeds.

Comparison of *pyriformis* (Ed. 4) with a specimen of *verrilli* (E. 39.100) of almost the same size (4.35 mm.) from the collection of the Oceanographic Institute of NhaTrang, shows that the first species is separated from the second by: (1) the different shape of the outline of the carapace, which on the second has its lateral borders more regularly convex from front to backward (Fig. 4*g*); (2) a larger space between the anterior end of the anterolateral angles of the carapace (Fig. 4*g*); in the second species, if the frontal margin properly so called (between the internal supraorbital angles) is as wide as in the first, the external orbital angles are nearer; (3) a stronger anteroposterior convexity of the dorsal surface; in the second species, the opposition between the anterior plan, which is sloping frontwards, and the posterior plan, which is sloping backwards, is much less accentuated; the species is more flattened dorsoventrally; (4) the chelipeds are comparatively shorter and higher, the morphology of wrist, propodus, and dactylus of *verrilli* is medium in its size between *T.* (*F.*) *pyriformis* and *C. coralliodytes* (Fig. 4*h*); (5) the 5th pereiopod is comparatively longer and more spinous, especially on *T.* (*F.*) *verrilli:* the whole length of carpus-propodus-dactylus is much shorter than on *T.* (*F.*) *pyriformis.* Edmondson uses that character of the 5th pereiopod in order to define *C. pyriformis,* and I have observed it myself. But in the present state of our knowledge, I am not sure of its worth as a character of specific differentiation: it is possible that it is liable to individual variation within a species.

FIG. 5. Carapaces and chelipeds of: *A.a, Troglocarcinus* (*Favicola*) *rugosus* (E. 39.108) 8 mm.; *B,b, Troglocarcinus* (*Favicola*) *helleri* (E. 38.677) 6 mm.; *C,c, Troglocarcinus* (*Favicola*) *verrilli* (E. 39.100) 4.2 mm.; *D,d, Troglocarcinus* (*Favicola*) *minutus* (Ed. 15) 2.5 mm.; *E,e, Troglocarcinus* (*Favicola*) *pyriformis* (Ed. 6) 3.25 mm.; *F,f, Troglocarcinus* (*Favicola*) *pyriformis* (Ed. 3) 3.5 mm.; *G,g, Troglocarcinus* (*Favicola*) *pyriformis* (Ed. 4) 4.1 mm.; *H,h, Cryptochirus coralliodytes* (E. 38.795) 4 mm.; *K,k, Cryptochirus bani* (E. 38.727) 6.5 mm.; *L, Cryptochirus coralliodytes* (Ed. 27) 5.6 mm.; *M, Cryptochirus pacificus* Edmondson, 4 mm.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Cryptochirus ? Pacificus ? Edmondson 1933
Fig. 5*M*

Cryptochirus pacificus Edmondson 1933, Bernice P. Bishop Mus. Occ. Pap., 10 (5): 8–10, fig. 2 a–j, pl. II.

The sixth tube in the Edmondson collection contained two female specimens under the name "*C. pacificus.*" Both were in bad condition, having lost their legs. One specimen has only its carapace without abdomen; the other has both carapace and abdomen, but the two parts are separated. Neither on the abdomen, nor on the carapace, can I find a trace of the first pair of pleopods, observation of which could permit a determining whether it is a *Troglocarcinus* or a *Cryptochirus.* On the abdomen, the 2nd and 3rd pairs of pleopods are still present.

Edmondson (1933) places the species as closely related to *C. rugosus* but more smooth on the carapace and its appendices. Moreover, according to him the median border of the ischium of the 3rd maxilliped is strongly convex, while it is straighter on other species. But reference to Edmondson's description and figures (1933) shows that the species is different from *T.* (*F.*) *rugosus, helleri, verrilli, pyriformis,* and *minutus* as described by Fize & Serene (1957).

On the contrary, it closely resembles *C. coralliodytes* and, more particularly, *C. bani.* The apparent relationship between *C. bani* and *C. pacificus* caused me to ask Dr. Edmondson to send me his specimens of *C. pacificus* in order to permit me to make a comparison. Their relationship is discussed in the following observations.

(1) The type of *C. pacificus* is 8 mm. long (Edmondson 1933) and this agrees with the size of *C. bani.*

(2) Edmondson's descriptions and figures of the species agree rather well with the morphology of *C. bani,* especially in: (a) the sloping anterior part of the dorsal surface of the carapace, the V-shaped elongated depressions on each side of the median line; and (b) the crescent-shaped depression with posterior concavity which separates the cardiac and gastric regions.

(3) Edmondson obtained his specimens on *Favia* sp. and *Meandra* (= *Platygyra*) *lamellina;* and Fize & Serene (1957) collected *C. bani* on *Favia speciosa.*

Those authors also collected *C. coralliodytes* var. *rubrolineata* on *Platygyra lamellina.* This variety is very near to *C. bani,* at least by reason of its large size. *C. pacificus* is very nearly related to these last two forms, very close between them. Perhaps all three of them are really only different forms of the same species.

C. pacificus is not much different from *C. bani* except that, in *pacificus,* the flattening of the sloping posterior part is clearly longer than the flattening of the anterior part. Just the contrary picture is shown by *C. bani*: the flattening of the anterior part extends as far as the groove which separates the cardiac and gastric regions, and the posterior part is shorter than the anterior. The *C. coralliodytes* (Ed. 27) of the present collection is not very different from these forms, but is not as distinctly marked on the sloping anterior part of the carapace by the V-shaped elongated depression mentioned by Edmondson (1933) on *C. pacificus,* which depression is found on *C. bani* also. To me that character does not seem to be sufficient for differentiating *C. pacificus* from *C. bani,* or from *C. coralliodytes* var. *rubrolineata,* or from *C. coralliodytes.* That depression, by its internal branch, leads to a groove, which separates anterolaterally the advancing of the gastric elevation towards the anterior border of the postero-orbital elevation, extending backwards the upper-internal angle of orbit; and, by its external branch, it leads to a groove, which separates the same elevation posterolaterally from the hepatic region of anterolateral borders. The more or less large producing of the branchs of that V-shaped depression, its more or less accentuated reliefs, seem to me to suggest the possibility of individual variations of *C. coralliodytes,* which is not yet so well known. The same is true for the more or less great development of the crescent-shaped depression with a posterior concavity which marks the separation of the gastric and the cardio-intestinal regions. Perhaps the same is true for the variations in proportion between the anterior part sloping frontwards and the posterior part sloping backwards; and for the more or less great height of the carapace in proportion to its length, the more or less great flattening of the posterior part. These are characteristics that the profiles of carapaces figured by Edmondson (1933) show clearly, and they reveal the differences between *C. pacificus* and *C. coralliodytes.*

It is proper, while we are discussing that subject, to point out the insufficient exactitude of the proportions in the outlines of the carapaces on the figures of Edmondson (1933), especially in figure 2 of *C. pacificus.* The ratio of the width of the carapace to its length, measured in that figure, is 1.78 while it is 1.32 in the other figure (Edmondson, 1933: pl. 2B). The latter ratio is approximately that found in *C. bani* and *C. coralliodytes* specimens of the same size, where it changes between 1.25 and 1.35. The figure of the male of *C. pacificus* suggests the idea of its close relationship to *C. coralliodytes.* Therefore, I think that *C. pacificus* as defined by Edmondson (1933) is near *C. bani* or *C. coralliodytes* var. *rubrolineata,* and perhaps in consideration of its large size is a form of *C. coralliodytes.*

Unfortunately the two specimens of *C. pacificus* which Dr. Edmondson sent to me do not allow me either to contradict or to confirm my impression. I have already mentioned their bad condition. But the larger specimen was only 4 mm. long, and that makes me doubt, in spite of the label, that it is the type to which Edmondson (1933) attributed a length of 8 mm. In order to define with certainty the characteristics of that species, specimens of 8 mm. must be observed and compared with specimens of the same size of *C. bani* and *C. coralliodytes.* Observations upon the pleiopods of the first pair, in female specimens, can also place the taxonomy of the species in a better perspective.

SUMMARY

Edmondson (1933) described four new species of *Cryptochirus* from the Hawaiian Islands: *C. rugosus, minutus, pyriformis,* and *pacificus.* Utinomi (1944) believed that these four species are only variations of *Cryptochirus coralliodytes,* and must be put in synonymy with that species. Fize and Serene (1957), in a revision of the Hapalocarcinidae, proposed a separation between the genus *Cryptochirus* and the genus *Troglocarcinus,* and pointed out that *C. rugosus* Edmondson 1933 and *C. minutus* Edmondson 1933 must be referred to the subgenus *Troglocarcinus* (*Favicola*).

The collection discussed in this paper was sent to the author by Professor Edmondson. Study of its specimens proved that *C. pyriformis* Edmondson 1933 should also be referred to *Troglocarcinus.* The bad state of preservation of the specimens does not permit a determination of the position of *C. pacificus* Edmondson 1933.

REFERENCES

EDMONDSON, C. H. 1925. Marine zoology of tropical central Pacific: Crustacea. Bernice P. Bishop Mus. Bull. 27: 32–35.

——— 1933. *Cryptochirus* of the central Pacific. Bernice P. Bishop Mus. Occ. Pap. 10 (5): 1–23.

FIZE, A., and R. SERENE. 1956. Note préliminaire sur huit espèces nouvelles, dont une d'un genre nouveau, d'Hapalocarcinidés. Bull. Soc. Zool. de France, t. 80, fasc. 5–6: 375–378, figs. 1, 2.

——— 1957. Les Hapalocarcinidés du Viet-Nam Mem. Inst. Ocean. NhaTrang, 10: 1–202, figs. 1–43, pls. 1–18.

HELLER, C. 1861. Beiträge zur Crustaceen-Fauna des Rothen Meeres. Sitzungsber. Math. Nat. Cl. Akad. Wissen. Wien. Bd. 43, Abt. I: 366–371.

HIRO, F. 1937. Studies on the animals inhabiting reef corals, I. *Hapalocarcinus* and *Cryptochirus.* Palao Trop. Biol. Stat. Studies 1 (1): 137–154, pls. 3.

——— 1938. A new coral-inhabiting crab: *Pseudocryptochirus viridis* gen. et sp. nov. (Hapalocarcinidae, Brachyura). Zoöl. Mag. (Japan) 50 (3): 149–151.

SHEN, C. J. 1936. Notes on the family Hapalocarcinidae (coral-infesting crabs) with descriptions of two species. Hong Kong Naturalist, Supplement 5: 21–26, 1 pl.

UTINOMI, H. 1944. Studies on the animals inhabiting reef corals, III. A revision of the family Hapalocarcinidae (Brachyura), with some remarks on their morphological peculiarities. Palao Trop. Biol. Stat. Studies 2 (4): 687–731.

Fish Poisoning: A Problem in Food Toxication

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INTEREST IN POISONOUS FISHES has intensified greatly in recent years. World War II brought many Americans and Europeans to tropical areas of the world where fish poisoning is common. Also, interest in the welfare of native populations of the Pacific islands has developed widely, and there is an impression that fish poisoning is increasing. In spite of an extensive literature, there is considerable confusion on the subject.

Some marine organisms are dangerous because of their venomous stings or bites, while others are poisonous to eat. Among the latter are shellfish of several kinds, including mussels, clams, and oysters. Some fin fishes also are poisonous to eat. They are intrinsically poisonous and, like the toxic shellfish, do not produce their undesirable effects through bacterial spoilage. Such fishes are the subject of this paper. The fish poisoning problem is especially insidious because of its inconsistencies. For example, a species is not always poisonous and therefore summarily rejected; it may be eaten safely in some localities and not in others, or at some times of year and not at others. Large specimens, otherwise attractive as food, are believed more likely to be dangerous than smaller ones.

Different from the usual fish poisoning episodes is Haffs' disease noted among fishermen along the Baltic Sea coast of East Prussia and at Lake Ysmen in Sweden (Schwimmer and Schwimmer, 1955). The more than a thousand victims had consumed eels, eel livers, and a few other kinds of fish. Animals that ate the fish also became ill and died. Selenium was once thought to be involved in the etiology (Berlin, 1948); toxic blue-green or other algae in the food chain of the fish have been suspected, also.

Another atypical episode occurred recently along the shores of a small bay in Japan, where local people were poisoned by eating fish and shellfish. Their affliction has been called Minamata disease after the name of the bay. Investigation[2] has shown the causative agent to be a mercury compound accumulated in the tissues of the sea food. Mercury was reaching the bay as a component of wastes discharged from a vinyl chloride manufacturing plant. Remedial waste handling measures recently installed at the plant, coupled with a ban on fishing, have been fairly successful in curbing the number of new cases.

Typical poisonous fishes are limited principally to the warm seas lying mostly between 30° N. and 30° S. They are most numerous around isolated islands far from continental shores, such as those of Micronesia, Melanesia, and Polynesia. In the Caribbean, they are common around the West Indies.

In spite of the numerous shore and reef fishes available as food in the tropic seas, potential toxicity is a deterrent to commercial harvest as well as to use by native populations. Because recognition of poisonous specimens presently requires tedious and time-consuming techniques, a tremendous poundage of potentially useful fish cannot be brought to market nor used freely to meet the food needs of local populations. This problem is far from solution at the present time.

HISTORY

Existence of poisonous fishes became much better known during World War II. They are believed to have killed more than 400 Japanese military personnel in Micronesia alone (Halstead, 1959). American military manuals warned against poisonous fishes, one (Smithsonian In-

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[1] Robert A. Taft Sanitary Engineering Center, Public Health Service, Department of Health, Education, and Welfare, Cincinnati, Ohio. Manuscript received February 21, 1961.

[2] Personal communication from Leonard T. Kurland, M.D., Dr. P. H., Chief, Epidemiology Branch, National Institute of Neurological Diseases and Blindness, Public Health Service, Bethesda, Md.

stitution, 1944) stating: "All these fish [with poisonous flesh] lack ordinary scales such as occur on bass, grouper, and sea trout. Instead, these poisonous fish are covered with bristles or spiny scales, strong sharp thorns, or spines, or are encased in a bony box-like covering. Some of these have naked skin, that is, no spines or scales. Never eat a fish that blows itself up like a balloon." Subsequent military literature has been revised in the light of more recent knowledge. Nevertheless, some service men by mistake have partaken of poisonous fishes, with painful result. A number of cases have been cited in the literature (Halstead, 1951, 1954). U. S. occupation or trusteeship of many Pacific islands has emphasized to Americans the problem of poisonous fishes.

Centuries ago, however, poisonous fishes already had made a mark in history. Captain Cook and several officers of HMS "The Resolution" almost ended their voyage in 1774 because they were poisoned from eating a puffer obtained from natives in New Caledonia (Courville *et al.,* 1958). Down through the years many articles have been written by persons whose scientific interests or economic pursuits have brought them in contact with the problem. Their reports of case histories invoke a healthy respect for the dangers of fish poisoning. The following examples show why.

Ciguatera

In May of 1956 in a rooming house at Fort Lauderdale, Florida, a fine-looking 6½-lb. barracuda (*Sphyraena* sp.) was taken from a deep freeze, where it had been kept since capture the day before, and prepared for the evening meal (Paetro, 1956). It was served to five guests and all of them became ill within 2 hr. Three of the victims were hospitalized. Recovery took from 2 to 6 weeks, with symptoms persisting in one case almost 4 months.

Puffer Poisoning

At about the same time, a 65-year-old tourist in south Florida ate the liver of a puffer (*Sphraeroides testudineus* Linnaeus) common in the area (Benson, 1956). Symptoms appeared within 5 min. and the victim died 45 min. after eating the fish.

Moray Eel Poisoning

At Saipan during May of 1949 several Filipinos captured a 6-ft. moray eel (*Gymnothorax flavimarginatus* [Ruppel]) which they dressed, sliced into steaks, and cooked, including the head (Khlentzos, 1950). All 57 persons who ate the fish became sick. After 3 days, 50 who were bedridden and unable to talk were taken on litters to the Saipan dispensary, and the sickest 17 of this group were moved by air to the general hospital at Guam. Two died, one after 14 days and the other after 20 days. In the others, recovery was prolonged, in some cases taking 2 months or more.

Scombroid Poisoning

In Hiroshima during the winter of 1953, three households bought dried mackerel pike (*Cololabis saira* Brevoort), known locally as "samma sakuraboshi," from a peddler (Kawabata *et al.,* 1955*a*). After broiling, the fish was eaten by 11 persons, who within 2½ hr. developed flushing of the face and upper half of the body, palpitation, severe headache, dizziness, and nausea. Fourteen outbreaks of this type of poisoning, involving 1,215 persons, occurred in Japan during a 2-yr. period ending October 1954 (Kawabata *et al.,* 1955*a*). In this fairly mild poisoning, victims commonly recover in a day or less.

STATUS OF FISH POISONING IN THE MARSHALLS

Although many species of fishes known to be poisonous occur in tropical areas, much attention has centered on the Marshall Islands. Starting in 1924, Matsuo, a Japanese medical officer, studied the poisonous fishes at Jaluit Atoll for a number of years (Matsuo, 1934). He listed 36 of 180 species there as poisonous. In 1941, Hiyama studied the fishes at Jaluit and wrote a superbly illustrated report (Hiyama, 1943). At that time, other island groups in the Pacific seemed little involved with fish poisoning, and even now Jaluit is considered by some as the center of the problem.

Scientific interest in the United States was stimulated by outbreaks in the Line Islands involving 95 persons out of a population of 224. Subsequent studies by Halstead and his associates (Halstead, 1959; Halstead and Bunker, 1954) led them to conclude that fish poisoning at Midway, Johnston, and the Line Islands rose to a peak in 1947 and has since declined. As recently as 1958, however, Marshallese of Majuro and Jaluit atolls believed that fish poisoning was still increasing and expressed their concern to the Trust Territory. As a result, an exploratory survey was made at request of Trust Territory officials to accomplish several objectives, including the following:

1. Define the extent of the fish poisoning problem in the Marshall Islands (especially at Majuro and Jaluit) in terms of human morbidity, and other epidemiologic characteristics available, in relation to the fishes involved and their toxicology.
2. Ascertain if poisonous fishes are currently available in the area for human consumption.
3. Collect sufficient information to permit development and proposal of a long-range definitive study of the problem, if indicated.

Epidemiological Characteristics

Epidemiological data came from reviews of Out-Patient Department (OPD) records of the Marshall Islands Memorial Hospital on Uliga Island of Majuro Atoll, questionnaires distributed in the Majuro area, and house-to-house surveys at a number of islands. Included were Darrit, Uliga, and Majuro islands of Majuro Atoll, and Jabor and Imroij islands of Jaluit Atoll. Survey conditions at Jaluit were difficult and less than satisfactory because of appalling damage and disruption caused by a recent typhoon.

OPD summaries for 1955–57 yielded information on the number of persons with fish poisoning and those with a diagnosis of gastrointestinal illness (Table 1). Respiratory illnesses, constituting a group of diseases unrelated to fish poisoning, were examined for comparison. During this period visits increased 60 per cent, whereas fish poisoning and gastrointestinal illnesses increased two to three times. Trends in incidence of respiratory illnesses also showed only a very slight increase and thus no apparent relationship to the other two. Information on population change that would be reflected in these trends was not at hand, but it was thought to be slight. There appears to be no reciprocal relationship between gastrointestinal illness and fish poisoning, suggesting that the former had stayed near its expected level and was not being misdiagnosed as fish poisoning. However, parallelism of the trend curves raises the question of whether fish poisoning may be mistaken for gastrointestinal illness. In August 1957 Trust Territory medical personnel distributed a questionnaire to all atoll dispensaries in the Marshalls. Use of this form identified the victim, described symptoms, treatment, and outcome, and gave the name, origin, and mode of handling of the fish. It is believed that such information has not been available in the past to students of the problem. Questionnaires for the area accessible to the hospital were selected as a comparable group susceptible of analysis. The following information is based on 91 cases.

Twenty-seven species of fishes were implicated in these outbreaks. Eleven cases were caused by red snapper (*Lutjanus vaigiensis* Quoy and Gaimard), 8 by rock cod (*Epinephelus fuscoguttatus* Forskal), 5 by mijmij (*Lethrinus microdon* Cuvier and Valenciennes), 4 by each of two other species, 3 by one species, 2 by each of seven, and each of the remainder by separate species.

The victims were in the following age groups:

AGE GROUPS	NO. OF PATIENTS	PER CENT OF TOTAL NUMBER	PER CENT OF TOTAL DISTRICT POPULATION OF AGE GROUP
0–5	5	8	39
6–14	2		
15–44	73	80	39.4
45+	10	11	21.4
unknown	1	–	–

The small number of victims under 14 yr. is striking, 8 per cent, since this age group constitutes 39 per cent of the population. Because common varieties of gastrointestinal diseases usually involve children more frequently than adults, these reported illnesses probably are not classical enteritis. Based on a year's data and a population of about 2,500, the fish poisoning attack rate was 9.3 per cent.

Of the persons who partook of the fishes in question, 76 per cent became ill; 24 per cent of them were hospitalized. The onset of symptoms ranged from 30 min. to 12 hr. after eating, with a median of 3 hr. Symptoms reported for the 91 victims were:

SYMPTOM	NO. OF PERSONS	PER CENT
numbness and tingling	52	57
muscle aches	9	10
nausea	45	49.5
vomiting	50	55
diarrhea	60	66
abdominal pain	54	59
weakness	27	30
dyspnea	8	9

In some island areas the view is expressed that only fishes taken on the outer reefs are likely to be toxic; elsewhere the view is reversed. Here 72 per cent came from the lagoon, 18 per cent from the reef. Obviously, selecting fish by place of capture is poor protection against poisoning. Although some fish were consumed within 30 min. of capture, others were kept for as long as 48 hr., so that spoilage seems a distinct possibility in some cases; 46 per cent were prepared by evisceration, but 40 per cent were not cleaned at all. Uncleaned fish commonly are eaten in their entirety.

The erratic distribution of fish poisoning among Pacific island groups still challenges interpretation. There is little reason to believe that fish taken in other coral reef areas are handled in a significantly different manner or with better sanitation than in the Marshalls. It is assumed that they also are left routinely at air temperature until consumed and that the extent of cleaning varies widely. Accordingly, fish handling is not considered a significant factor, and it is more likely that distribution of poisoning reflects the intrinsic toxicity of the fishes, acquired in the ocean or reef environment from which they came.

During recent years fish poisoning has been common in the vicinity of Majuro Atoll, but absent at Koror in the Palau Islands lying at the same latitude 2,000 mi. west (Table 1). In public health statistics for the entire Trust Territory, fish poisoning episodes are included in the accident category. The accident rate in the Marshalls is higher by at least 50 per cent than the rate for the entire Trust Territory. These pieces of information, though limited, still suggest a greater prominence of fish poisoning in the Marshalls than elsewhere.

Survey Information

At Rita and Uliga islands, 35 families with a total membership of 375 persons were visited to obtain information on their experiences with fish poisoning during the previous year. During the questioning it became obvious that at least some persons differentiated common diarrheal disease from fish poisoning. Fourteen per cent

TABLE 1

SUMMARY OF MARSHALL ISLANDS MEMORIAL HOSPITAL DISPENSARY (OPD) REPORTS

YEAR	TOTAL OPD PATIENT VISITS	GASTROINTESTINAL ILLNESSES	FISH POISONING	RESPIRATORY ILLNESSES
1955, last half	3,439	97	22	862
1956	7,696	190	100	2,304
1957	11,686	791	211	1,615

SUMMARY OF KOROR HOSPITAL (PALAU ISLANDS) DISPENSARY (OPD) INFORMATION

YEAR	TOTAL OPD PATIENT VISITS	GASTROINTESTINAL ILLNESSES	FISH POISONING	RESPIRATORY ILLNESSES
1956	23,604	1,105	NR*	
1957	31,355	1,220	NR	
1958 (Jan.–Apr.)	9,143	511	NR	

* NR = No cases reported.

of the persons questioned reported that they had been victims of fish poisoning; 6 per cent were hospitalized and the other 94 per cent reported to the OPD for treatment.

Rock cod (*Epinephelus fuscoguttatus* Forskal), red snapper (*Lutjanus vaigiensis* Quoy and Gaimard), mullet (*Chelon vaigiensis* Quoy and Gaimard), and rabbitfish (*Siganus puellus* Schlegel) were each involved in only three incidents although many families normally ate these fish. Similar data on Majuro Island gave an attack rate of 15 per cent for the previous year. Here the implicated fishes were rock cod (probably *Anyperodon leucogrammicus* Cuvier and Valenciennes), scavenger (*Lethrinus* sp.), and parrotfish (*Callyodon pulchellus* Ruppel).

Information obtained from native populations is filled with inconsistencies and is difficult to interpret. In some cases a fish pointed to as toxic would be accepted readily and used as food. Taboos and customs add confusion. Much difficulty results from faulty communication and the language barrier, especially as to names of fishes. Toward alleviating this problem, it was necessary to translate Marshallese names to English and technical names, although this did not solve the problem completely.

Availability of Poisonous Fishes

In most efforts to ascertain the presence of poisonous fishes in a given area, it has been common practice to capture as many fish as possible and subject them to animal assays. Fish tissues were fed to cats, rats, mice, chickens, mongooses, and other animals, or tissue extracts were injected intraperitoneally into mice. Obtaining an understanding of the logistic problems to be faced in a future on-the-spot intensive study of the problem was a main reason for collecting fishes and undertaking exploratory tests to determine their toxicity. It provided a first-hand, thorough, personal "feel" for the obstacles to be encountered by future investigators, and suggested solutions. Concurrently, some idea of the availability of poisonous fishes was obtained.

Fishes were taken at Majuro and Jaluit atolls by spearing, poisoning, or angling, and a few were obtained by Marshallese fishermen using throw nets. There were various collecting stations representing lagoon, outer reef, and oceanic habitats. Of the many fishes collected, 66 specimens representing 41 species from Majuro Atoll and 41 specimens representing 26 species from Jaluit Atoll were selected for study. Some were assayed by mouse injection, others by both mouse injection and cat feeding. The mouse assay method is the same as used in assaying for paralytic shellfish poison (McFarren, 1959). It is known to be applicable to puffer fish poison (Hori, 1957; Hashimoto and Migita, 1951), and other investigators (Hiyama, 1943; Halstead and Schall, 1955) have used a similar method for other species of fishes and presumed it to be applicable.

In our tests each of three mice were injected with 1 ml. of the supernatant fluid obtained by centrifuging an aqueous acid extract of ground whole fish, muscle tissue, or visceral organs such as liver, ovaries, or intestines. Mouse responses were observed thereafter for at least 18 hr.

Fishes were prepared for cat-feeding tests by cooking small pieces of muscle or other organ for 30 min.; 100 g. of such material offered to a mature cat previously fasted for 24 hr. was always eaten readily; occasionally 200 g. were fed without difficulty. Puffers (*Tetraodon hispidus* Linnaeus), although available, were not tested with cats because positive mouse response was sufficient indication that fed cats would become ill (Murtha *et al.*, 1958).

Test results are summarized in Table 2. In all, 171 preparations were used, 124 extracts from 98 specimens injected into mice and 47 portions from 43 specimens fed to cats. These represented 51 different species. Of this total only 3 specimens of puffer (*Tetraodon hispidus* Linnaeus) were clearly toxic to mice, while 4 specimens—3 of red snapper (*Lutjanus gibbus* Forskal) and 1 scavenger (*Lethrinus miniatus* Bloch and Schneider)—caused illness in cats. On the basis of the tests used, only 7 of 98 specimens comprising 3 of 51 species tested could be considered potentially toxic to humans. Actually, the muscle of only 2 of the puffers was found toxic and the viscera of the third only mildly toxic. The muscle of another red snapper and of 6 other species of the snapper family (Lutjanidae) were nontoxic by cat-feeding test (Table 2).

TABLE 2

Summary of Bioassay Data for Specimens from Majuro and Jaluit Atolls

SPECIMEN NO.	NAME	PORTION TESTED	MOUSE RESPONSE*	CAT RESPONSE*
1	*Gymnothorax pictus* Ahl	viscera	—	NT
		muscle	—	NT
2	*G. pictus* Ahl	whole	—	NT
3	*G. pictus* Ahl	ovaries, viscera	—	NT
		muscle	—	NT
11	*Rhinecanthus aculeatus* (Linnaeus)	whole	—	NT
12	*Chelon vaigiensis* (Quoy & Gaimard)	whole	—	NT
12A	*C. vaigiensis* (Quoy & Gaimard)	whole	D	NT
14	*Tetraodon hispidus* Linnaeus	muscle	—	NT
		liver	D	NT
		viscera	+	NT
15	*Euthynnus alteratus* (Rafinesque)	muscle	—	NT
		liver	D	NT
16	*Caranx melampygus* Cuvier	muscle	—	NT
		viscera	—	NT
17	*Sphyraena barracuda* (Walbaum)	muscle	—	NT
18	*S. forsteri* Cuvier and Valenciennes	muscle	—	NT
19	*Variola louti* (Forskal)	muscle	—	NT
20	*V. louti* (Forskal)	muscle	—	NT
21	*V. louti* (Forskal)	viscera	—	NT
22	*Epinephelus merra* Bloch	whole	—	NT
23	*E. merra* Bloch	muscle	D	NT
24	*Halichoeres trimaculatus* (Quoy & Gaimard)	whole	—	NT
25	*Mulloidichthys samoensis* (Gunther)	whole	D	NT
		viscera	D	NT
26	*Lutjanus monostigmus* (Cuvier & Valenciennes)	whole	—	NT
		viscera	—	NT
27	*Arca* sp. (ark shellfish)	whole	—	NT
28	*Echidna nebulosa* (Ahl)	whole	—	NT
29	*Scarus jonesi* (Streets)	muscle	—	NT
		viscera	—	NT
30	*S. harid* Forskal	muscle	—	NT
		viscera	+	NT
31	*Hepatis triostegus* (Linnaeus)	whole	—	NT
32	*Hyporhamphus laticeps* (Gunther)	whole	—	NT
33	*Epinephelus macrospilos* (Bleeker)	viscera	D	NT
34	*Trochus* sp. (trochus shellfish)	whole	+	NT
		viscera	+	NT
35	*Anyperodon leucogrammicus* (Cuvier)	viscera	—	NT
36	*Chaetodon ephippium* Cuvier	whole	—	NT
37	*C. auriga* Forskal	whole	—	NT
38	*Holocentrus praslin* (Lacepede)	whole	—	NT
39	*Acanthurus leucosternon* Bennett	whole	—	NT
40	*Abudefduf septemfasciatus* Cuvier & Valenciennes	whole	—	NT
41	*Belone platyura* Bennett	whole	—	NT
42	*Gymnothorax flavimarginatus* Ruppel	whole	—	NT
43	*Acanthocybium solandri* (Cuvier)	muscle	—	NT
		viscera	D	NT
44	*Lutjanus gibbus* (Forskal)	muscle	D	NT
		viscera	D	NT
45	*Epinephelus fuscoguttatus* (Forskal)	muscle	—	—
		viscera	D	NT
46	*Lutjanus gibbus* (Forskal)	muscle	—	NT
		viscera	D	NT

TABLE 2—*Continued*

SPECIMEN NO.	NAME	PORTION TESTED	MOUSE RESPONSE*	CAT RESPONSE*
46A	*L. gibbus* (Forskal)	muscle	—	NT
46B	*L. gibbus* (Forskal)	muscle	—	NT
46C	*L. gibbus* (Forskal)	muscle	—	—
47	*L. kasmira* (Forskal)	whole	—	NT
48	*Epinephelus kohleri* Schultz	whole	—	NT
49	*Turbo* sp. (top shellfish)	whole	D	NT
51	*Aprion virescens* Valenciennes	viscera	—	—
52	*Euthynnus pelamis* (Linnaeus)	viscera	—	NT
53	*Trachinotus bailloni* (Lacepede)	muscle	—	NT
54	*Germo alalunga* (Bonnaterre)	muscle	—	NT
55	*Plectropomus truncatus* Fowler	muscle	D	—
56	*Lutjanus* sp.	ovaries	—	NT
		gills, viscera	D	NT
57	*Conomurex* sp.	whole	D	NT
58	*Lutjanus gibbus* (Forskal)	muscle	D	NT
59	*Abudefduf saxatilis* (Linnaeus)	muscle	—	NT
60	*Chelon vaigiensis* (Quoy & Gaimard)	muscle	D	NT
61	*Mulloidichthys samoensis* (Gunther)	muscle	D	NT
62	*Lutjanus vaigiensis* (Quoy & Gaimard)	whole	D	NT
63	*Tetraodon hispidus* Linnaeus	muscle	++	NT
		liver	+	NT
64	*Epinephelus* sp.	broth	D	—
65	*Scarus* sp.	muscle	—	NT
66	*Gymnothorax pictus* Ahl	muscle	—	—
67	*Epinephelus fuscoguttatus* (Forskal)	muscle	—	—
		fat around viscera	—	NT
69	*Lutjanus gibbus* (Forskal)	muscle	NT	+
70	*Sphyraena barracuda* (Walbaum)	muscle	—	—
71	*Lutjanus monostigmus* Cuvier & Valenciennes	muscle	—	—
72	*Gerres argyreus* (Bloch & Schneider)	muscle	—	—
73	*Lutjanus* sp.	muscle	—	—
74	*Lethrinus miniatus* (Forster)	muscle	—	+
75	*Tetraodon hispidus* Linnaeus	muscle	++	NT
80	*Acanthocybium solandri* (Cuvier)	muscle	—	—
		liver	—	NT
81	*Euthynnus alteratus* (Rafinesque)	muscle	—	—
		liver	—	NT
82	*Epinephelus* sp.	muscle	—	—
83	*Euthynnus alteratus* (Rafinesque)	muscle	—	NT
84	*Aprion virescens* Valenciennes	muscle	—	—
85	*Plectropomus truncatus* Fowler	muscle	—	—
86	*Sphyraena barracuda* (Walbaum)	muscle	—	—
		ovaries, liver	—	—
87	*Lutjanus gibbus* (Forskal)	muscle	—	—
88	*Hepatis triostegus* (Linnaeus)	whole	—	—
89	*Mulloidichthys samoensis* (Gunther)	muscle	—	NT
90	*Kyphosus cinerascens* (Forskal)	muscle	—	—
		viscera	D	NT
91	*Lutjanus gibbus* (Forskal)	muscle	—	+
92	*Sphyraena barracuda* (Walbaum)	muscle	—	—
93	*Epinephelus fuscoguttatus* (Forskal)	muscle	—	—
94	*Caranx lugubris* Poey	muscle	—	—
95	*Variola louti* (Forskal)	muscle	—	—

TABLE 2—*Continued*

SPECIMEN NO.	NAME	PORTION TESTED	MOUSE RESPONSE*	CAT RESPONSE*
96	*Elagatis bipinnulatus* (Quoy & Gaimard)	muscle	—	—
97	*Lutjanus kasmira* (Forskal)	muscle	—	NT
98	*L. gibbus* (Forskal)	muscle	—	++
99	*Plectropomus oligacanthus* Bleeker	muscle	—	—
100	*Variola louti* (Forskal)	muscle	—	—
101	*Aprion virescens* (Valenciennes)	muscle	—	—
102	*A. virescens* (Valenciennes)	muscle	—	—
103	*Lethrinus* sp.	muscle	—	—
104	*L. miniatus* (Schneider)	muscle	—	—
105	*L. miniatus* (Schneider)	muscle	—	—
106	*Caranx melampygus* Cuvier & Valenciennes	muscle	—	—
107	*C. melampygus* Cuvier & Valenciennes	muscle	—	—
108	*Grammatorcynus bilineatus* (Ruppel)	muscle	—	—
109	*G. bilineatus* (Ruppel)	muscle	—	—
110	*Elagatis bipinnulatus* (Quoy & Gaimard)	muscle	—	—
111	*Neothunnus albacora macropterus* (Temminck & Schlegel)	muscle	—	—
112	*N. sexfasciatus* (Quoy & Gaimard)	muscle	—	—
113	*Caranx melampygus* Cuvier & Valenciennes	muscle	—	—
		total 126		

* — = negative
\+ = positive
D = toxicity doubtful
NT = not tested

None of the specimens found toxic by cat test gave a clearcut indication of toxicity when injected into mice. Hashimoto (1956) found a similar relationship with barracuda (*Sphyraena picuda* Bloch and Schneider). When mice were injected with aqueous extract, or even when fed the muscle, their response was very slight, whereas cats became severely ill or died after eating. Hashimoto also showed that the toxin in barracuda apparently is fat-soluble, because it could be extracted with ether. In Hawaii, Banner and Boroughs (1958) studied the toxin from a snapper (*Lutjanus bohar* Forskal) and found it insoluble in water but soluble in 90 per cent ethanol and some other solvents. Essentially similar characteristics were found by McFarren and Bartsch (1960) for the toxins of red snapper (*Lutjanus gibbus* Forskal) and a scavenger (*Lethrinus miniatus* Bloch and Schneider) from Jaluit Atoll. They also found that such poison can be assayed successfully by intraperitoneal injection of mice, using the oily residue obtained by concentration of an ethyl ether extract. All of these observations indicate that water extraction of macerated fish tissues, followed by centrifuging and intraperitoneal injection of the supernatant into mice, cannot be a valid test. Prompt positive mouse responses, when they occur, apparently result from toxic substances suspended or emulsified in the extract. Unfortunately, therefore, published data on distribution of ciguatera-producing fishes and their toxin intensity based on the customary mouse test are subject to question.

There can be no doubt, however, that some poisonous fishes are present in Majuro and Jaluit atolls. This has been demonstrated by assay for the poison of puffers (*Tetraodon hispidus* Linnaeus), red snappers (*Lutjanus gibbus* Forskal), and scavengers (*Lethrinus miniatus* Bloch and Schneider). In addition, information from the literature (Hiyama, 1943) and from questioning local populations implicate the last two in poisoning episodes. The puffer, of course, is not used as food, and considerable selectivity is exercised in taking other fish for consumption. Even so, toxic specimens seem less common than findings of others would lead one to believe.

Are More Species Becoming Toxic?

During conversations and surveys among the Marshallese, it was often heard that a given species had become toxic only recently and that more kinds of fishes are toxic now than in the past. Information from the present study was examined in relation to that obtained by Japanese workers (Matsuo, 1934; Hiyama, 1943) at Jaluit Atoll in 1934 and 1941. Some general indication of the situation was obtained, in spite of the necessity to use Marshallese names which apparently are not only inconsistent but are applied to more than a single species. Accordingly, both the Marshallese name and the best judgment of the technical equivalent are given in Table 3.

Obviously, these earlier and later data are not strictly comparable, because of method of collection and the profound social, economic, and occupational changes among the Marshallese since 1941. Nevertheless, it is interesting that the number of implicated fishes at Jaluit has changed only from 18 to 22 during the 24-yr. period. The number of species implicated at Majuro was 23, but composition at one place varied somewhat from the other, so that Jaluit and Majuro together had 32. Of the 91 poisoning episodes cited earlier, the principal fishes concerned were already toxic in 1934 or 1941, as shown by the following list of those causing two or more incidents:

FISH	NO. OF INCIDENTS	REPORTED TOXIC		
		1934	1941	1958
jato (*Lutjanus vaigiensis* Quoy and Gaimard)	11	X	X	X
kuro (*Epinephelus fuscoguttatus* Forskal)	8	–	X	X
mijmij (*Lethrinus microdon* Cuvier and Valenciennes)	5	–	–	X
liele (*Rhinecanthus aculeatus* Linnaeus)	4	X	X	X
marea (identity questionable)	4	?	?	X
kur (identity questionable)	3	?	?	X
lane (*Caranx melampygus* Cuvier)	2	X	X	X
jawe (*Promicrops lanceolatus* Bloch)	2	X	X	X
kie (*Monotaxis grandoculis* Forskal)	2	X	X	X
yol (*Chelon vaigiensis* Quoy and Gaimard)	2	–	–	X
ikmouj (identity questionable)	2	?	?	X
lejebjeb (identity questionable)	2	?	?	X
malae (identity questionable)	2	?	?	X

It is concluded that there is no striking evidence that species that have been untainted in the past have suddenly become poisonous.

Undoubtedly, throughout the course of history, persons involved in fish poisoning have wondered how fishes become toxic. Numerous ideas have been expressed—from fish eating manchineel berries dropping onto the water to uptake of copper from natural deposits or sunken ships. Now it seems generally agreed that fishes become poisonous through influences existing in the reef environment. This has been stated many times, but never so clearly or in such logical sequence of steps as by Randall (1958) in a recent review of ciguatera: (a) toxin must originate in the environment because only fishes in a restricted area are toxic, while those of similar size elsewhere are not; (b) in affected areas not all species are toxic, and, because food and feeding habits are the principal variables, their food is a likely source of toxin; (c) the food is probably benthic, because toxic specimens of a species occur with it but not in open seas where only plankton are available; (d) if the benthic food is algae, it must be small to accommodate the delicate mouth structures of some poisonous fishes; (e) blue-green algae, sometimes toxic, are suspect; (f) violently poisonous large predaceous fishes presumably accumulate toxin from their less toxic prey, and they can retain the toxin for a long time after being separated from that source; (g) the course of events in many places suggests that benthic organisms at the base of a toxic food chain grow well in areas recently denuded or disrupted by catastrophic events such as violent storms.

TABLE 3

TOXIC FISHES AS INDICATED BY FISH POISONING EPISODES OR VERBAL REPORTS (1934, 1941, and 1958)

MARSHALLESE NAME	SCIENTIFIC NAME	JALUIT			MAJURO 1958
		1934 Matsuo*	1941 Hiyama*	1958	
Ban	*Lutjanus gibbus* (Forskal) *L. bohar* (Forskal)	+	+	+	+
Barot, baret	*Abudefduf septemfasciatus* Cuvier & Valenciennes	—	+	—	—
Bejerak	*Kyphosus* sp.	—	—	—	+
Betwettak	not known	+	+	+	—
Ikaboe molmol	*Scomber japonicus* Houttuyn	—	—	—	+
Ikbwij	*Caranx lessonii* Cuvier & Valenciennes *Trachinotus bailloni* (Lacépède)	+	+	+	+
Ikmouj	*Scarus harid* Forskal	—	—	+	+
Ikuit	*Plectropomus leopardus* (Lacépède)	+	—	—	—
Ilmok	*Gerres baconensis* Evermann & Seale	—	—	—	+
Jab, jato	*Lutjanus bohar* (Forskal) *L. vaigiensis* (Quoy & Gaimard) *L. gibbus* (Forskal)	+	+	+	+
Jalia	*Lethrinus miniatus* (Schneider)	+	+	+	—
Jawe	*Promicrops lanceolatus* (Bloch) *Plectropomus truncatus* Fowler	+	+	+	+
Jo	*Mulloidichthys auriflama* (Forskal)	—	—	—	+
Jome	*M. samoensis* (Gunther)	+	—	+	+
Jujukip	*Sphyraena picuda* Bloch & Schneider *S. forsteri* Cuvier & Valenciennes	+	+	+	—
Julae	*Plectropomus oligocanthus* Bleeker	+	+	+	—
Jure	*Sphyraena barracuda* (Walbaum)	+	+	+	—
Katak	not known	+	+	+	—
Kie, kielotan	*Monotaxis grandoculis* (Forskal)	+	+	+	+
Kuban	*Hepatis triostegus* (Linnaeus)	—	—	+	—
Kuro	*Epinephelus fuscoguttatus* (Forskal)	—	+	+	+
Lane, deltokrok	*Caranx melampygus* Cuvier & Valenciennes	+	+	+	+
Laum	*Aprion virescens* Valenciennes	—	+	—	—
Lejebjeb	*Epinephelus* sp.	—	—	—	+
Lemejine	not known	+	—	+	—
Liele, bub	*Rhinecanthus aculeatus* (Linnaeus)	+	+	+	+
Malle	*Siganus puellus* (Schlegel)	—	—	—	+
Mamennie	*Lethrinus* sp.	+	+	+	—
Mera, alowor	*Scarus jonesi* (Streets)	—	+	+	+
Mijmij	*Lethrinus microdon* Cuvier & Valenciennes	—	—	—	+
Momo	*Epinephelus macrospilos* (Bleeker)	—	—	—	+
Net	*Lethrinus variegatus* Cuvier & Valenciennes	—	+	—	—
Pelak, Berak	*L. kallopterus* Bleeker	—	—	—	+
Rewa	*Caranx fulvoguttatus* (Forskal)	—	—	—	+
Tiebro-ael	*Acanthurus nigricans* (Linnaeus)	—	+	+	+
Ulinno, Ilino	not known	+	+	+	—
Yol	*Chelon vaigiensis* (Quoy & Gaimard)	—	—	—	+
	Total	18	21	22	23

* *See* References.

PRESENT KNOWLEDGE OF FISH POISONS

Ciguatera

Fish most commonly incriminated in ciguatera are barracuda and snappers, although various reef fishes such as sea bass, groupers, and many others have frequently been implicated (Halstead, 1959). Symptoms in humans vary greatly, but usually appear in 1–10 hr. Numbness of lips and mouth occurs first, followed by tingling of the lips and extremities. Initial symptoms sometimes include a metallic taste, nausea, vomiting, abdominal cramps, and diarrhea. Generally the victim becomes extremely weak and prostrate, and in extreme cases muscular aches and pains are pronounced. Temperature sense may be reversed so that hot objects feel painfully cold and cold objects hot. A general inability to coordinate muscular movements may develop, and paralysis, muscular aches, and itching sensations may persist for several weeks or even months. In severe cases, complete recovery from weight losses, sensory disturbances, and weakness may require several years.

Recent research by Hashimoto (1956), Banner and Boroughs (1958), and McFarren and Bartsch (1960) indicates that barracuda poison and snapper poison are similar and perhaps identical. The poison is insoluble in water but is soluble in 90 per cent ethanol and certain other solvents, including acetone and diethyl ether. Beyond the knowledge that it will withstand boiling and is soluble in certain organic solvents, its chemical, pharmacological, and physical properties are still to be investigated.

Because of the recent discovery that ciguatera poison is not soluble in water, and because of possible toxic effects of salt in the extracts, much of the past assay data on ciguatera poison is questionable. Shortage of cats and the questionable validity of the mouse injection test led Banner and Boroughs to use the imported mongoose. Feeding tests with this animal showed it to be an acceptable test animal. They also noted that mice fed toxic fish were less sensitive to ciguatera poison than cats or mongooses. However, a successful assay may be done by injecting oil from a concentrated ether extract of the cooked fish into mice (McFarren and Bartsch, 1960).

Puffer Poison

Efforts by Japanese workers since 1909 have resulted in useful methods for extraction, purification, and characterization of puffer poison, known as tetrodotoxin (Tahara, 1910, Yokoo and Morosawa, 1955; Tsuda *et al.*, 1958; Tsuda and Kawamura, 1952*a, b,* 1953). In human cases the onset of symptoms is generally rapid and violent (Halstead, 1958). Malaise, pallor, dizziness, paresthesia of the lips and tongue, and ataxia frequently develop in 10 to 45 min. Hypersalivation, profuse sweating, extreme weakness, headache, subnormal temperature, decreased blood pressure and a rapid weak pulse also appear early. Nausea, vomiting, and diarrhea may or may not occur. The paresthesia may subsequently involve the fingers and toes and finally other parts of the body, causing victims to complain of feeling as if they are floating. Respiratory distress becomes prominent, and muscular twitching, tremor, and incoordination become progressively worse. With approaching death, the eyes become fixed and glassy, and convulsions occur. The victims usually remain conscious and mentally acute. Death results from respiratory paralysis usually in 6 to 24 hr.

Japanese workers assay the poison in dilute acetic acid and/or methanol and generally use subcutaneous injection, whereas recent studies (McFarren and Bartsch, 1960) indicate that puffer poison can be assayed in much the same manner as paralytic shellfish poison.

Moray Eel Poison

Practically no information is available concerning the chemical or pharmacological properties of moray eel (*Gymnothorax*) poison. Similarity of symptoms with those of ciguatera suggests a common poison (Randall, 1958) but it is now known that ciguatera poison is not water-soluble, whereas gymnothorax poison probably is. In studying gymnothorax poisoning, Ralls and Halstead (1955) used water or methanol acidified to pH 4.0 with acetic acid to obtain extracts for injection into mice. Appearance of prompt symptoms including hypoactivity, respiratory distress, convulsions, and death by respiratory arrest strongly suggest a water-soluble gymnothorax poison; water extracts from ciguatera-producing species are not known to cause such symptoms. Although puffer poison also is water-soluble, symptoms of gymnothorax poison do not seem identical to puffer poisoning. As with ciguatera and puffer poisoning, the initial symptoms of gymnothorax poisoning may include tingling and numbness about the lips, tongue, hands, and feet, sometimes followed by nausea, vomiting, a metallic taste, diarrhea, and abdominal pain, as in ciguatera. The characteristic signs of gymnothorax poisoning, however, appear to be the absence of thoracic respiration, with pronounced abdominal breathing, profuse perspiration, excessive mucus production, purposeless movements, violent convulsions, and an extended period with absence of reflexes. Rapid respiration, rapid pulse, and high fever may develop. Khlentzos (1950) has reported dizziness, blurred vision, tremors of the hands, sensory changes in the legs, interosseous atrophy, muscular weakness, ulnar palsy, foot drop, radial weakness, deviation of the tongue, and a loss of voice probably due to laryngospasm. In severe intoxication, death did not occur until after 14 to 25 days.

Scombroid Poison

Recent Japanese studies (Kawabata *et al.*, 1955*a, b, c,* 1956) have shown that scombroid poisoning is an allergy-like food poisoning caused by the presence in the incriminated fish of an unusual amount of histamine and another more powerful vagus stimulant, called saurine. Large amounts of histamine and saurine are not naturally present in fish but apparently are produced by the action of certain strains of the bacterium, *Proteus morganii,* under conditions giving no obvious signs of putrefaction. Susceptible fishes are tuna, mackerel, bonita, and skipjack.

Isolation of saurine was accomplished by paper chromatography of a crude methanol extract leached from minced fish (probably *Cololabis saira* Brevoort). The newly isolated vagus stimulant was clearly differentiated from histamine and was tentatively named saurine. Saurine is insoluble in ether, acetone, benzene, chloroform, and absolute alcohol, although easily extracted with 80 per cent alcohol.

The physiological and pharmacological actions of saurine were determined by skin reactions in rabbits, shock symptoms in guinea pigs, and antagonism against anti-allergic drugs. These studies indicated that saurine has an additive effect to histamine and is different from acetylcholine. In humans, ½ to 2 or 3 hr. usually elapse after eating deteriorated scombroid fishes before appearance of symptoms, which include reddening of the face and the upper half of the body, exanthema like those of allergy, severe headache, and palpitation. Fever and diarrhea may accompany the illness in a few cases, and victims may become nauseated but rarely vomit.

PLAN FOR STUDY

Information now available emphasizes the need for further intensive and long-range studies of fish poisoning. Comprehensive studies will yield information of value to all places presently involved and eventually will also benefit areas other than those now known to be affected. Continuing epidemiologic studies should be intensified and coordinated with biochemical and biological approaches. Only by such an approach are significant advances likely within a reasonable period. Six principal phases are recommended:

1. Collection and analysis of epidemiologic data should be devised to observe incidence trends and establish more clearly the relationship of symptoms with species of fishes involved, their origin, and mode of handling. At present, considerable confusion surrounds the relationship of potentially toxic fishes to illness in humans. No systematic analysis exists of any large series of cases to indicate how many types of poisoning there actually are. Symptoms may be numerous and varied, and therefore a controlled analysis of clinical observations relating them to species and laboratory studies is of paramount importance. Fish poisoning incidence trends also should be evaluated in relation to weather, water characteristics, and other environmental phenomena in an effort to detect any significant influences they may have.

2. Because treatment of victims at present is only symptomatic and involves a multiplicity

of medications, a phase of study should be devoted to developing more effective therapy. The Trust Territory is now pursuing this objective.

3. To obtain toxic fish specimens for study, advantage should be taken of the normally occurring fish poisoning episodes among Marshallese and other populations in poisonous fish areas. In past studies the general procedure has been to collect hundreds of fishes and test all of them for toxicity by an assay procedure of some kind. Such costly and time-consuming effort to obtain one or two toxic specimens is exceedingly inefficient. Information thus obtained can only relate toxicity to the response in test animals, and it fails to provide the more important knowledge of human symptoms in response to the toxin of a specific fish. No investigator thus far has established a systematic procedure that will provide simultaneously pertinent information on symptoms in humans, knowledge of the causative fish's environment, symptoms in laboratory animals fed a part of the same specimen used for other analyses, and a record of human patient responses to a given therapy.

4. Because present assay procedures are inadequate, a simple on-the-spot test must be developed to determine if a fish is safe to eat, and to relate the quantity of poison present in a fish to the quantity that will cause human illness.

5. For a more rational approach to diagnosis and therapy and a better understanding of the biological activity of fish toxins, pharmacologic studies are needed to determine the physiologic response of test animals to fish toxins, and their mode of action. Studies will require large quantities of poisonous fish material, collection of which will pose difficulties.

6. The formation of toxins in fishes appears to be a response to some influence in the environment, perhaps involving feeding habits and susceptibility of the fish species. No way is known to predict toxicity in fishes at a given locality. Ecologic study is proposed to determine if there is some dependable relationship between one or more identifiable variables in the environment and the appearance of toxic fishes. If such relationships are discovered, poisoning episodes could be prevented by avoiding susceptible groups of fishes accordingly, or possibly by controlling the causes of toxicity.

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REFERENCES

BANNER, A. H., and H. BOROUGHS. 1958. Observations on toxins of poisonous fishes. Proc., Soc. Exper. Biol. & Med. 98: 776–778.

BARTSCH, A. F., R. H. DRACHMAN, and E. F. MCFARREN. 1959. Report of a Survey of the Fish Poisoning Problem in the Marshall Islands. BSS. 117 pp.

BERLIN, R. 1948. Hoff disease in Sweden. Acta Med. Scand. 129: 560.

BENSON, JEROME. 1956. Tetraodon (blowfish) poisoning. J. Forensic Sciences 1: 119–125.

COURVILLE, DONOVAN A., BRUCE W. HALSTEAD, and DONALD W. HESSEL. 1958. Marine biotoxins: Isolation and properties. Chemical Reviews, pp. 235–248.

HALSTEAD, BRUCE W. 1951. A medical-military problem. Research Reviews, Office of Naval Research, pp. 10–16.

——— 1954. A note regarding the toxicity of the fishes of the skipjack family, Katsuwonidae. Calif. Fish & Game 40: 61–63.

——— 1958. Poisonous fishes. PHR 73: 302–312.

——— 1959. Dangerous Marine Animals. Cornell Maritime Press, Cambridge, Md. 146 pp.

——— and NORMAN C. BUNKER. 1954. A survey of the poisonous fishes of Johnston Island. Zoologica 39: 61–77.

——— and DONALD W. SCHALL. 1955. Report on the poisonous fishes captured during the Woodrow G. Krieger Expedition to the Galapagos Islands. In: Essays in the Natural Sciences in Honor of Captain Allan Hancock, Univ. of Southern Calif. Press, Los Angeles, pp. 147–172.

HASHIMOTO, YOSHIRO. 1956. A note on the poison of a barracuda, *Sphyraena picuda* Bloch & Schneider. Bull. Japan. Soc. Scientific Fisheries 21: 1153–1157.

——— and M. MIGITA. 1951. Quantitative analysis method for fugu (puffer) toxin. Bull. Japan. Soc. Scientific Fisheries 16: 341–346.

HIYAMA, YOSHIO. 1943. Poisonous Fishes of the South Seas. [In Japanese.] Translated by W. G. Van Campen, in: Special Scientific Report, Fisheries No. 25, U.S. Dept. Interior, Fish & Wildlife Service, Washington, D. C., 1950.

HORI, HIROYOKI. 1957. Histopathologic study of crystalline tetrodotoxin, Report No. 1. Observation on acute intoxication in the mouse. Annual Report, Inst. Food Microbiology, Chiba University, Japan 10: 70–71.

KAWABATA, T., K. ISHIZAKA, and T. MIURA. 1955*a*. Studies on the allergy-like food poisoning associated with putrefaction of marine products, I. Episodes of allergy-like food poisoning caused by "samma sakuraboshi" (dried seasoned saury) and other kinds of marine products. Japan. J. Med. Sci. & Biol. 8: 487–501.

——— ——— ——— 1955*b*. Studies on the allergy-like food poisoning associated with putrefaction of marine products, II. Separation of causative substance and some of its chemical characteristics. Japan. J. Med. Sci. & Biol. 8: 503–519.

——— ——— ——— 1955*c*. Studies on the allergy-like food poisoning associated with putrefaction of marine products, III. Physiological and pharmacological action of "saurine," a vagus stimulant of unknown structure recently isolated by the authors, and its characteristics in developing allergy-like symptoms. Japan. J. Med. Sci. & Biol. 8: 521–528.

——— ——— ——— and T. SASAKI. 1956. Studies on the food poisoning associated with putrefaction of marine products, VII. An outbreak of allergy-like food poisoning caused by "sashimi" of *Parathunnus mebachi* and the isolation of causative bacteria. Bull. Japan. Soc. Scientific Fisheries 22: 41–47.

KHLENTZOS, CONSTANTINE T. 1950. Seventeen cases of poisoning due to ingestion of an eel, *Gymnothorax flavimarginatus*. Am. J. Trop. Med. 30: 785–793.

MATSUO, RYUICHI. 1934. Report of an investigation of poisonous fishes at Jaluit I. In: Collected Medical Reports on Endemic Diseases of the South Sea Islands, 2nd ed., South Seas Office, pp. 309–326. [In Japanese.]

MCFARREN, EARL F. 1959. Report on collaborative studies of the bioassay for paralytic shellfish poison. J. Assoc. Offic. Agri. Chemists 42: 263–271.

——— and A. F. BARTSCH. 1960. Application of the paralytic shellfish poison assay to poisonous fishes. J. Assoc. Offic. Agri. Chemists 43: 548–554.

MURTHA, E. F., D. E. STABILE, and J. H. WILLS. 1958. Some pharmacological effects of puffer poison. J. Pharm. Exper. Thera. 122: 247–254.

PAETRO, SIDNEY. 1956. Food poisoning caused by the great barracuda. PHR 71: 933–938.

RALLS, R. J., and B. W. HALSTEAD. 1955. Moray eel poisoning and a preliminary report on the action of the toxin. Am. J. Trop. Med. & Hyg. 4: 136–139.

RANDALL, JOHN E. 1958. A review of ciguatera, tropical fish poisoning, with a tentative explanation of its cause. Bull. Marine Science, Gulf and Caribbean 8: 236–267.

SCHWIMMER, M., and D. SCHWIMMER. 1955. The Role of Algae and Plankton in Medicine. Grune & Stratton, Inc., New York City. 85 pp.

SMITHSONIAN INSTITUTION. 1944. Survival on Land and Sea. Publications Branch, Office of Naval Intelligence, U.S. Navy.

TAHARA, Y. 1910. Uber das Tetrodon-Gift. Biochem. Ztschr. 30: 255–275.

TSUDA, K., and M. KAWAMURA. 1952*a*. The constituents of the ovaries of globefish, VI. Purification of globefish poison by chromatography. J. Pharmaceutical Soc. Japan 72: 187–190.

——— ——— 1952*b*. The constituents of the ovaries of globefish, VII. Purification of tetrodotoxin by chromatography. J. Pharmaceutical Soc. Japan 72: 771–774.

——— ——— 1953. The constituents of the ovaries of globefish, VIII. Studies on tetrodotoxin. Pharmaceutical Bull., Pharmaceutical Soc. Japan 1: 112–113.

——— ——— and R. HAYATSU. 1958. On the constitution of tetrodotoxin. Chemical & Pharmaceutical Bull. 6: 225–226.

YOKOO, A., and S. MOROSAWA. 1955. Studies on the toxin in globefish, No. 5. Comparison with tetrodotoxin. J. Pharm. Soc. Japan 75: 235–236.

Types of Occurrence of Nontronite and Nontronite-like Minerals in Soils[1]

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NONTRONITE, the iron-rich dioctahedral mineral of the montmorillonite group, is rarely found in soils. A number of montmorillonite clays having a high content of iron oxide have been found in subsoils. These occurrences are located at Toowoomba, Queensland, Australia; Waipata, South Island, New Zealand; Molumolu, Fiji; and at a number of sites in the Hawaiian Islands. These clays occur as relatively pure mineral aggregates and therefore are well segregated from their matrix. The type of occurrence provided material of homogeneous chemical and mineral compositions. The iron oxide content of these clays ranged from 9 to 32 per cent and indicates a wide range of iron substitution in the octahedral position. These clays occur under a wide range of climatic conditions, as evidenced by rainfall variation of 13 to 120 inches per year. Likewise, they occur in both early and late stages of weathering and, because of that, they occur in different mineral associations of primary minerals, other 2:1 clays, kaolin, iron oxides, and bauxite.

The purpose of this report is to describe the mode of the occurrence of these clays, the climatic environment, the weathering stage and mineral association, and their chemical and mineral composition.

The occurrence of nontronite in weathering basalt has been described by Allen and Schied (1946) in Washington. These nontronites are dioctahedral montmorillonite clays in which there is a full substitution of iron in the octahedral position. There is a similarity in the occurrence of some of the clays described in this report to the nontronite of Manato, Washington.

DESCRIPTION OF NONTRONITE OCCURRENCES

The description of the occurrences of nontronite and nontronite-like minerals will relate both their mode of occurrence and the climatic and weathering environments under which they exist. The climatic environment is divided into three types. The mineral weathering conditions are determined by the climatic conditions. The descriptions are as follows.

Semi-Arid Conditions

1. Lualualei, Oahu, Hawaii. A yellowish-green nontronite was found as one of the first products of weathering of olivine and as fragmental crystalline coatings on olivine in a picrite basalt, oceanite. It occurred in several boulders of a weathering picrite basalt exposed in the road cut across from the new Permanente Cement Plant on the Kolekole Pass Road. In many of the weathered olivine pockets in the rock, the unweathered green olivine crystals occurred in the center surrounded by yellowish-green, waxy-surfaced aggregates of nontronite. There is evidence that the nontronite may occur as pore fillings after weathering of the nontronite. Similar pore fillings with montmorillonite have been described by Sherman and Uehara (1956). The area receives about 15 inches of rainfall per year.

2. Road cut at Molumolu near Nandi, Fiji. Nontronite occurs as light yellowish-brown coating on peds and slickenslide surfaces. It also is impregnated in the pores of the peds. The soil of the peds is a black, sticky montmorillonite clay. The very nature of the occurrence suggested that the nontronitic clay was a secondary deposition of material from percolating leaching

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waters. This material was identified as nontronite by the New Zealand Division of Scientific and Industrial Research Laboratories. The rainfall in this area is between 15 and 20 inches per year.

Moderate Rainfall Areas

1. Waipata, South Island, New Zealand. This nontronite occurred as dark greenish-brown, elongated, waxy-coated mineral aggregates under a ledge of weathering basalt. This site was a protected accumulation area under a basalt boulder where the material would lose water slowly while continually receiving additional dissolved and suspended materials in the percolating waters. The mineral aggregates were extremely homogeneous in physical appearance. The climate was cool temperate, and the area received approximately 35 inches of rainfall per year.

2. Toowoomba, Queensland, Australia. This nontronite occurs as waxy, greenish-brown mineral aggregates in a lens near the top of a well-weathered basalt. The mineral aggregates occur both as elongated aggregated coatings on weathered basalt fragments and as independent units. The mineral aggregates are homogeneous and appear to be secondary deposition. The area is located due west of Brisbane and probably receives 35 inches of rainfall per year. Climate is subtropical.

Humid Tropical Rainforest Areas

1. Kahakuloa, West Maui, Hawaii. A greenish-yellowish-brown, waxy nontronite occurs as continuous layer coating in water drainage channels in a weathering oligoclase andesite of the Honolua flows of West Maui. This layer may be in close contact with halloysite clays. The climate is tropical and the rainfall is about 80 inches per year.

2. Nuuanu Pali, Oahu, Hawaii. Two samples of nontronite were collected from the contact zone of a vertical dike complex in the road cut on the windward side of the famous Pali on Oahu. The nontronite occurs as a layer at the contact zone of the dike. It is a waxy, greenish-gray-brown to greenish-brown mineral aggregate breaking into slightly curved aggregates with sharp points. The internal fracture faces are not always waxy in appearance. The climate is tropical with a rainfall of about 65 inches per year.

3. Wailua Reservoir, Kauai, Hawaii. In studying a weathered basalt boulder which had an unweathered rock core, green, waxy crystal aggregates were found. On further investigation, the crystals were quite numerous at the weathering contact zone and also in various locations in the highly weathered matrix of the shell of the weathered boulder. The nontronite was found in the following locations in this weathering rock system: (a) green, waxy nontronite crystals were found in the protective pockets in the rock and at the weathering contact zone; (b) waxy, green nontronite nodules occurred as pore fillings in the weathered portion of the rock; and (c) yellowish-green, waxy mineral aggregates occurred as segregated material in the weathered portion of the rock. The weathered portion of the rock is a ferruginous bauxite. The sample used in this study is contaminated with some gibbsite. The occurrence of these two minerals together is unique in nature. This area is a true humid tropical area with an annual rainfall of 100 inches or more.

CHEMICAL COMPOSITION OF NONTRONITES

The chemical composition of the nontronites was determined by standard sodium carbonate fusion. The results of the chemical analysis are given in Table 1. In considering the chemical analysis of these nontronites, some of the samples were difficult to collect without impurities. The samples collected at Lualualei may contain some olivine; the samples collected at Kahakuloa, Maui, may contain some halloysite and gibbsite; the Molumolu sample may contain some of the montmorillonite clay; and lastly the Wailua sample does have gibbsite impregnated in it. The gibbsite interfingering was clearly discerned by petrographic examination of thin sections. However, in each case every effort was made to obtain as pure a sample as possible.

The samples from Lualualei and Toowoomba have a high content of magnesium. Some of the magnesium in the Lualualei sample may come from the olivine which contains 46 per cent MgO. The samples collected at Molumolu and Waipata have moderate amounts of MgO,

TABLE 1

THE CHEMICAL COMPOSITION OF NONTRONITES SAMPLED UNDER A WIDE RANGE OF CLIMATIC AND WEATHERING ENVIRONMENTS

CONSTITUENT	SEMIARID		MODERATE RAINFALL		HUMID TROPICAL				STANDARD NONTRONITE
	Lualualei Valley, Oahu, Hawaii	Molumolu, Fiji	Waipata, S. Island, New Zealand	Toowoomba, Queensland, Australia	Kahakuloa, Maui, Hawaii	Nuuanu Pali, Oahu, Hawaii		Wailua Game Refuge, Kauai, Hawaii	
	weathering product after olivine	clay coating, skins, impregnations	under weathering basalt boulder	pockets in subsoil of lateritic soil formed from basalt	mineralized drainage channel	volcanic dike weathered basalt	contact zone to dike in weathered basalt	weathered basalt boulder	
	%	%							
SiO_2	48.20	52.28	48.54	48.74	33.35	39.04	43.69	26.40	45.83
Al_2O_3	7.02	21.43	16.88	21.02	22.65	23.73	17.65	28.00	5.05
Fe_2O_3	16.39	9.95	15.52	8.82	31.52	17.13	14.18	26.26	36.44
TiO_2	0.58	0.92	0.77	0.53	0.35	3.01	2.61	2.01	0.49
CaO	4.26	1.18	2.30	1.29	0.01	0.55	3.52	0.10	2.20
MgO	17.12	4.39	6.72	10.71	0.21	0.69	0.75	0.73	1.14
K_2O	0.00	1.52	0.21	0.08	0.12	0.00	0.16	0.00	0.00
Na_2O	0.53	2.43	0.37	0.48	1.29	0.49	3.01	0.00	0.00
MnO	0.16	0.06	0.03	0.06	0.08	0.34	0.20	0.08	0.02
P_2O_5	0.00	0.07	0.04	0.21	0.05	0.04	0.03	0.11	—
Loss on Ignition	6.87	8.67	9.94	10.86	10.70	12.78	9.65	15.77	9.12

4.4 and 6.7 per cent respectively. All of the other samples are low in magnesium.

The Fe_2O_3 content of the nontronites and nontronite-like samples ranged from 8.8 to 31.5 per cent. The samples collected at Toowoomba and Molumolu had the lowest Fe_2O_3 content, 8.8 and 9.9 per cent respectively. The Fe_2O_3 content of the samples collected at Lualualei, Waipata, and Nuuanu Pali ranges from 14.2 to 17.1 per cent. The samples collected at Kahakuloa, Wailua, and the *standard nontronite* sample from Manato, Washington, have a much higher Fe_2O_3 content. The Wailua nontronite contains gibbsite; and, if the sample were corrected for its gibbsite content, the Fe_2O_3 would probably equal that of the other samples. The correction is made by using the increase in per cent lost on ignition as indication of gibbsite content.

The alumina content is high (16.9 to 28.0 per cent) in all samples except the Lualualei sample and the standard nontronite sample.

The silica content ranges from 43.7 to 52.3 per cent in all samples except the samples collected at Kahakuloa and Wailua, which contained 33.4 and 26.4 per cent respectively.

Only the samples collected at Waipata, New Zealand, have a calcium content comparable to the standard nontronite sample from Manato, Washington. The samples collected at Lualualei and one at the Nuuanu Pali had a much higher content of calcium, and all others were considerably lower.

The high titanium content in the three Hawaiian samples is a residual enrichment from the parent basalt, which has a high titanium content, as pointed out by Cross (1915).

MINERAL IDENTIFICATION OF NONTRONITE

Examination of the X-ray data shows two pertinent features of the Wailua clay: first, that the clay is a montmorillonite type clay; and, second, a more conjectural one, that the ion substitution in the octahedral layer might be ferruginous in nature. X-ray analysis of the oriented, glycerol-solvated clay showing a strong 001 basal reflection at 17.7Å, verifies the first, but the second statement requires some explanation.

The diffraction pattern in Figure 1 is that of powder samples, but the strong 001 line indicates some degree of preferred orientation in that plane. An increase in the b-axial length of the montmorillonite group of minerals in the order montmorillonite—nontronite—saponite clays had been suggested by Brindley (1951). Measurement of the 060 index for Wyoming bentonite, Washington nontronite, and the Wailua clay shows a sequence: Wyoming bentonite—nontronite—Wailua nontronite. The axial length of the Wailua clay is intermediate to that of Wyoming bentonite and Washington nontronite. The b-axial length of nontronite and saponite are, however, so alike that it is impossible to differentiate between these two minerals by X-ray technique alone. Chemical data must be used to support any claim to the identification of the mineral.

DISCUSSION OF RESULTS

The data presented in this report show a wide range in the chemical composition of the nontronite or nontronite-like minerals. If one were to use the degree of substitution of iron in the octahedral position as the criterion, then not all of these 2:1 minerals could be considered nontronite. If a 50 per cent or more substitution of iron were used as a criterion for nontronite, the minerals from Toowoomba and Lualualei would not qualify. The sample at Toowoomba cannot be considered to be a nontronite; but probably, at best, it would be a magnesium nontronite or more likely an iron saponite. This was borne out by the X-ray diffraction pattern for this sample in that it favored a trioctahedral structure more than the Wailua sample's pattern. The other low iron oxide-containing mineral was the sample from Molumolu, Fiji. However, here the magnesium content is low. Thus, a dioctahedral structure is possible with a low iron substitution.

All other samples contained sufficient iron oxide content to support a 50 per cent or more substitution of iron in the octahedral position.

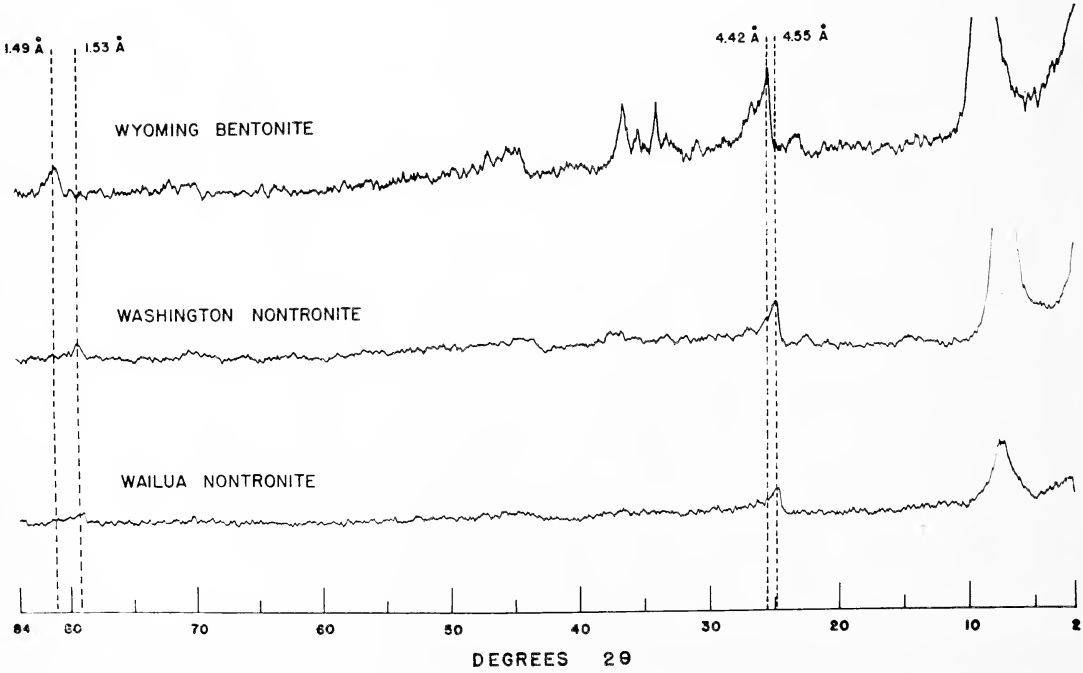

FIG. 1. X-ray diffractometer traces of Wyoming bentonite, Washington nontronite, and Wailua nontronite.

The X-ray diffraction patterns favor the nontronite identification. The sample from Wailua, Kauai, had a pattern almost identical with that of the standard nontronite from Manato, Washington.

The occurrence of nontronite in these locations suggests several interpretations of the weathering processes which are involved. The mode of occurrence suggests that both the climatic environment and the type of weathering system have a strong effect on the nature of the clay mineral formed. In each instance, these clay minerals have formed as secondary minerals with more or less complete separation from other minerals. Even in the Lualualei sample, the nontronitic clay has clearly separated from olivine.

The Fe_2O_3 content of these clays has ranged from 8.8 to 31.5 per cent. The Fe_2O_3 content probably reflects the concentration of active Fe in the weathering system rather than any other factor. The high Fe_2O_3 content in the Lualualei sample and its high magnesium content reflect the release of ions from the decomposing olivine and the possible migration of Fe from the weathering matrix to the cavity produced by loss of volume of the olivine. The source of iron must come from the matrix, as the olivine is iron poor. Sherman and Uehara (1956) have described a 2:1 montmorillonitic clay having a high content of Fe_2O_3 occurring after olivine in the same type of rock. Since their clay had a much lower MgO content, we suggest that in time Fe will replace Mg and produce a nontronitic clay.

The content of bases is higher in the dryer areas. This is what one would expect. The low base content of the nontronite samples from the humid area suggests that these clays have formed under conditions of strong leaching and good drainage. The high content of Fe_2O_3 in these clays further suggests that the concentration of Fe has been sufficiently high and continuous to produce a high degree of Fe inclusion in the crystal lattice. However, the stability of this mineral in this type of a system would not be expected in this environment favorable for weathering and leaching. Stability would have to arise from the presence of a continuous source of silica and Fe to maintain the stability of the nontronite mineral, or otherwise some other protective system must exist, such as an impervious coating of either halloysite, iron oxide, or gibbsite. The stability of the nontronites found at Kahakuloa and Nuuanu Pali can be explained by the former condition, in that they occur in a position in which leachates from adjacent weathering rocks move through or near these clays. These leachates may contain sufficient Fe and Si to maintain the stability of the nontronite. In the Kahakuloa area there is evidence that the nontronite will decompose with the loss of SiO_2, and iron oxide mineral will form. A similar system has been proposed by Bates (1960) for the halloysite-gibbsite system in the same weathering rock formation. There is an indication in these occurrences that nontronite might be more stable than heretofore observed by workers.

The weathering rock from the Wailua sample has been the object of many investigations. Abbott (1958) and Sherman *et al.* (1962) have described the bauxitic weathering of this rock. The weathering of this rock is characterized by its rapid loss of bases and desilication. Almost at the contact zone with the rock core, the bases have been reduced to trace quantities, and the SiO_2 has been reduced from 40 per cent in the rock to 2 per cent in the weathering product. The nontronite mineral aggregates, and nodular pore fillings, have almost identical X-ray patterns with that of the standard nontronite sample. The nontronites occurring near the weathering contact zone owe their stability to the protective effects of the rock. The stability of the nontronite pore filling and aggregates in the weathering matrix is more of a puzzle. The close association with gibbsite has been observed in the X-ray diffraction patterns as well as in thin sections. At this point, the stability of nontronite in this association cannot be explained except that it must be more resistant to decomposition than was previously suspected. However, there is a suggestion that the nontronite will decompose to iron oxide minerals in time. Iron oxide minerals occurring as pore filling or replacements are numerous in similar locations in the weathering matrix, thus suggesting the eventual decomposition of nontronite by desilication.

SUMMARY

This study describes the mode of occurrence of eight nontronite and nontronite-like minerals occurring in Australia, New Zealand, Fiji, and Hawaii. Each of the minerals has a relatively high content of Fe_2O_3, ranging from 8.8 to 31.5 per cent. Six of these minerals contain sufficient Fe_2O_3 to be considered a nontronite.

The chemical composition suggests that the degree of iron substitution in the octahedral position is related to the concentration of the Fe. The iron oxide content of these 2:1 layered silicate minerals appears to increase as weathering of silicate minerals approach completion.

X-ray diffraction supports the identification of nontronite. The sample from a ferruginous bauxite boulder gave X-ray patterns almost identical to that of a standard nontronite sample from Manato, Washington.

The occurrence of nontronite in a bauxite suggests that the stability of the mineral must be due either to the concentration of Fe and Si in the percolating waters, or to possible protective mineral coatings, or to greater resistance to weathering and leaching than has been previously considered.

REFERENCES

ABBOTT, A. T. 1958. Occurrence of gibbsite on the island of Kauai, Hawaiian Islands. Econ. Geol. 53: 842–853.

ALLEN, V. T., and V. E. SCHIELD. 1946. Nontronite in the Columbia River Region. Am. Mineral. 31: 294–312.

BATES, T. F. 1960. Rock weathering and clay formation in Hawaii. Mineral Ind. 29(8): 1–6.

BRINDLEY, G. W. 1951. X-ray identification and crystal structures of clay minerals. Mineralogical Society, London, England. 345 pp.

CROSS, W. 1915. Lavas of Hawaii and their relations. U. S. Geol. Survey Prof. Paper 88. 97 pp.

SHERMAN, G. DONALD, and GORO UEHARA. 1956. The weathering of olivine basalt in Hawaii and its pedogenic significance. Soil Sci. Soc. Amer. Proc. 20: 337–440.

SHERMAN, G. DONALD, W. M. JOHNSON, J. D. CADY, H. IKAWA, and N. BLOMBERG. In press. The characteristics of the Halii soils of the Aluminous Ferruginous Latosols.

A Survey for Alkaloids in Hawaiian Plants, III

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In continuation of our systematic survey for alkaloids in Hawaiian plants[2] we have collected and tested additional plant species on Oahu, Hawaii, Maui, and Kauai. Of the 71 samples in the present report, 15 represent species which had been tested by us previously. These results are included here since 13 of these samples were collected at different locations and 2 gave test results at variance with previous findings. All specimens were collected from living plants. In parts I and II of this survey testing for alkaloids was carried out as described by Webb (1949, 1952) in his classical phytochemical study of the Australian flora. In following up some positive tests as indicated in the survey with actual isolation of alkaloids on a preparative scale, it has been noted by us and by others (*e.g.*, Raffauf, 1958) that extraction and testing as done for the survey led occasionally to erroneous conclusions. For the present work an extraction procedure was used which more nearly parallels those commonly employed in preparative work. This was followed by a crude separation of the quaternary bases from all others. Both portions were then tested with Mayer's reagent, which is considered to be the most selective of the customary alkaloid reagents. It may be noted that Yeh *et al.* (1959), in their recent phytochemical study of the Taiwan flora, also have used this modified procedure.

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METHODS

The following procedure is the one which is recommended by Raffauf (1958).

A 20 g. sample of dried plant parts was ground in a Waring blender with the addition of some 95 per cent ethanol. The material was then extracted with 150 ml. of boiling ethanol for 2 hr. The insoluble plant parts were removed by suction filtration and the alcoholic filtrate was evaporated to dryness on a steam bath under reduced pressure. The residue was dissolved by stirring with a mixture of 50 ml. ether and 50 ml. of 5 per cent hydrochloric acid. Part of the aqueous acidic extract containing the nonquaternary alkaloids was tested with Mayer's reagent. The validity of a positive alkaloid test was confirmed by adding powdered sodium chloride to another portion of the acidic extract. If the addition of sodium chloride caused turbidity, the solution was clarified before being tested with Mayer's reagent.

The ammoniacal layer of the initial separation which contained the quaternary bases was acidified with a few drops of concentrated hydrochloric acid and then tested with Mayer's reagent. A positive test was confirmed by the addition of sodium chloride.

The precipitates were evaluated on a + to ++++ basis by visual comparison with the following standards. A solution of brucine in 2 per cent hydrochloric acid at a concentration of 0.4 mg/ml corresponds to +; 1.3 mg/ml is equivalent to ++; 4 mg/ml is equivalent to +++; and any precipitate larger than that is assigned ++++.

The standard for quaternary alkaloids was a 2 per cent hydrochloric acid solution of isoreserpiline methochloride. A concentration of 0.05 mg/ml was assigned +; 0.17 mg/ml, ++; 0.5 mg/ml, +++; and more than 0.5 mg/ml was assigned ++++.

Preparation of Mayer's reagent was described by Swanholm *et al.* (1959).

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[1] Department of Chemistry, University of Hawaii, Honolulu. Manuscript received April 3, 1961.

[2] Part II of this series appeared in *Pacific Science* 14(1): 68–74.

RESULTS AND DISCUSSION

Table 1 lists the results of the alkaloid tests which were carried out on 71 plant species representing 56 genera and 39 families. Six of the 7 new species in Rutaceae which have been tested show a large enough alkaloid content to merit further investigation as does *Sophora chrysophylla,* a newly tested member of Leguminosae.

KEY TO ABBREVIATIONS IN TABLE 1

The results of the spot tests are given in the following order in abbreviated form:

BINOMIAL, accepted botanical name; authority is omitted to conserve space.

LOCAL NAME, Hawaiian or vernacular name, if known.

LOCALITY, nearest town or other prominent map feature.

DATE COLLECTED, date of actual collection in the field.

DATE TESTED, date of actual application of spot test.

PLANT PART(S), B—bark, Br—branchlet, F—fruit, Fl—flower, L—leaf, R—root or underground part, RB—root bark, St—stem.

TABLE 1

RESULTS OF SPOT TESTS FOR ALKALOIDS

(Plants listed alphabetically within each taxon)

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES		COMMENTS
						HCl	NH_4OH	
AMARANTHACEAE								
Charpentiera elliptica	papala	Waianae, Oahu	12/59	13/1/61	L,Br	–	+	endemic genus
C. obovata	papala	Auahi, Maui	28/8/58	13/4/59	L,B	++	tr	endemic genus
Charpentiera sp.	papala	Waianae, Oahu	4/11/58	15/4/59	L,B	tr	–	endemic genus
ANACARDIACEAE								
Rhus chinensis var. *sandwicensis*	Hawaiian sumach, neneleau	Waianae, Oahu	12/59	31/1/61	L	–	++	endemic variety
APOCYNACEAE								
Pteralyxia macrocarpa	kaulu	Waianae, Oahu	4/11/58	21/2/59	L	–	+	a sample from the Koolau range was tested in Part II endemic genus
				15/11/58	B	–	–	
				3/2/59	St,B	+	tr	
				13/1/59	RB	–	–	
				27/1/59	B	–	tr	
AQUIFOLIACEAE								
Ilex anomala	kawa‘u	Pupukea Trail, Oahu	11/59	20/1/61	L	–	–	a sample from Aiea was tested in Part I endemic species

TABLE 1—*Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COL-LECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES		COMMENTS
						HCl	NH_4OH	
ARALIACEAE								
Cheirodendron gaudichaudii	olapa	Auahi, Maui	28/8/58	22/4/59	L		–	endemic species
C. ugadense	olapa	Manuka, Hawaii	11/58	17/4/59	L,St,F	++	–	endemic species
Reynoldsia mauiensis	ohe, ohe makai	Ulupalakua, Maui	28/8/58	10/2/59	L	–	–	endemic species
				2/2/59	B	–	tr	
R. sandwicensis		Ewa, Oahu	10/58	10/11/58	L,St,B	–	–	
Tetraplasandra hawaiiensis	ohe	Manuka, Hawaii	11/58	30/4/59	L	–	tr	endemic species
			11/58	17/4/59	B,F	tr	–	
T. meiandra	ohe	Manuka, Hawaii	11/58	17/4/59	L	–	–	endemic species
BOMBACACEAE								
Pachira insignis		Manuka, Hawaii	11/58	15/4/59	B,L	+	–	introduced species
CHENOPODIACEAE								
Chenopodium oahuense	‘aweoweo, ‘aheahea	Waianae, Oahu	12/59	13/1/61	L,Br,F	++	+	a sample from another location tested in Part I endemic species
COMPOSITAE								
Argyroxiphium sandwicense	silversword, pohinahina ahinahina	Haleakala, Maui	20/8/58	16/4/59	L	–	–	endemic genus
				18/3/59	B	–	tr	
CONVOLVULACEAE								
Jacquemontia sandwicensis	pa‘u-o-Hi‘i-aka, kakua-o-Hi‘i-aka	Blowhole, Oahu	10/59	20/1/61	Br	–	+	a sample from another location was tested in Part I endemic species
EPACRIDACEAE								
Styphelia tameiameiae	pukeawe, mai‘ele, kawau	Waianae, Oahu	11/58	6/5/59	St	–	–	indigenous, but widespread
				6/5/59	L	–	–	
ERICACEAE								
Vaccinium sp.	‘ohelo	Haleakala, Maui	26/8/58	27/2/59	L,F,St	–	–	
EUPHORBIACEAE								
Antidesma pulvinatum	ha‘a, hame, mehame	Manuka, Hawaii	11/58	16/5/59	L,B	–		a sample from Oahu was tested in Part I endemic species
Euphorbia heterophylla	‘akoko, koko	Waianae, Oahu	12/59	17/1/61	L,Br	–	tr	introduced weed
Euphorbia sp.	akoko, koko	Auahi, Maui	28/8/58	15/4/59	B	–	–	

TABLE 1—*Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES		COMMENTS
						HCl	NH$_4$OH	
GERANIACEAE								
Geranium cuneatum var. *tridens*	hinahina	Haleakala, Maui	26/8/58	5/1/59	R,L,St,B	–	–	endemic species
GOODENIACEAE								
Scaevola chamissoniana	naupaka-kuahiwi	Pupukea, Oahu	11/58	14/2/59	L,B	–	++	endemic species
S. frutescens	naupaka-kahakai	Punaluu, Oahu	8/59	7/10/59	B,F	–	–	indigenous, but wide-spread
				14/3/60	L	–	+	
S. glabra	ohenaupaka	Kokee, Kauai	12/4/60	4/60	L,St	+		endemic species
GRAMINEAE								
Oplismenus hirtellus	honohono maoli, basket grass	Oahu	4/11/58	14/5/59	L		–	introduced species
LABIATAE								
Phyllostegia grandiflora	kapana	Pupukea Trail, Oahu	11/59	24/1/61	L,St	–	++	a sample from the Waianae range tested in Part I endemic species
LEGUMINOSAE								
Papilionatae								
Canavalia galeata	puakauhi, ‘awikiwiki	Firebreak Trail, Waianae Mts., Oahu	11/58	12/1/59	B	+		endemic species
Erythrina sandwicensis	wiliwili	Ulupalakua, Maui	27/8/58	14/3/59	Fl,L	–	–	
				14/3/59	B	tr	tr	
Sophora chrysophylla	mamane	Haleakala, Maui	26/8/58	10/2/59	L	+++		endemic species
				7/1/59	B	++	++	
LILIACEAE								
Dracaena aurea	halapepe	Auahi, Maui	28/8/58	23/2/59	B	–	tr	endemic species
				23/2/59	L	–	–	
				10/3/59	F,Fl	tr	tr	
LOBELIACEAE								
Clermontia arborescens	oha wai	Pupukea, Oahu	10/58	8/1/59	L	–	–	endemic genus
MALVACEAE								
Hibiscadelphus hualalaiensis	hau kuahiwi	Manuka, Hawaii	11/58	17/4/59	L	–	–	endemic genus
Kokia rockii	koki‘o	Manuka, Hawaii	11/58	20/4/59	L	tr	–	endemic genus
Sida fallax	‘ilima	Blowhole, Oahu	10/59	31/1/61	L,B;Br	–	+	a sample from another location tested in Part I indigenous, but wide-spread

TABLE 1—*Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COL-LECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES		COMMENTS
						HCl	NH_4OH	
MORACEAE								
Pseudomorus sandwicensis	a‘ia‘i	Firebreak Trail, Waianae Mts., Oahu	4/11/58	17/2/59	B	–	–	endemic species
MYRSINACEAE								
Myrsine lessertiana	kolea	Firebreak Trail, Waianae Mts., Oahu	11/58	12/3/59	B,L	–	–	endemic species
		Makawao, Maui	26/8/58	6/5/59	B,F,L	–		
MYRTACEAE								
Metrosideros collina ssp. *polymorpha*	‘ohi‘a-lehua	Puna, Hawaii	11/58	10/3/59	L,St	–	–	a sample from Oahu was tested in Part I endemic subspecies
NYCTAGINACEAE								
Ceodes umbellifera	papala, kepau	Pupukea, Oahu	11/59	31/1/61	L	tr	+	endemic species
OLEACEAE								
Osmanthus sandwicensis	pua, olopua	Waianae, Oahu	12/59	20/1/61	L,F	+	++++	a sample from the Koolau range was tested in Part I endemic species
		Waianae, Oahu	12/59	20/1/61	B,Br	+	+++	
		Manuka, Hawaii	11/58	15/4/61	L,St,Fl	–	+	
PALMAE								
Pritchardia beccariana	loulu	Manuka, Hawaii	11/58	27/4/59	L		+	endemic species
PASSIFLORACEAE								
Passiflora triloba		Kaaawa, Oahu	11/58	20/4/59	L	–	tr	introduced species
PITTOSPORACEAE								
Pittosporum eugenoides	ho‘awa	Manuka, Hawaii	11/58	16/4/59	L,B	–	–	
P. hosmeri	ho‘awa	Puna, Hawaii	11/58	17/4/59	L	–	–	endemic species
P. kauaiense	ho‘awa	Kokee, Kauai	12/59	28/1/61	L,B	+	+	endemic species
P. spathulatum	ho‘awa	Pupukea, Oahu	11/59	28/1/61	L,B	+	+	endemic species
POLYPODIACEAE								
Elaphoglossum reticulatum	ekaha	Pupukea Trail, Oahu	11/59	18/1/61	L	–	–	endemic species
				18/1/61	R	–	+++	
Microlepia setosa	palai, palapalai	Waianae, Oahu	12/59	24/1/61	L,Br,St	tr	tr	retest of a new sample

TABLE 1—*Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COL-LECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES		COMMENTS
						HCl	NH_4OH	
RHAMNACEAE								
Alphitonia ponderosa	kauila, kauwila, o'e	Auahi, Maui	28/8/58	23/4/59	L,B,F	–	–	endemic species
Colubrina oppositifolia	kauila	Manuka, Hawaii	11/58	17/4/59	L	–	–	endemic species
RUBIACEAE								
Bobea elatior	'ahakea	Pupukea Trail, Oahu	11/59	11/1/61	L	+	++	a sample from Aiea was tested in Part I endemic genus
Gardenia remyi	nanu	Manuka, Hawaii	11/58	20/4/59	L	–		endemic species
Gouldia terminalis	manono	Kokee, Kauai	12/59	17/1/61	L,Br	tr	+	a sample from Manoa was tested in Part I endemic genus
Straussia sp.	kopiko	Kokee, Kauai	12/59	31/1/61	L	+	+	endemic genus
		Makawao, Maui	26/8/58	14/3/59	L	+	tr	
				23/2/59	B	–	–	
RUTACEAE								
Fagara dipetala	heae	Kokee, Kauai	12/4/60	4/60	F,L,St	+++		endemic species
		Kokee, Kauai	12/4/60	4/60	L	+++		
		Kokee, Kauai	12/4/60	4/60	B	++++		
F. kavaiensis	a'e, hea'e	Kokee, Kauai	12/4/60	4/60	L,St	++		
Pelea anisata	mokihana, mokehana	Kokee, Kauai	12/4/60	4/60	L,B	+		endemic species
P. barbigera	uahea Pele	Kokee, Kauai	12/4/60	4/60	L,B	+++		endemic species
P. haleakalae		Waikamoi, Maui	26/8/58	16/4/59	B	+	tr	endemic species
				10/3/59	L	++	++	
				9/3/59	St	tr	tr	
P. nealae		Kokee, Kauai	12/4/60	4/60	L,St	+		endemic species
Platydesma remyi	pilo-kea	Kokee, Kauai	12/4/60	4/60	L	++++		endemic genus
SANTALACEAE								
Santalum ellipticum	'ili-ahi	Waianae, Oahu	12/59	28/1/61	L,Br	tr	++	endemic species
SAPINDACEAE								
Alectryon macrococcus	mahoe	Auahi, Maui	28/8/58	20/4/59	B,F,L	–	–	endemic species
Dodonaea eriocarpa	'a'ali'i, kumakani	Kokee, Kauai	12/59	13/1/61	L,Br	+	+	indigenous, but wide-spread
Sapindus oahuensis	'aulu, kaulu	Waianae, Oahu	12/59	28/1/61	L,B,Br	–	+	retest of a new sample
				27/1/59	B	–	–	endemic species

TABLE 1—*Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COL-LECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES		COMMENTS
						HCl	NH_4OH	
SAPOTACEAE								
Nesoluma polynesicum	keahi	Firebreak Trail, Waianae Mts., Oahu	11/58	27/1/59	B	–	–	indigenous
		Waikamoi, Maui	26/8/58	14/3/59	L	–	tr	
				20/4/59	B	–	–	
Sideroxylon rhynchospermum	ala‘a	Auahi, Maui	8/58	20/4/59	L	–	–	endemic species
SAXIFRAGACEAE								
Broussaisia arguta	kanawao	Pupukea Trail, Oahu	11/59	13/1/61	L	–	+	another sample was tested in Part II endemic genus
STERCULIACEAE								
Waltheria americana	hi‘aloa, ‘uhaloa, kanakaloa	Blowhole, Oahu	10/59	31/1/61	L,Fl	+	+++	indigenous, but wide-spread
				12/1/61	B	+	–	
				12/1/61	L	tr	–	
THYMELAEACEAE								
Wikstroemia furcata	‘akia	Kokee, Kauai	12/4/60	4/60	L,B	+		endemic species
URTICACEAE								
Pipturus albidus	mamake, mamaki	Waianae, Oahu	12/59	25/1/61	L,St,F	–	–	a sample from the Koolau range tested in Part I endemic species

REFERENCES

Raffauf, R. F. 1958. Private communication.

Swanholm, C. E., H. St. John, and P. J. Scheuer. 1959. A survey for alkaloids in Hawaiian plants, I. Pacific Sci. 13(3): 295–305.

Webb, L. J. 1949. An Australian phytochemical survey, I. Alkaloids and cyanogenetic compounds in Queensland plants. Bull. Coun. Sci. Industr. Aust. 241: 1–56.

——— 1952. An Australian phytochemical survey, II. Alkaloids in Queensland flowering plants. Bull. Coun. Sci. Industr. Res. Aust. 268: 1–99.

Yeh, P. Y., L. C. Lin, and S. S. Yang. 1959. The alkaloid contents of plants in Taiwan (I). J. Taiwan Pharm. Assoc. 11(1): 4–7.

Revision of the Genus *Pandanus* Stickman, Part 8
The Hong Kong Coastal *Pandanus*

HAROLD ST. JOHN[1]

Pandanus remotus sp. nov. (sect. *Pandanus*)
Figs. 43–46

DIAGNOSIS HOLOTYPI: Arbori ad 3 m. alti, truncis 15 cm. diametro sublaevibus saepe decumbentibus et copsis densis formantibus, radicibus fulturosis paucis et parvis, foliis 95–160 cm. longis 4.5 cm. latis ligulatis sed in base amplectentibus et 7 cm. latis longiter in apice acuto diminuentibus fragilibus et faciliter transruptibus base inerme sed parte subbasalis cum serris luteis 3.5–5 mm. longis 6–20 mm. distantibus in medio serris 2–4 mm. longis 5–12 mm. distantibus parte subapicale cum serris 0.5–1 mm. longis 3–10 mm. distantibus nervo mediale cum serris adscendentibus subulatis simulantibus sed minoribus, syncarpiis in flore 4 cm. longis late ellipsoideis cum bracteis albis numerosis amplectentibus maximis 53 cm. longis 3 cm. latis, syncarpio in fructu terminali, pedunculo 19–20 cm. longo tereto in basi pluribracteato eis ocreatis; syncarpiis 23 cm. longis 20 cm. diametro ellipsoideo, axili in fructu carnoso et succifero et celeriter multo contracto et solum fibris paucis remansis, phalangibus plusminusve 50 et 4.2–4.6 cm. longis 2.1–3 cm. latis 1.6–2.6 cm. crassis dimidia supera cuneata lateribus laevibus planis vel subcurvatis sublucidis luteis in sicco brunneis sed sinibus aurantiacis apice convexo sinibus lateralibus carpellorum vadosis sed ad mediam productis sinibus apicalibus centralibus 3–4 mm. profundis dimidia infera valde distenta carnosa lutea saccharosa, carpellis 7–10 plerumque 8–9 subaequalibus apicibus liberis conico-pyramidalis tertia supera suboblata eis marginalis asymmetricis et paene divergentibus, stigmatibus 1.5–2 mm. longis ovalibus lineatis obliquis centripetalibus, endocarpio mediali osseoso obscure mahogani-colorato in latere 0.5–1.5 mm. lato, seminibus 10 mm. longis 4 mm. diametro ellipsoideis, mesocarpio supero cavernoso medulloso et fibroso, mesocarpio infero carnoso et valde fibroso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Trees 3 m. tall, the trunk 15 cm. in diameter, nearly smooth, often decumbent, forming dense thickets; prop roots few and small; leaves 95–160 cm. long, 4.5 cm. wide, though at the very base widening to 7 cm. at the clasping part, ligulate, long tapering to an acute tip, texture fragile, so, easily and often torn across, the very base unarmed, but just above it subulate serrate, the yellowish teeth 3.5–5 mm. long, 6–20 mm. apart, at the middle the teeth 2–4 mm. long, 5–12 mm. apart, near the tip the teeth 0.5–1 mm. long, 3–10 mm. apart, the midrib with similar, ascending, but smaller subulate teeth; inflorescence of staminate trees pendent, terminal, 40–50 cm. long, and the panicle 3–5 cm. wide, sweet fragrant; bracts white, divergent, the lowest ones 44–53 cm. long, 3.6 cm. wide, the lower half linear-lanceolate, the upper half a slender, tapering subulate tip, the midrib unarmed, but the margins appressed subulate serrate, the uppermost bract 5–7 cm. long, 6–8 mm. wide; lateral spikes numerous, 4–5.5 cm. long, borne on stalks up to 15 mm. long; staminal columns 5–15 mm. long, racemose, the lower half naked; filaments 1.5–2.5 mm. long; anthers 3–4 mm. long, linear-oblong, bearing an apical projection of the connective 1–1.2 mm. long, subulate; pistillate inflorescence with white bracts; pistillate flowering heads broad ellipsoid, 4 cm. long, surrounded by numerous white bracts, the largest ones 53 cm. long, 3 cm. wide; in fruit the syncarps terminal, on a peduncle 19–20 cm. long, terete, and at base with several ochreate bracts, naked above; syncarps 23 cm. long, 18–20 cm. in diameter, ellipsoid, the core at maturity juicy, fleshy, and almost wholly rotting and shrinking, leaving but very little fiber; phalanges 50 or more in number, 4.2–4.6 cm. long, 2.1–3 cm. wide, 1.6–2.6 cm. thick, upper half cuneate, with sides smooth,

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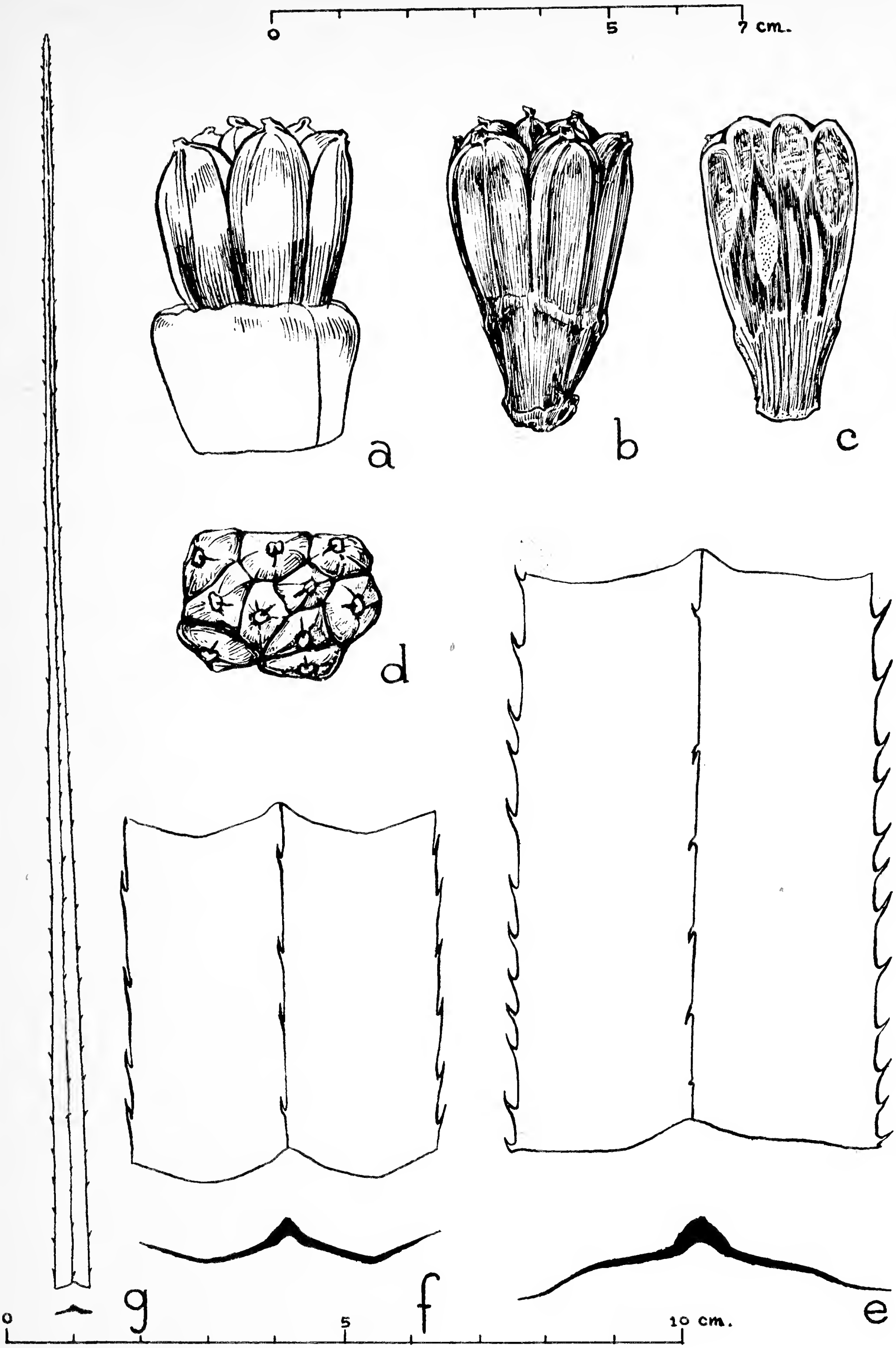

FIG. 43. *Pandanus remotus,* from holotype. *a,* Ripe phalange, lateral view, × 1; *b,* dried phalange, lateral view, × 1; *c,* phalange, longitudinal section, × 1; *d,* phalange, apical view, × 1; from topotype, *St. John 26,322, e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf tip, lower side, × 1.

FIG. 44. *Pandanus remotus,* holotype, showing syncarp.

plane or gently curved, a little shiny, yellow with orange creases, drying brownish, the apex convex, the lateral carpel sutures shallow but distinct down to the middle, the central apical sutures 3–4 mm. deep, the lower half conspicuously enlarged and swollen with orange, juicy flesh, on the one drawn when fresh at the midsection the upper part was 1.8 cm. in diameter while the fleshy lower part was 3 cm. in diameter, on drying the fleshy enlargement largely vanishes except for shoulders on each angle at the juncture and fleshy traces below that; pulp of the base very sweet and with a faint peach flavor but then with an irritating after taste; carpels 7–10, mostly 8–9, subequal, their apices conic-pyramidal, the upper ⅓ somewhat oblate, the marginal ones asymmetric and a little divergent; stigmas 1.5–2 mm. long, oval, creased, oblique, centripetal, below it the proximal suture extending ½ way to valley bottom; endocarp median, dark mahogany-colored, bony, that around the outer seeds 0.5–1.5 mm. thick; seeds 10 mm. long, 4 mm. in diameter, ellipsoid; upper mesocarp fibrous and cavernous between membranous cross partitions; lower mesocarp fleshy and very fibrous.

HOLOTYPUS: Hong Kong: Shek-o Bay, sands at top of beach, forming thickets, July 19, 1956, *H. St. John 25,930* (BISH).

SPECIMENS EXAMINED: Same data, staminate plant, *St. John 25,929* (BISH); same locality. Oct. 20, 1959, *St. John 26,322* (BISH); Hong Kong, Ringgold & Rodgers Expedition, 1853–56, *C. Wright* (US).

DISCUSSION: The striking feature of this species is the fleshy distention of the base of each fruiting phalange. Their large expansion causes the phalanges to be widely separated on the head. This type of fruiting structure was almost unknown in the *Pandanus* species of the central and eastern Pacific, but is now frequently found on the islands near the Asiatic coast. Two of this group from Mindanao, Philippines, were described by Martelli as *P. coronatus* forma *coronatus,* and forma *minor.* The first differs from ours in its more conic carpel apices, larger stigmas, and its phalange length of 3.5 cm. The forma *minor* differs in its low convex carpel apices and its phalange length of only 3 cm. In both the swollen fleshy base is smaller than in ours, but they were described and figured from dried material, so this point is uncertain.

The new specific epithet is from the Latin, *remotus,* distant, in allusion to the widely separated phalanges of the syncarp.

FIG. 45. *Pandanus remotus,* paratype, *St. John 25,929,* staminate plant with white inflorescence.

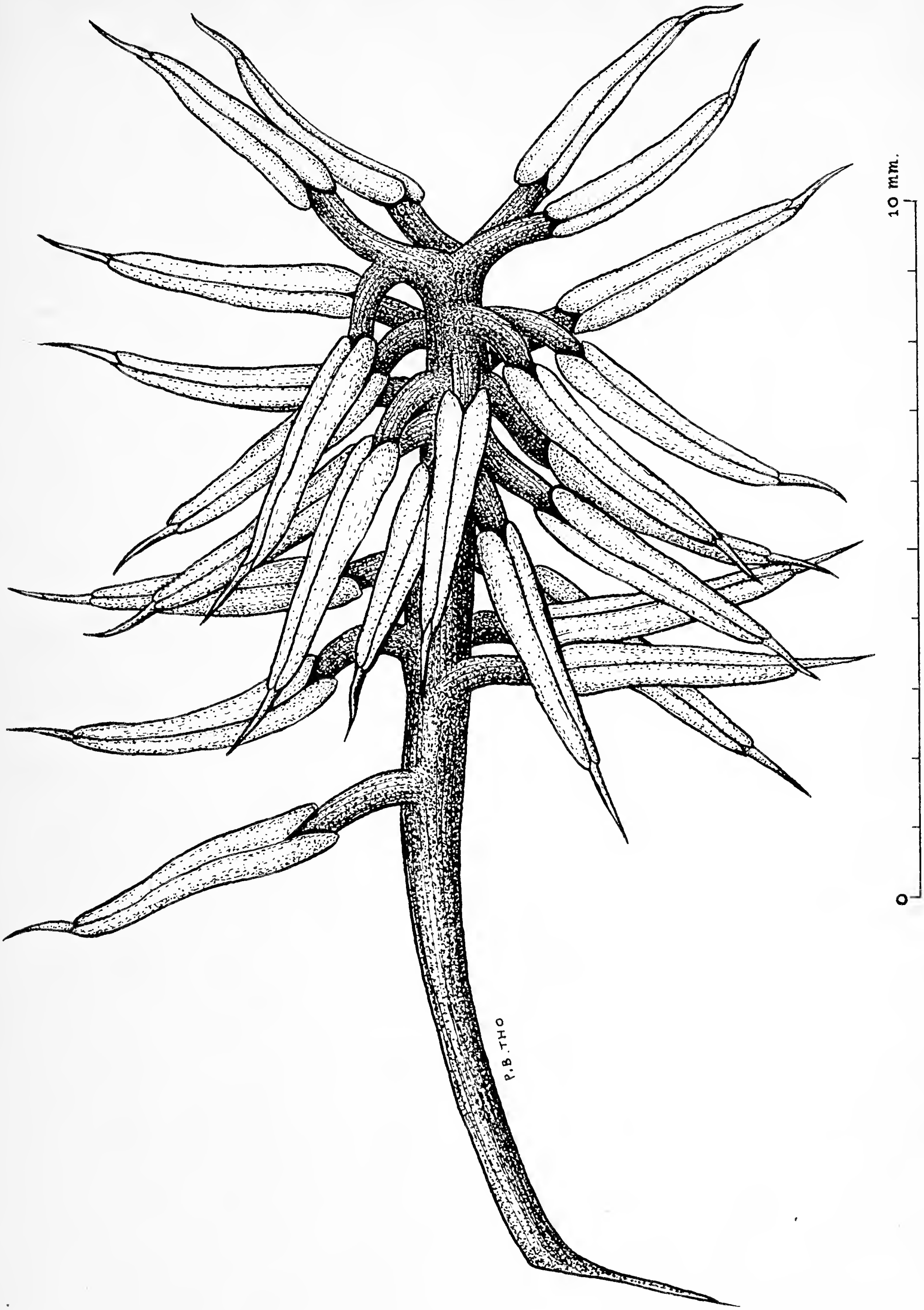

FIG. 46. *Pandanus remotus,* paratype, *St. John 25,929,* staminate column, × 10.

Revision of the Genus *Pandanus* Stickman, Part 9
Three New *Pandanus* Species from Queensland, Australia

HAROLD ST. JOHN[1]

Pandanus gemmiferus sp. nov. (sect. *Australibrassia*)
Figs. 47–52

DIAGNOSIS HOLOTYPI: Arbor 8 m. alta 15 cm. diametro, cortice brunneo sublaeve in arboribus veteribus aliquando gemmiferis sed ramis omnibus plerumque infra foliis helices tribus 6–8 gemmarum, deinde post 6–7 nodas et cicatricem pedunculi helices tribus reversas in gemmis cum 6–15 foliis ad 3–7 cm. longis subintegris ferrentibus, deinde post intervallam helices tribus etiam reversis gemmae foliosae cum circa 43 foliis exterioribus bracteosis sed interioribus 25–45 cm. longis 4.6–6.4 mm. latis ad basem inermibus circa mediam marginibus cum aculeis 0.8–1 mm. longis 2–9 mm. distantibus subulatis luteis, foliis principalibus 2.26–2.30 m. longis 5 cm. latis coriaceis supra rotundato-sulcatis marginibus subrevolutis plerumque 4.5 cm. latis ligulatis sed in quarto supero sensim diminuentibus ad apicem subulatam eo 3 mm. lato in regione 10 cm. ex apice basi amplexicauli integri et inerme per 11–13 cm., proxima basi marginibus cum aculeis 1.5–2 mm. longis 3–10 mm. distantibus valde subulatis adscendentibus apicibus brunneis, midnervo proximo inermi, in sectioni mediali marginibus cum aculeis 1.5–2 mm. longis 3–6 mm. distantibus subulatis adpressi-ascendentibus, midnervo infra cum aculeis 1.5 mm. longis 13–55 mm. distantibus tenuiter subulatis adscendentibus adpressis, circa apicem marginibus et midnervo infra cum serrulis 0.3–0.5 mm. longis 1.5–3 mm. distantibus, pedunculo terminali 50 cm. longo 2 cm. diametro cernuo folioso, syncarpio 25 cm. longo 18 cm. diametro cylindrico rubro, phalangibus 5–5.6 cm. longis 4–4.4 cm. latis 3.4–3.7 cm. crassis obovoideo-subglobosis subcompressis 4–5-angulosis lateribus laevibus lucidis subconvexis, parte 3/5 supera libera apice rotundato, regione stigmatis 12–15 mm. latis concavis, suturis lateralibus nullis, sinibus apicalibus centralibus 2 mm. profundis angustis, carpellis 13–17, apicibus congregatis anguste pyramidalibus marginalibus obliquis inflexis et truncatis, stigmatibus 1.5–2 mm. longis cordatis vel deltoideis nigris papillosis verticalibus centripetalibus, sinibus proximalibus ½ ad fondam extentis, endocarpio mediali solido mahogani-brunneo latere interiori lucido lateribus exterioribus 4–5 mm. crassis, seminibus 13–15 mm. longis 3–4 mm. diametro fusiformibus, mesocarpio apicali cavernoso fibrosoque et cum membranis medullosis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 8 m. tall, 15 cm. in diameter; bark brown, rather smooth, but with remote, low, rounded warts, on old trunks rarely bearing a few adventitious shoots; most branches bearing below the terminal plume of leaves three spirals of green, flattened, scaly, axillary buds, 6–8 in a series, then after an interval of 6–7 nodes and a peduncle scar, the spiral series of buds resume but in reverse direction, these buds having developed into leafy sprouts with 6–15 leaves, the inner ones the largest, 3–7 cm. long, 3–4 mm. wide, linear lanceolate, coriaceous, mostly entire but near the apex the margins and midrib below serrulate; then after a similar interval of bare nodes and a peduncle scar, there is found a third series of 6–9 axillary sprouts, of about 43 leaves, the outer lanceolate scale-leaves, the inner and younger ones 25–45 cm. long, 4–11.5 mm. wide, near the base unarmed, at the middle the margins only with ascending prickles 0.8–1 mm. long, 2–9 mm. apart, subulate, yellowish; near the apex the margins and midrib below with ascending prickles 0.4–0.5 mm. long, 1–3 mm. apart, subulate, pale but with brownish tips, these oldest sprouts being mature are detached

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[1] B. P. Bishop Museum, Honolulu 17, Hawaii, U.S.A. Manuscript received October 17, 1960.

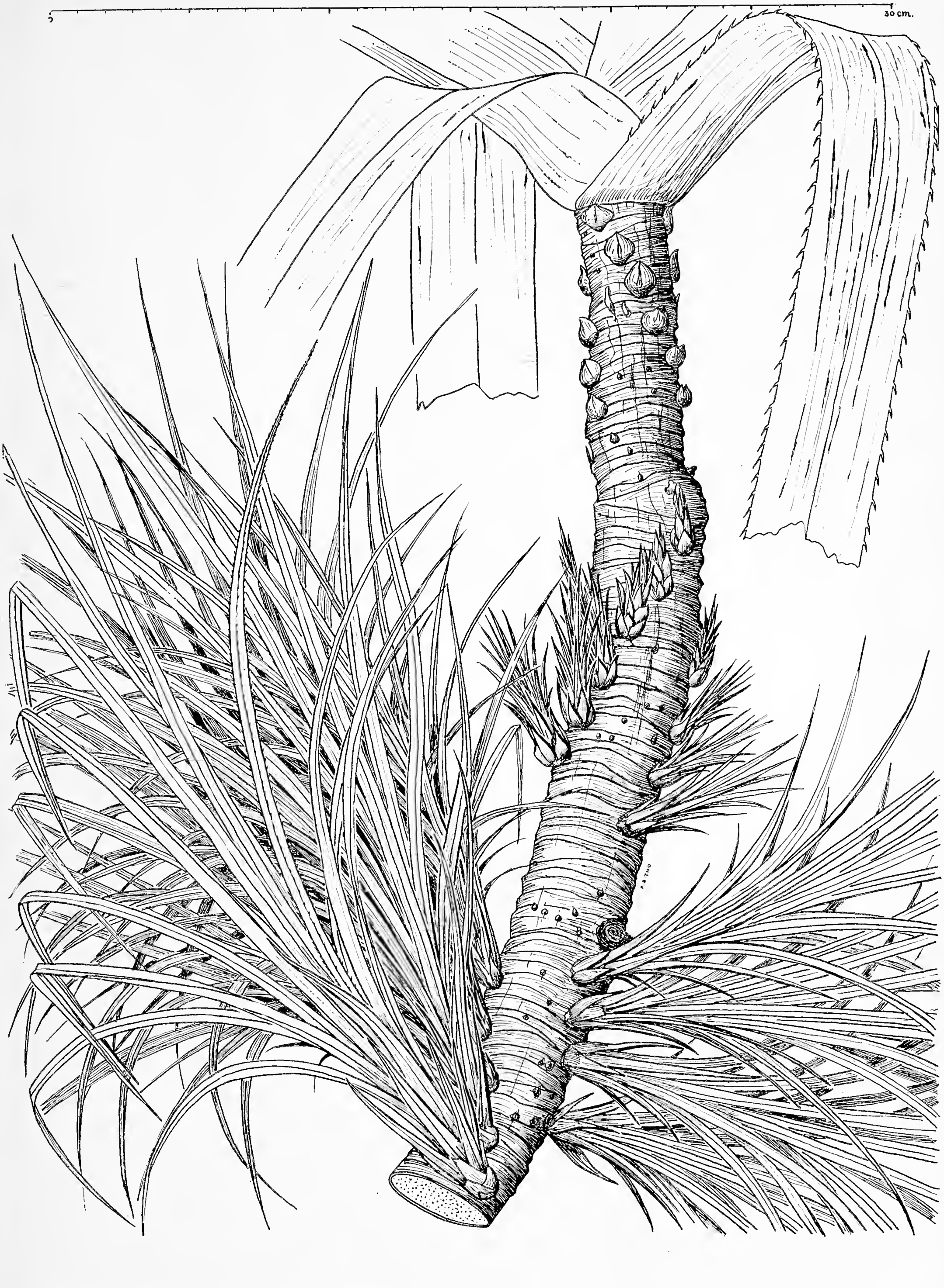

FIG. 47. *Pandanus gemmiferus* St. John, from *St. John 26,276.* A branch with three series of adventitious buds in reversing spirals, × 41/100.

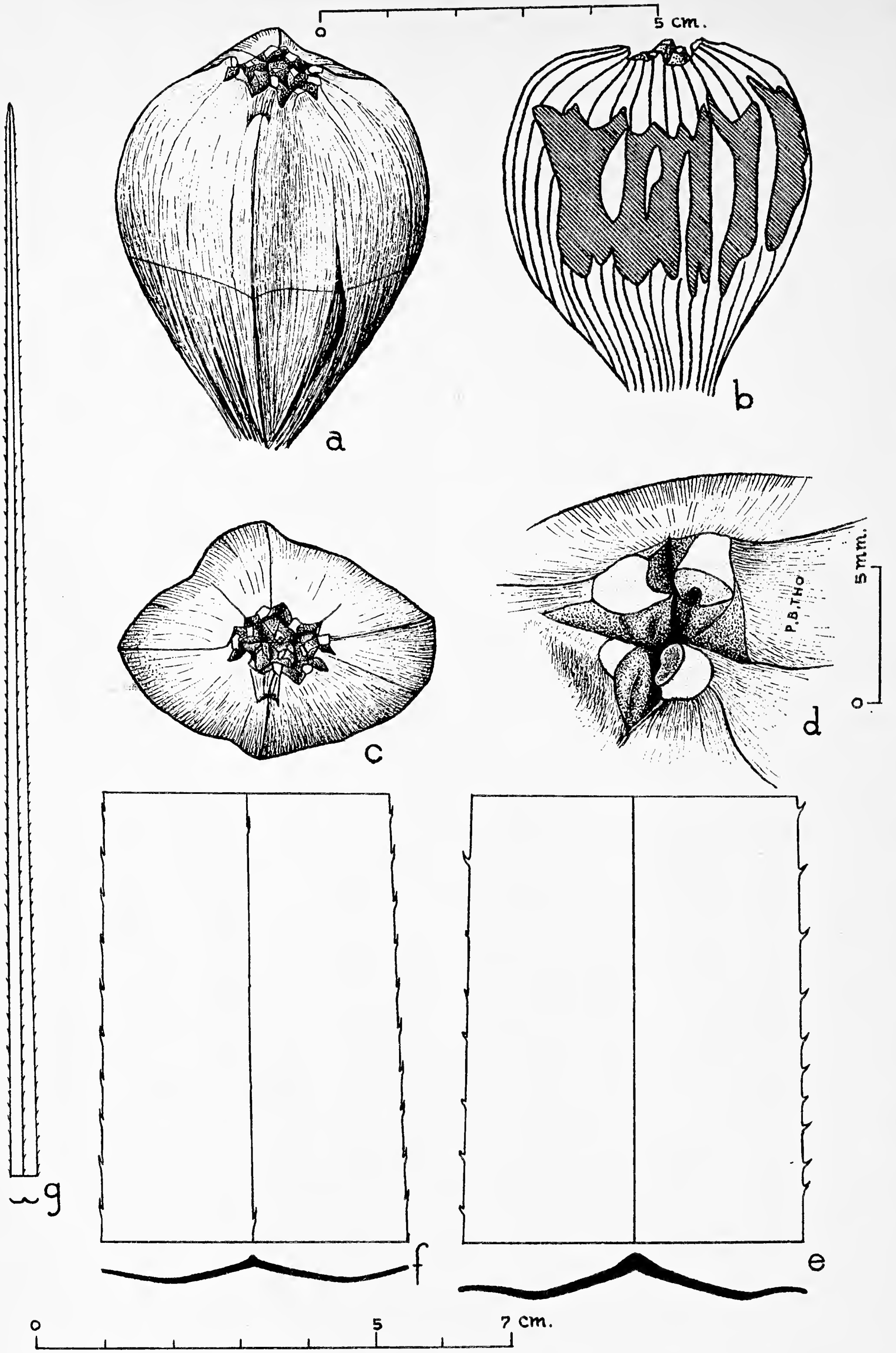

FIG. 48. *Pandanus gemmiferus* St. John, from the holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices and stigmas, oblique view, × 4; *e,* leaf, lower side near base, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

at a touch or blow, fall to the ground where they readily take root; leaves 1.69–2.30 m. long, 5–5.7 cm. wide, coriaceous, above with a broad, half-rounded, central furrow and slightly revolute sides, the blade about 4.5 cm. wide for most of its length, ligulate, but in the apical quarter gradually tapering to the long subulate apex which 10 cm. down is 3 mm. wide, the base amplexicaul, unarmed and entire for 11–13 cm.; near the base the margins with prickles 1.5–4 mm. long, 3–10 mm. apart, stout subulate, ascending, brown tipped; nearby midrib unarmed and so almost to middle; at midsection the margins with prickles 1.5–3 mm. long, 3–6 mm. apart, subulate, appressed ascending; the midrib below with prickles 1.5 mm. long, 13–55 mm. apart, slender subulate, ascending, flat appressed; near the apex the margins and midrib below with serrulations 0.3–0.5 mm. long, 1.5–3 mm. apart; the almost basal leaves of young vigorous plants 2.35 m. long, 6.5 cm. wide, almost to the base the midrib below with prickles 3–4.5 mm. long, 6–15 mm. apart, stout subulate, arcuate, reflexed; at midsection the midrib below with prickles 2–3 mm. long, 4–11 mm. apart, ascending; and the tip 10 cm. down 1.5 mm. wide, but in other details the juvenile leaves similar to the others; peduncle terminal, 50 cm. long, 2 cm. in diameter, nodding, leafy bracted; syncarp observed in 1951 to be 23–25 cm. long, 10–18 cm. in diameter, with many persistent leafy bracts, cylindric, red, the core 3-sided, the rind fibrous, firm and persistent, the center soft and evanescent; phalanges 4.2–5.6 cm. long, 3.2–4.4 cm. wide, 2.9–3.7 cm. thick, obovoid-subglobose, slightly compressed, 4–5-sided, the sides smooth, shining, gently convex, upper 3/5 free, apex rounded to the stigmatic cluster which is 12–15 mm. wide and concave; lateral sutures none; apical central sinuses narrow, 2 mm. deep from the base of the stigma (3–4 mm. from its apex); carpels 13–17, their apices crowded, narrow pyramidal, the marginal ones oblique, inflexed, and truncate; stigmas 1.5–2 mm. long, cordate to deltoid, black, papillose, on the proximal face of the apex, vertical and centripetal, the proximal crease running about half-way to the valley bottom; endocarp median, massive, mahogany brown, the inner surface shining, the lateral walls 4–5 mm. thick; seeds 13–15 mm. long, 3–4 mm. in diameter, fusiform; apical mesocarp cavernous, traversed by strong fibers and with medullary membranes; basal mesocarp fibrous and fleshy.

Fig. 49. *Pandanus gemmiferus* St. John, from *St. John 26,276.* Base of trunk and prop roots.

HOLOTYPUS: Australia, North Queensland, Cairns, Fresh Water Creek, moist forest by stream, near intake, 500 ft. alt., Jan. 29, 1958, *H. St. John 26,238* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, Cairns Intake, Freshwater Creek, Nov. 18, 1953, *H. Flecker 14,558* (Herb. North Queensland Nat. Hist. Club); Lake Eacham, 4 miles N. W. of Yungaburra, rain forest by lake shore, with *Brassaia actinophylla, Mallotus, Blepharicarya,* and *Freycinetia,* 2,450 ft. alt., Feb. 11, 1958, *H. St. John 26,276* and *26,276A* (BISH).

DISCUSSION: *P. gemmiferus* is a member of the section *Australibrassia* and in that group finds its closest relative, *P. conicus* St. John of

Queensland. This species has its phalanges 6–6.2 cm. long, 4–4.5 cm. wide, upper half free; carpels 12–14; stigmas 2–3 mm. long; blades 2.7–3.25 m. long, 4.4 cm. wide, the apex 1 mm. wide at the point 10 cm. down; bark of the trunk with stout, upturned prickles; and the tree not bearing active, axillary shoots. On the other hand, *P. gemmiferus* has the phalanges 3.2–4.4 cm. long, 2.9–3.7 cm. wide, the upper 3/5 free; carpels 13–17; stigmas 3–4 mm. long; blades 1.69–2.30 m. long, 5–5.7 cm. wide, the apex 3 mm. wide at the point 10 cm. down; bark of the trunk smooth but with low, rounded warts; and the tree with abundant, leafy, axillary shoots.

This is a very remarkable species. It, like *P. reversispiralis* St. John of Vietnam, has a phyllotaxy of three spirals, reversing direction following each peduncle. However, unlike that Asiatic species, *P. gemmiferus* has active axillary, adventitious buds. The youngest spirals of six to eight buds are mere, flattened, scaly things. The second have grown to leafy shoots, the inner and largest leaves of which are 3–7 cm. long. The third are of vigorous, leafy shoots, each with about 43 leaves, the largest of which are 25–45 cm. long. At a blow or even a touch these fall to the ground where they may take root and start new plants. At Lake Eacham the ground under the *Pandanus* trees was carpeted by fallen, axillary shoots, rooting and growing vigorously. So far as known, this is the first species in the genus with gemmipary and active vegetative propagation.

FIG. 50. *Pandanus gemmiferus* St. John, from *St. John 26,276*. Main trunks with masses of adventitious, leafy buds.

The new epithet is from the Latin, *gemma,* a bud; *fero,* to produce; in reference to the spectacular production of lateral, leafy buds.

Pandanus kurandaensis sp. nov. (sect. *Pandanus*)
Figs. 53–55

DIAGNOSIS HOLOTYPI: Arbor 10 m. alta 20 cm. diametro, cortice trunci et radicorum fulturosorum cum radicillis adpresse adscendentibus 2–4 cm. longis et furcatis obtectis, radicibus fulturosis 5 dm. longis 3 cm. diametro, ligno trunci pallidi duri, foliis 1.41–1.91 m. longis 7–8 cm. latis coriaceis supra in media sulcatis ligulatis sensim ex basi in apice subulato diminuentibus eo in puncto 10 cm. ex apice 3–3.5 mm. lato, basi per 17–20 cm. inermi tum marginibus cum aculeis 2–3 mm. longis 3–7 mm. distantibus subulatis adscendentibus brunneis, midnervo infra fere ad mediam inermi, in sectione mediali marginibus cum aculeis 1.2–1.5 mm. longis 4–11 mm. distantibus adpresse adscendentibus, midnervo infra cum aculeis simulantibus et 11–19 mm. distantibus, circa apicem marginibus cum aculeis 0.2–0.3 mm. longis 1.5–3 mm. distantibus divergentibus crasse subulatis brunneis, midnervo infra cum aculeis 0.5–0.8 mm. longis 5–10 mm. distantibus subulatis adscendentibus, syncarpio 12–14 cm. longo ovoideo, phalangibus 4.5–5.3 cm. longis 2.4–3.8 cm. latis 2.5–3 cm. crassis apparente rubris cuneatis apice late truncatis vel subconvexis multiangulosis, lateribus cum angulis secundariis multis dense papillosis, parte ½ supera libera, suturis lateralibus distinctis sed angustis, sinibus centralibus apicalibus 6–8 mm. pro-

FIG. 51. *Pandanus gemmiferus* St. John, from *St. John 26,276.* A branch with the adventitious, leafy buds, held by the forester, Edward Volk.

fundis, carpellis 8–13 apicibus adscendentibus sed minime divergentibus eis marginalibus anguste conicis et cum plana oblique truncata parva terminali ad stigmatem vicini vel eam praecipitanti, eis centralibus lanceoloideis acutis, stigmatibus 1–2 mm. longis ovalibus sulcatis nigris papillosis centripetalibus obliquis vel verticalibus, sutura proximali ad fondam extenta, endocarpio mediali mahogani-colorato osseoso solido marginibus lateralibus 2.5–3 mm. crassis, seminibus 14–17 mm. longis 3 mm. diametro anguste ellipsoideis, mesocarpio apicali in carpella quaque cavernoso cum fibris paucis et membranis medullosis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 10 m. tall, 20 cm. in diameter; bark of trunk and prop roots shaggy with appressed ascending rootlets 2–4 cm. long and branching; prop roots 5 cm. long, 3 cm. in diameter; wood pale, dense and hard; leaves 1.41–1.91 m. long, 7–8 cm. wide, coriaceous, above with a median furrow, ligulate, gradually tapering from the base into deltoid subulate apex which 10 cm. down is 3–3.5 mm. wide, near the base beginning 17–20 cm. up the margins with prickles 2–3 mm. long, 3–7 mm. apart, subulate, ascending, brown; the midrib below unarmed almost to the middle; at the midsection the margins with prickles 1.2–1.5 mm. long, 4–11 mm. apart, appressed ascending; the midrib below with similar prickles 11–19 mm. apart; near the apex the margins with prickles 0.2–0.3 mm. long, 1.5–3 mm. apart, divergent, stout subulate, brown; the midrib below with prickles 0.5–0.8 mm. long, 5–10 mm. apart, subulate, ascending; syncarp 12–14 cm. long, ovoid; phalanges 4.5–5.3 cm. long, 2.4–3.8 cm. wide, 2.5–3 cm. thick, apparently reddish, cuneate, the apex broad truncate or perceptibly curved,

FIG. 52. *Pandanus gemmiferus* St. John, from *St. John 26,276.* A branch showing the three reversing spirals of adventitious buds.

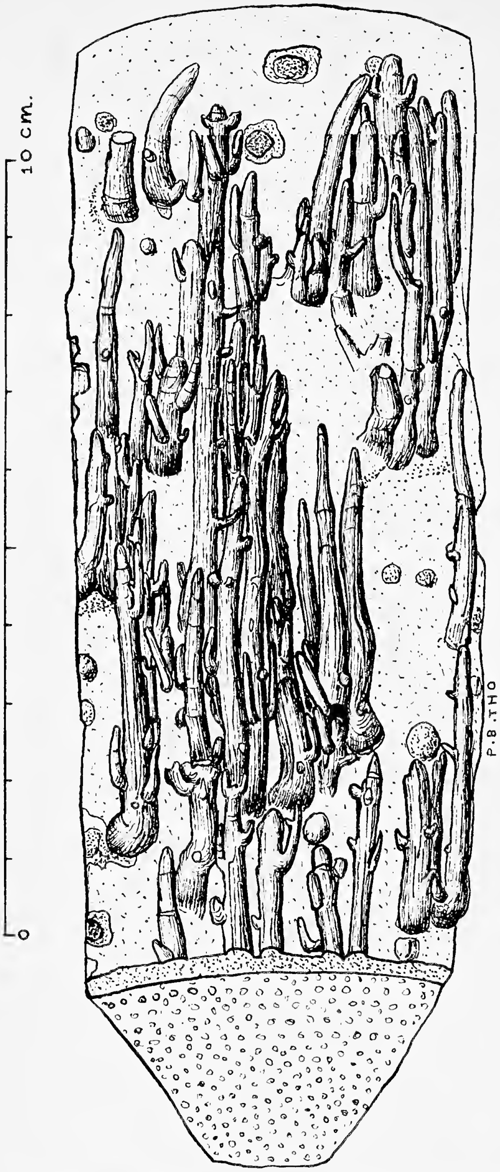

FIG. 53. *Pandanus kurandaensis* St. John, from the holotype. Lateral view of trunk, showing bark and appressed ascending adventitious rootlets, × 1.

many-angled, the sides with many secondary angles, closely papillose, upper ½ free, lateral sutures distinct but narrow; apical central sinuses 6–8 mm. deep; carpels 8–13, the apices ascending but slightly diverging, the outer narrowly conic with a small terminal oblique truncate plane leading to and often projecting over the stigma, the central ones lanceoloid, acute; stigmas 1–2 mm. long, oval, creased, blackish, papillose, centripetal, oblique or vertical, exposed on the proximal face or below the apical tooth; proximal crease extending to valley bottom; endocarp median, mahogany-colored, bony, massive, the lateral margins 2.5–3 mm. thick; seeds 14–17 mm. long, 3 mm. in diameter, narrowly ellipsoid; apical mesocarp forming in each carpel a cavern with a few longitudinal fibers and delicate medullary membranes; basal mesocarp fibrous and fleshy. Staminate trees similar to the pistillate; trunk 13 m. tall, 24 cm. in diameter; crown widely branched; bark of trunk and prop roots with many appressed ascending rootlets; leaves 1.75–1.89 m. long, 6–6.5 cm. wide, ligulate, coriaceous, above furrowed and in section M-shaped, gradually tapering from near the base to the long subulate apex about 30 cm. long and 10 cm. down only 1 mm. wide, the base amplexicaul, entire, and the margins unarmed for 23–43 cm., the lowest marginal prickles 1–1.9 mm. long, 5–10 mm. apart, heavy based, arcuate, ascending, subulate, pale; the midrib unarmed, at the midsection the margins with prickles 1–1.7 mm. long, 2–32 mm. apart, subulate, appressed ascending, brown tipped; the nearby midrib unarmed; near the apex the margins with serrae 0.2–0.5 mm. long, 2–5 mm. apart, subulate tipped; the nearby midrib below with similar serrae but these 3–6 mm. apart; staminate inflorescences terminal, nodding, 1 m. long, leafy bracted; peduncle 14–17 cm. long, 7–8 mm. in diameter, fleshy; lower bracts 90–95 cm. long, 4.8–5 cm. wide, the lower third slightly expanded and pale, the rest foliaceous, narrowing to the long subulate tip; median bracts 23 cm. long, 3 cm. wide, lanceolate, coriaceous but white; flowering part of spike 30 cm. long, bearing 15–20 lateral racemes, these 4–10 cm. long, 3 cm. in diameter, cylindric, densely flowered; stamens 10–20 in racemes, the fused axis 5–7 mm. long; free filament tips 1–2 mm. long; anthers 2–3 mm. long, bearing terminal subulate connective prolongation 0.4–0.6 mm. long.

HOLOTYPUS: Australia, North Queensland, Davies Creek, 12 miles W. of Kuranda, fringing forest by stream, with *Tristania laurina,* and *Eucalyptus tereticornis,* 1,270 ft. alt., Feb. 10, 1958, *H. St. John 26,271* (BISH).

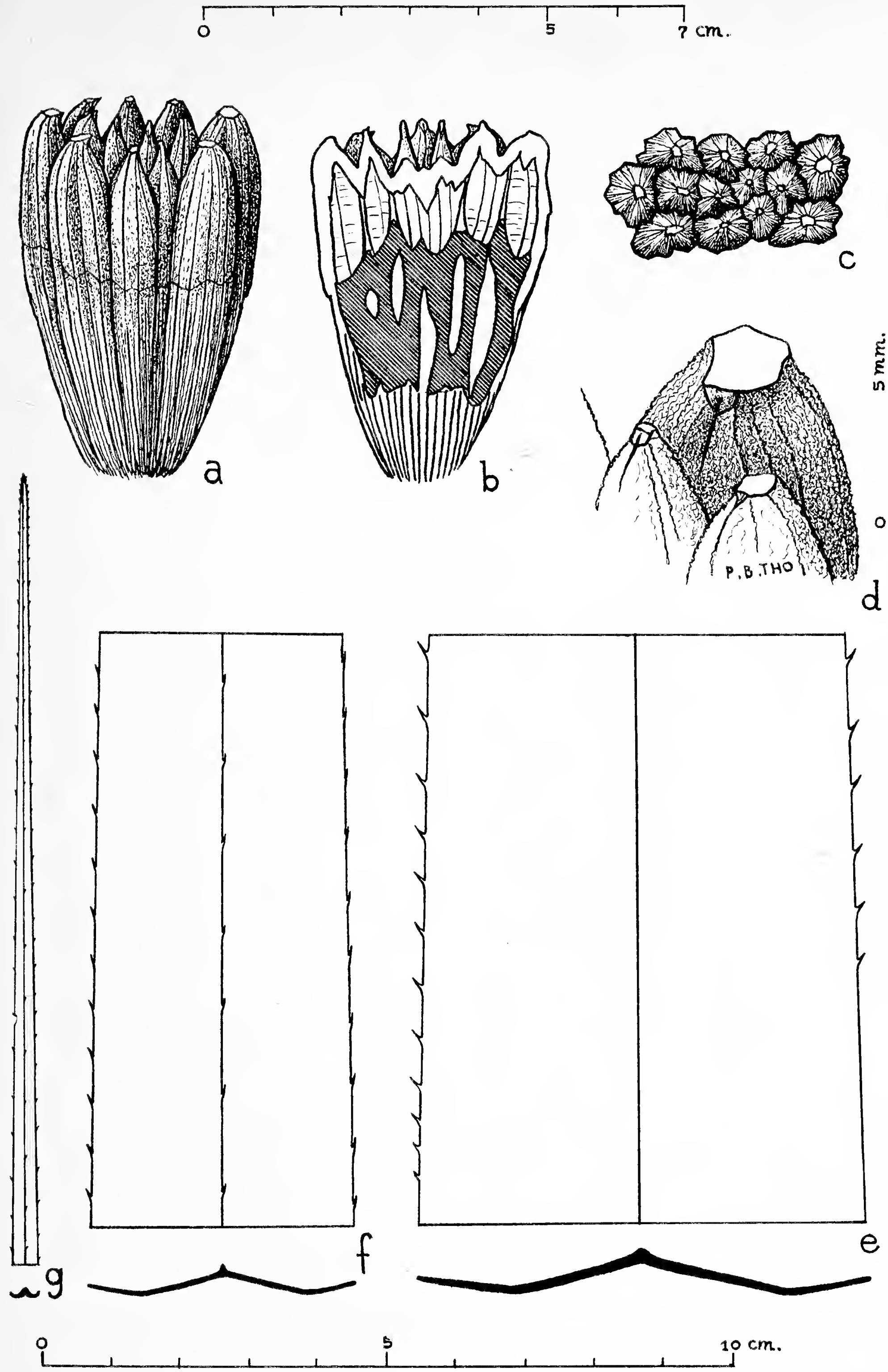

FIG. 54. *Pandanus kurandaensis* St. John, from the holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices and stigmas, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

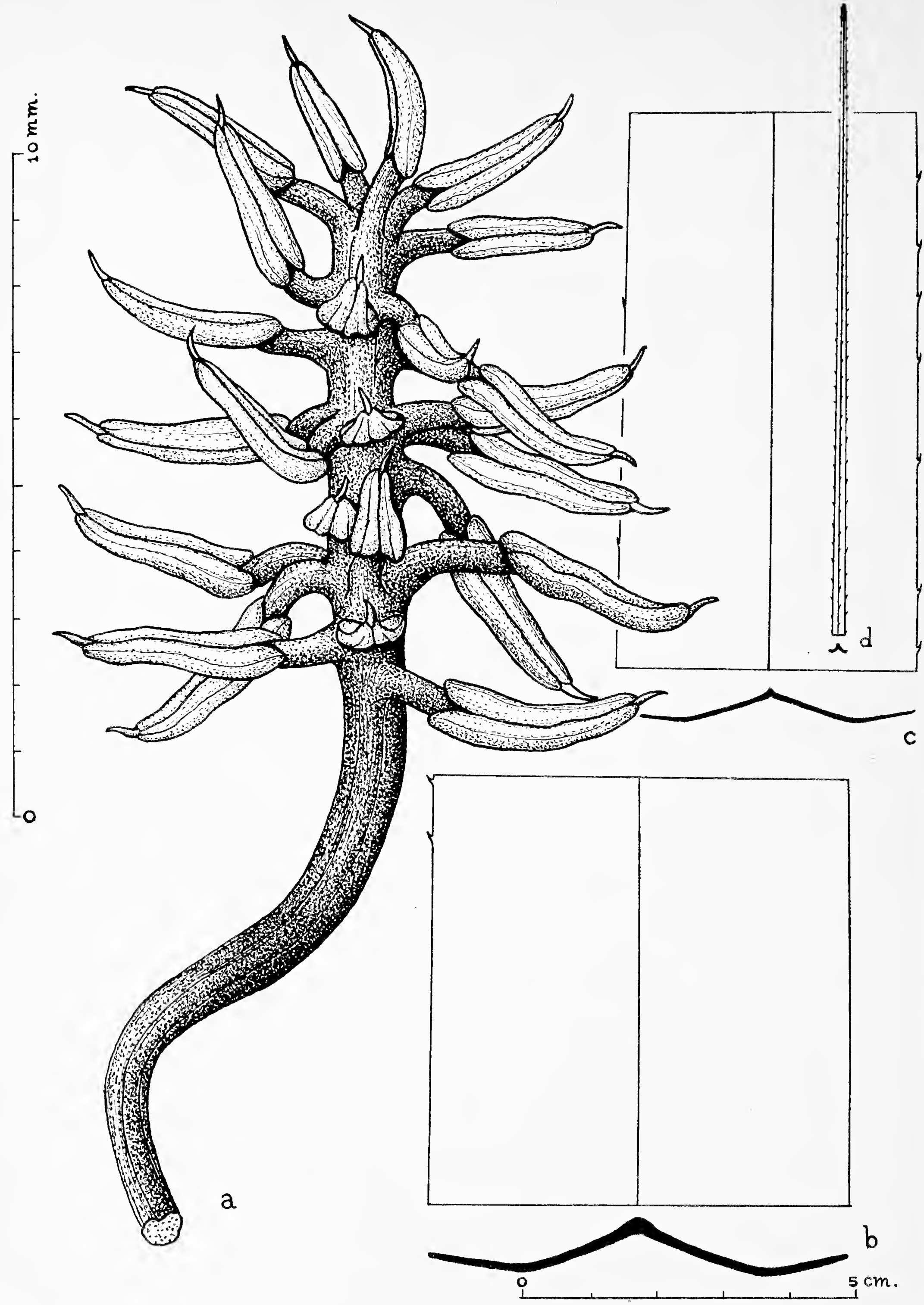

FIG. 55. *Pandanus kurandaensis* St. John, from *St. John 26,272. a,* Column of stamens, × 10; *b,* leaf base, lower side, × 1; *c,* leaf middle, lower side, × 1; *d,* leaf apex, lower side, × 1.

SPECIMENS EXAMINED: Australia, North Queensland, 12 miles W. of Kuranda, fringing forest by stream, staminate tree growing with the pistillate ones, 1,270 ft. alt., Feb. 10, 1958, *H. St. John 26,272* (BISH).

DISCUSSION: *P. kurandaensis* is a member of the section *Pandanus.* Its only close relative seems to be represented by *St. John 26,240* from Australia, a species as yet undescribed.

Only one species was present in the area, occurring in the strips of forest by the streams in the bottoms of narrow valleys. Pistillate trees were abundant; so also were staminate trees which at a glance seemed identical, in stature and shape, and in the rootlet-clothed trunks and prop roots. On close study, however, there are apparent several sex-linked differences in the foliage. The leaves of the staminate trees are narrower at base, but broader at the middle, the margins of base and middle are much less spiny, and the midrib below at the middle is unarmed. Despite these differences in foliage, the author who was also the collector, is certain that these two, male and female, are a pair, representing one species.

Many of the fallen phalanges were minus the upper half which had been chewed off by white-tailed rats seeking the edible, oily seeds.

The new epithet is the Latin adjective, *medialis,* middle, given in reference to the median position of the endocarp.

Pandanus rivularis sp. nov. (sect. *Pandanus*)
Figs. 56–59

DIAGNOSIS HOLOTYPI: Arbor 10 m. alta 20 cm. diametro, ramis dichotomis, cortice brunneo sublaeve, trunco ramisque dense etiam junioribus cum radicillis adpresse adscendentibus 1.5–2.5 cm. longis obtectis, radicibus fulturosis nullis, foliis 1.68–1.81 m. longis 6–7.6 cm. latis supra in media sulcatis coriaceis ligulatis in media extrema in apice acuto diminuentibus eo in 10 cm. ex apice 16 mm. lato, basi amplexicauli et per 17–25 cm. inermi deinde marginibus cum aculeis 2.5–4 mm. longis 2–5 mm. distantibus valde arcuato-subulatis obscure brunneis, midnervo proximo inermi, in sectione mediali marginibus cum aculeis 1–2 mm. longis 6–13 mm. distantibus subulatis adpressis, midnervo infra cum aculeis simulantibus paucis remotis, circa apicem aculeis 0.5–0.7 mm. longis subulatis divergentibus vel semiadscendentibus eis marginali 1.5–2.5 mm. distantibus illis midnervi infra in hoc nullis in eo 3–5 mm. distantibus, inflorescentia foeminea terminale cernua foliosa, pedunculo 45 cm. longo obtuse trigono ad apicem incrassato et 2 cm. diametro, syncarpio unico 23 cm. longo 18 cm. diametro late ellipsoideo brunneo-rubro cum 91 phalangibus eis 5.1–5.3 cm. longis 2.7–3.6 cm. latis (in geminis 4.3–4.4 cm. latis et cum 19–20 carpellis) 1.8–2.8 cm. crassis cuneatis compressis et in sectione plerumque oblongis cum 5–6 angulis majoribus, lateribus exponitis subconvexis densiter papillosis excepta in apice, lateribus quaeque carpellae cum 2–4 angulis secundariis et valleculis, parte ½ supera libera, apice truncato, suturis lateralibus distinctis in parte ⅔ supera sed angustis, sinibus apicalibus centralibus 4–7 mm. profundis, carpellis 9–11 apicibus erectis semiorbiculari-pyramidalibus ceteris marginalibus cum concavite distali subhorizontali, stigmatibus 1.5–2 mm. longis suborbicularibus ad reniformibus valde obliquis centripetalibus papillosis pallide brunneis, sinu proximali breve plerumque ¼–½ distantia ad fondam extenta, endocarpio in parte 2/5 infera solido obscure mahogani-colorato osseoso lateribus lateralibus 4–6 mm. crassis, seminibus 14 mm. longis 3.5 mm. diametro ellipsoideo, mesocarpio apicali in quaque carpella cavernoso cum fibris validis marginalibus et membranis medullosis, mesocarpio basali parvo sed fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 10 m. tall, 20 cm. in diameter; crown with dichotomous branching; bark brown, rather smooth, but even on youngest branches and densely on older stems and trunk more or less covered by appressed ascending rootlets 1.5–2.5 cm. long; prop roots none; leaves 1.68–1.81 m. long, 6–7.6 cm. wide, above with a broad central furrow, coriaceous, ligulate, tapering in outer half to an acute apex which 10 cm. down is 16 mm. wide, the base amplexicaul unarmed for 17–25 cm., then the margins with prickles 2.5–4 mm. long, 2–5 mm. apart, stout arcuate subulate, dark brown; the nearby midrib unarmed; at the midsection the margins with prickles 1–2 mm. long, 6–13 mm. apart, sub-

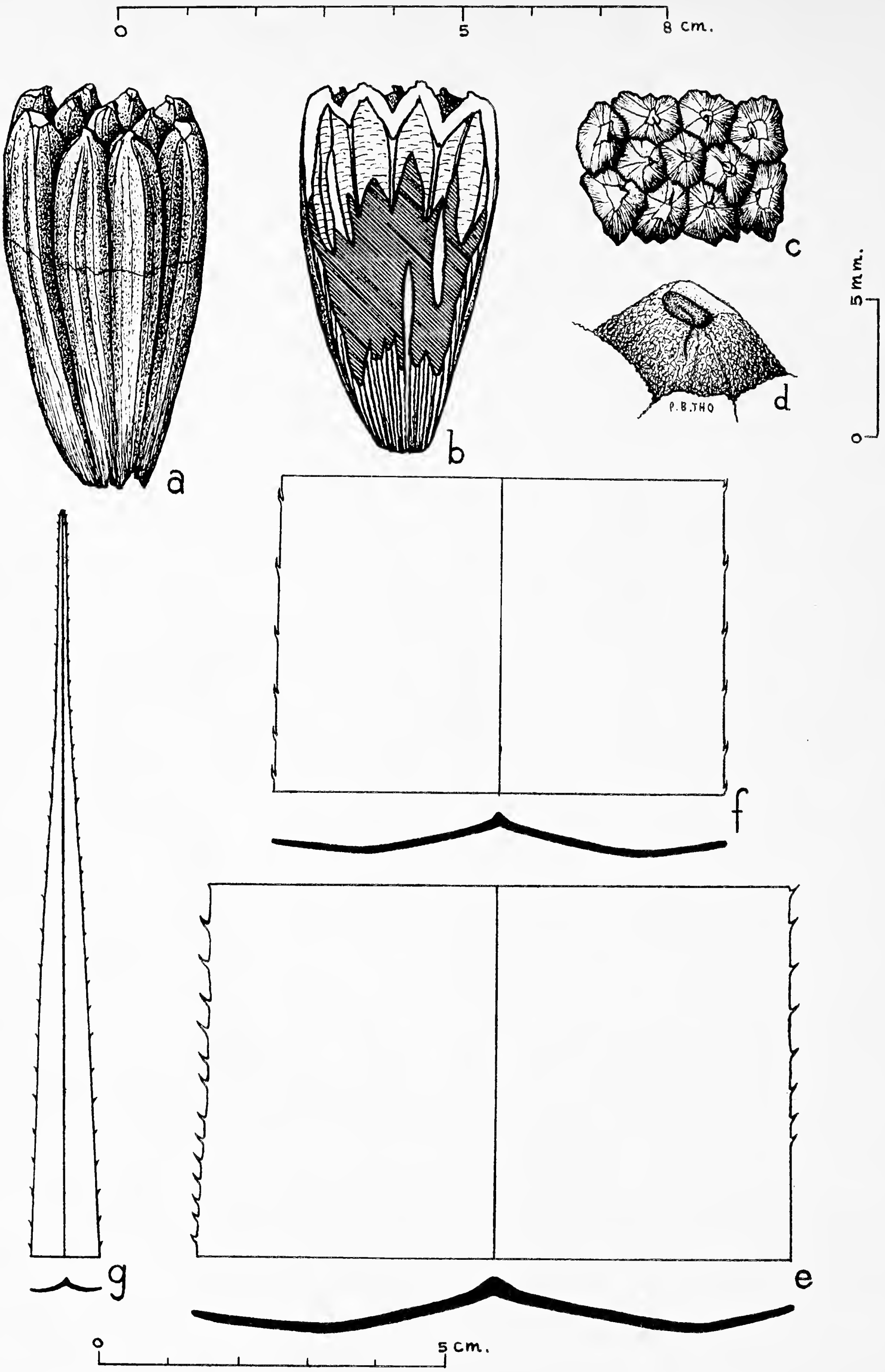

FIG. 56. *Pandanus rivularis* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex and stigma, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

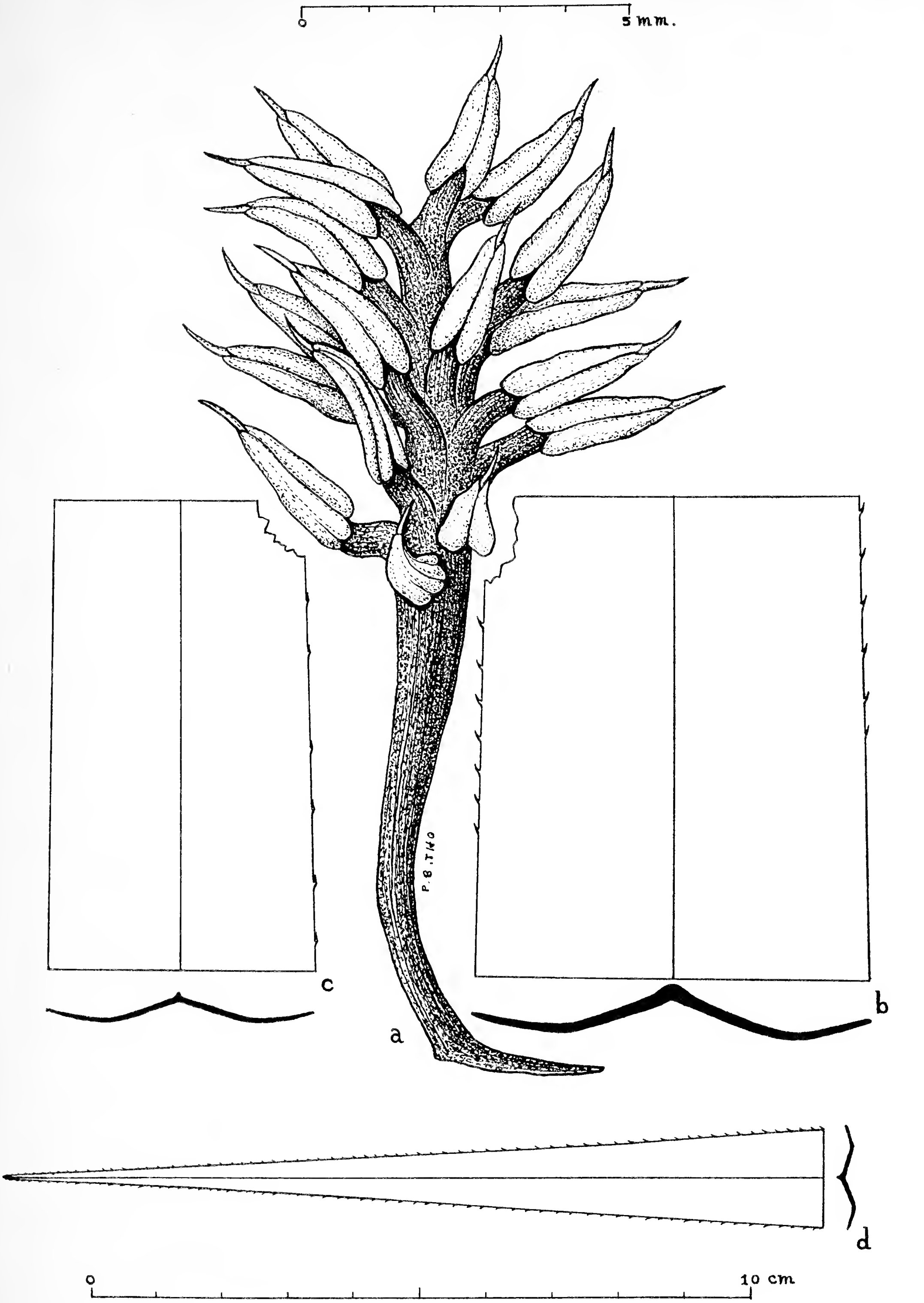

FIG. 57. *Pandanus rivularis* St. John, from *St. John 26,241*. *a*, Column of stamens, × 10; *b*, leaf base, lower side, × 1; *c*, leaf middle, lower side, × 1; *d*, leaf apex, lower side, × 1.

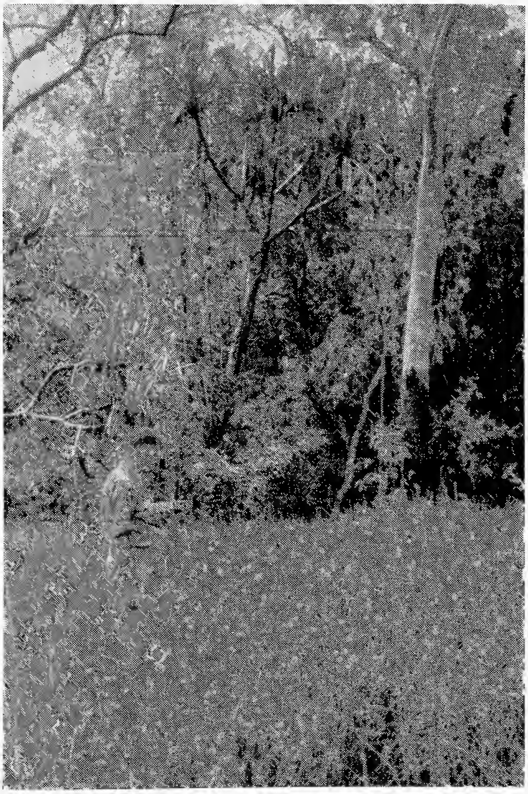

FIG. 58. *Pandanus rivularis* St. John, from holotype, in its habitat, and showing Dr. S. T. Blake.

ulate, appressed; the midrib below with few remote, similar prickles; near the tip the prickles 0.5–0.7 mm. long, subulate, divergent or somewhat ascending, those of the margins 1.5–2.5 mm. apart, those of the midrib below in places none, in others 3–5 mm. apart; pistillate inflorescence terminal, nodding, leafy bracted; peduncle 45 cm. long, obtusely triangular, in diameter increasing upwards and near the apex 2 cm. in diameter; syncarp solitary, 23 cm. long, 18 cm. in diameter, broadly ellipsoid, brownish red, bearing 91 phalanges, these 5.1–5.3 cm. long, 2.7–3.6 cm. wide (in doubles 4.3–4.4 cm. wide and with 19–20 carpels), 1.8–2.8 cm. thick, wedge-shaped, compressed, in cross section mostly oblong, with 5–6 major angles, the sides gently convex, densely papillose on exposed parts except at summit, the sides of each carpel with 2–4 secondary angles and valleys, upper ½ or nearly that part free, apex truncate; lateral sutures distinct but narrow down to lower ⅓, apical central sinuses 4–7 mm. deep; carpels 9–11, the apices erect, semiorbicular-pyramidal, some of the marginal ones with a concavity nearly horizontal and distal of the stigma; stigmas 1.5–2 mm. long, suborbicular to reniform, sharply oblique, centripetal, papillose, light brown; proximal crease short, mostly running ¼–½ way to valley bottom; endocarp centering in lower 2/5, extensive, darkish mahogany-colored, bony, the lateral walls 4–6 mm. thick; seeds 14 mm. long, 3.5 mm. in diameter, ellipsoid; apical mesocarp outlined by heavy fibers, forming in each carpel a cavern with wide, white, medullary membranes; basal mesocarp small, but fibrous and fleshy. Staminate trees 7 m. tall, 20 cm. in diameter; prop roots 30–40 cm. long, the surface with ascending rootlets; leaves 1.06 m. long, 5.5–6 cm. wide, similar but near the base the margins with spines 1.5–2 mm. long, 4–7 mm. apart, subulate, ascending, brownish tipped; the midrib un-

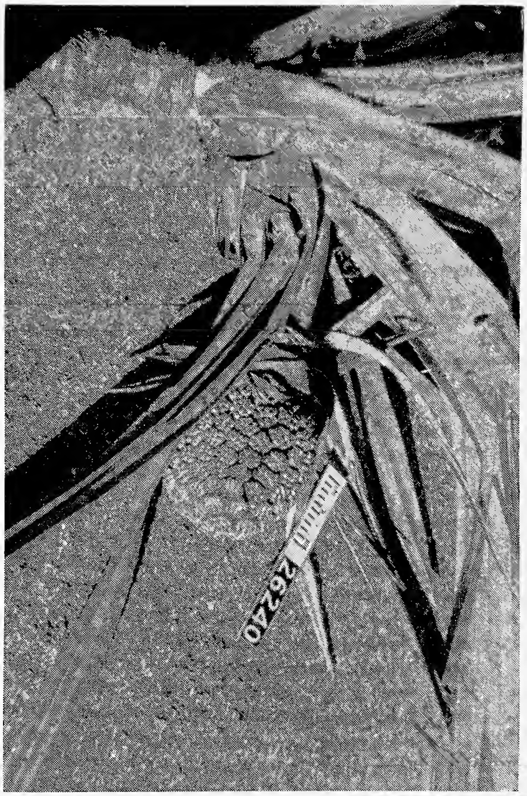

FIG. 59. *Pandanus rivularis* St. John, from the holotype, showing fruiting branch.

armed near the base, middle, and tip; at midsection the spines similar on one margin but lacking on the other; near the apex the margins with serrae 0.2–0.3 mm. long, 1.5–3 mm. apart; the midrib unarmed; staminate inflorescence terminal, nodding, 40–50 cm. long; peduncle fleshy, its bracts caducous; lowest floral bract 80 cm. long, the lower half lanceolate, 3 cm. wide, white, the upper half long subulate, both minutely subulate toothed; median bracts 20 cm. long, 3 cm. wide, white, lanceolate; staminate spikes numerous, sessile, 3–5 cm. long, 2 cm. in diameter; staminate column 10–15 mm. long, the lower half naked; free filament tips 1–1.5 mm. long; anthers 2–2.5 mm. long, lanceolate, bearing an apical prolongation of the connective 0.6–0.8 mm. long, subulate.

HOLOTYPUS: Australia, North Queensland, Endeavour River, Jansons Crossing, 8 miles W. of Cooktown, fringing forest by river, along brackish (?) streams, with *Heritiera, Rhizophora, Dillenia alata,* and *Randia sessilis,* 20 ft. alt., Jan. 31, 1958, *H. St. John 26,240* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, Endeavour River, same locality, habitat, and date as above, staminate tree, *H. St. John 26,241* (BISH).

DISCUSSION: *P. rivularis* is a member of the section *Pandanus.* In that section one finds its closest relative in *P. kurandaensis* St. John of Queensland, which species has the prop roots 50 cm. long, 3 cm. in diameter; leaves 7–8 cm. wide, the subulate apex 3–3.5 mm. wide at the point 10 cm. down from the tip, the marginal prickles near the apex 0.2–0.3 mm. long; the syncarp 12–14 cm. long, ovoid; phalanges with apical central sinuses 6–8 mm. deep; stigmas 1–2 mm. long, oval; and the proximal crease extending to the valley bottom. On the other hand, *P. rivularis* lacks prop roots; has the leaves 6–7.6 cm. wide, the subulate apex 16 mm. wide at the point 10 cm. down from the tip, marginal prickles near the apex 1–2 mm. long; syncarp 23 cm. long, broadly ellipsoid; phalanges with apical central sinuses 4–7 mm. deep; stigmas 1.5–2 mm. long, suborbicular to reniform; and the proximal crease running ¼–½ way to the valley bottom.

The new epithet is the Latin adjective, *rivularis,* by a small stream, chosen to describe the habitat of the species.

Revision of the Genus *Pandanus* Stickman, Part 10
New *Pandanus* Species from Vietnam

HAROLD ST. JOHN[1]

DURING THE YEAR 1959–60 the writer has actively collected and studied *Pandanus* in Vietnam. The following novelties are here reported.

Pandanus hueensis sp. nov. (sect. *Pandanus*) Figs. 60–63

NOM. VERN.: "dua."

DIAGNOSIS HOLOTYPI: Arbor 7 m. alta 15 cm. diametro, cortice brunneo cum radicillis 1–2.5 cm. longis paucis adscendentibus, radicibus fulturosis 30–40 cm. longis 2.5 cm. diametro paucis, foliis 1.45–1.58 m. longis 4.7–5.5 cm. latis coriaceis ligulatis supra intense viridibus infra pallidioribus et glaucis in sectio sinuatis in apice trigono subulato sensim longiter diminuentibus eo 10 cm. ex apice 2.2 mm. lato basi clausa integra et amplexicaule sed ex 8–10 cm. marginibus cum spinis 2–4 mm. longis 3–10 mm. distantibus toto albis vel cum apicibus brunneis subulatis arcuatis adscendentibus, midnervo infra cum spinis 2–2.5 mm. longis 12–30 mm. distantibus subulatis in basi incrassatis valde reflexis, in regione medialis marginibus cum spinis 3–4 mm. longis 3–13 mm. distantibus subulatis adpresse adscendentibus, midnervo infra cum spinis 1.5–2.5 mm. longis 12–18 mm. distantibus adpresse adscendentibus, circa apice marginibus et midnervo infra cum serris mucronatis 0.5–0.7 mm. longis 2–4 mm. distantibus, syncarpiis solitariis terminalibus, pedunculo 30 cm. longo folioso obtuse triangularibus, syncarpio 28 cm. longo 20 cm. diametro late elliptico-ovoideo sed triangularibus, centro 5 cm. diametro ellipsoideo 143 phalangibus ferrento eis 7.4–8 cm. longis 3–4.6 cm. latis 2.8–3.6 cm. crassis anguste oblongo-oblanceoloideo quando submaturis in apice aurantiascentibus lateribus laevibus lucidis planatis vel subcurvatis 4–7-angulatis parte supera ⅓ libera apice subconvexo suturis lateralibus nullis, sinibus centralibus apicalibus 3.5–5 mm. profundis dimidia infera V-formatis, carpelis 4–9 plerumque 6–7 apicibus pyramidalibus sed in phalangiis parvis et minoribus apicibus anguste pyramidalibus et apice subrostratis sed in eis majoribus apicibus oblato-pyramidalibus, stigmatibus 2.5–3.5 mm. longis suborbicularibus ad reniformibus obscure brunneis sulcatis apicalibus contripetalibus inclinatis, sutura proxima lata et ½–⅔ ad fondam extenta, endocarpio in tertia supera 2 cm. longo osseoso brunneo pagina interiori lucida marginibus lateralibus 2 mm. crassis, seminibus 14–15 mm. longis 5 mm. diametro ellipsoideis, mesocarpio apicali in carpella quoque cavernoso 10–18 mm. longo cum fibris paucis et membranis medullosis albis multis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 7 m. tall, 15 cm. in diameter; bark brown, with a few appressed ascending rootlets 1–2.5 cm. long; prop roots few, 30–40 cm. long, 2.5 cm. in diameter; leaves 1.45–1.58 m. long, 4.7–5.5 cm. wide, coriaceous, ligulate, bright green above, below slightly paler and glaucous, in section sinuate, gradually long tapering to the subulate, trigonous apex, this 10 cm. down only 2.2 mm. wide, the enclosed base amplexicaul and entire, but beginning 8–10 cm. up the margin with spines 2–4 mm. long, 3–10 mm. apart, wholly white or with brown tips, subulate, arcuate, ascending; the midrib below, beginning 8 cm. up, with spines 2–2.5 mm. long, 12–30 mm. apart, broad based subulate, sharply reflexed; at midsection the margin with spines 3–4 mm. long, 3–13 mm. apart, subulate, appressed ascending; the midrib below with spines 1.5–2.5 mm. long, 12–18 mm. apart, appressed ascending; near the tip the margins and midrib below with mucronate serrations 0.5–0.7 mm. long, 2–4 mm. apart; syncarp single, terminal; peduncle 30 cm. long, leafy bracted, obtusely 3-angled; syncarp

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[1] B. P. Bishop Museum, Honolulu 17, Hawaii, U. S. A. Manuscript received November 7, 1960.

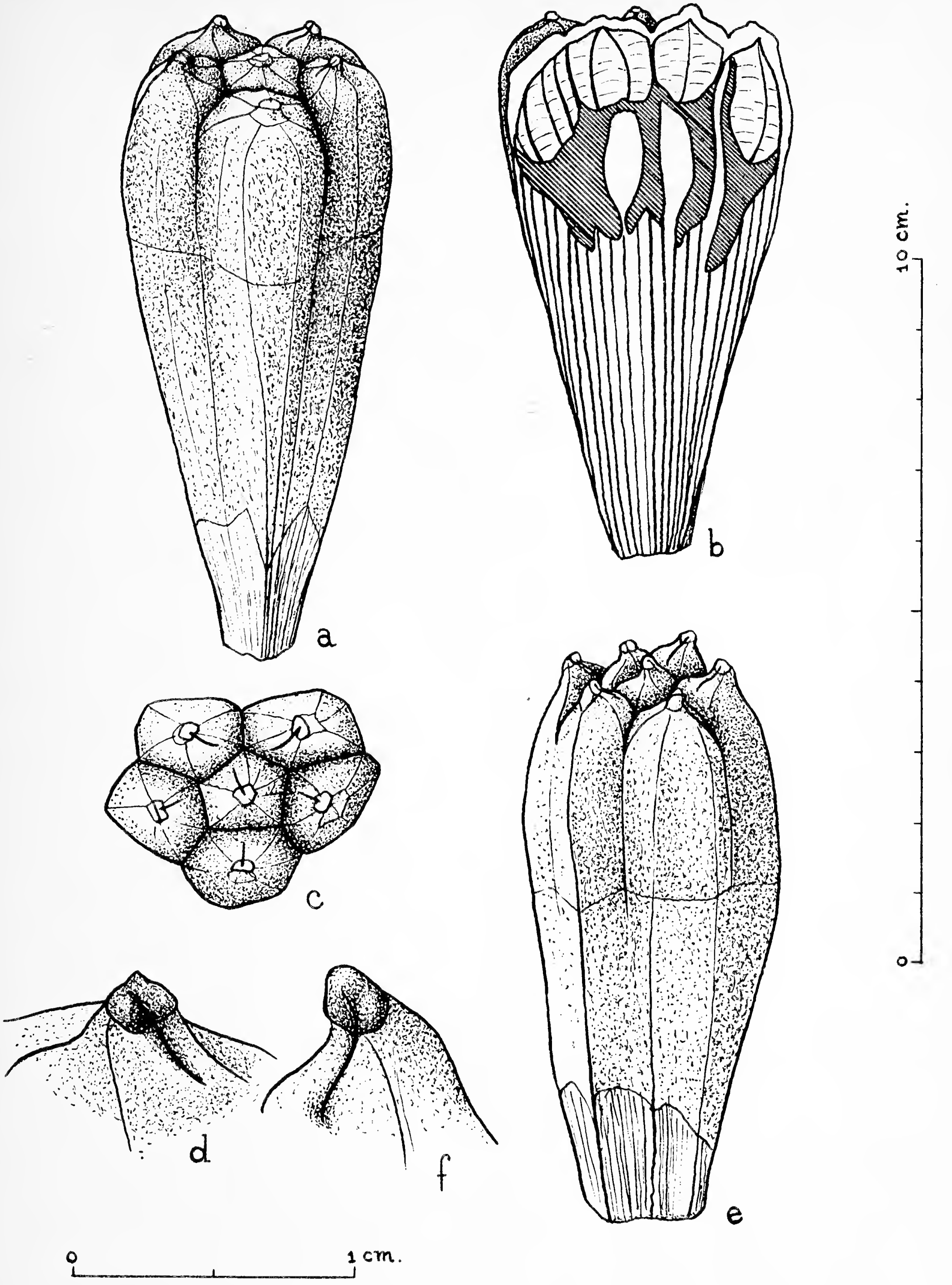

FIG. 60. *Pandanus hueensis,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* stigma and carpel apex of broader phalange, oblique view, × 4; *e,* narrower phalange, lateral view, × 1; *f,* stigma and carpel apex of narrower phalange, oblique view, × 1.

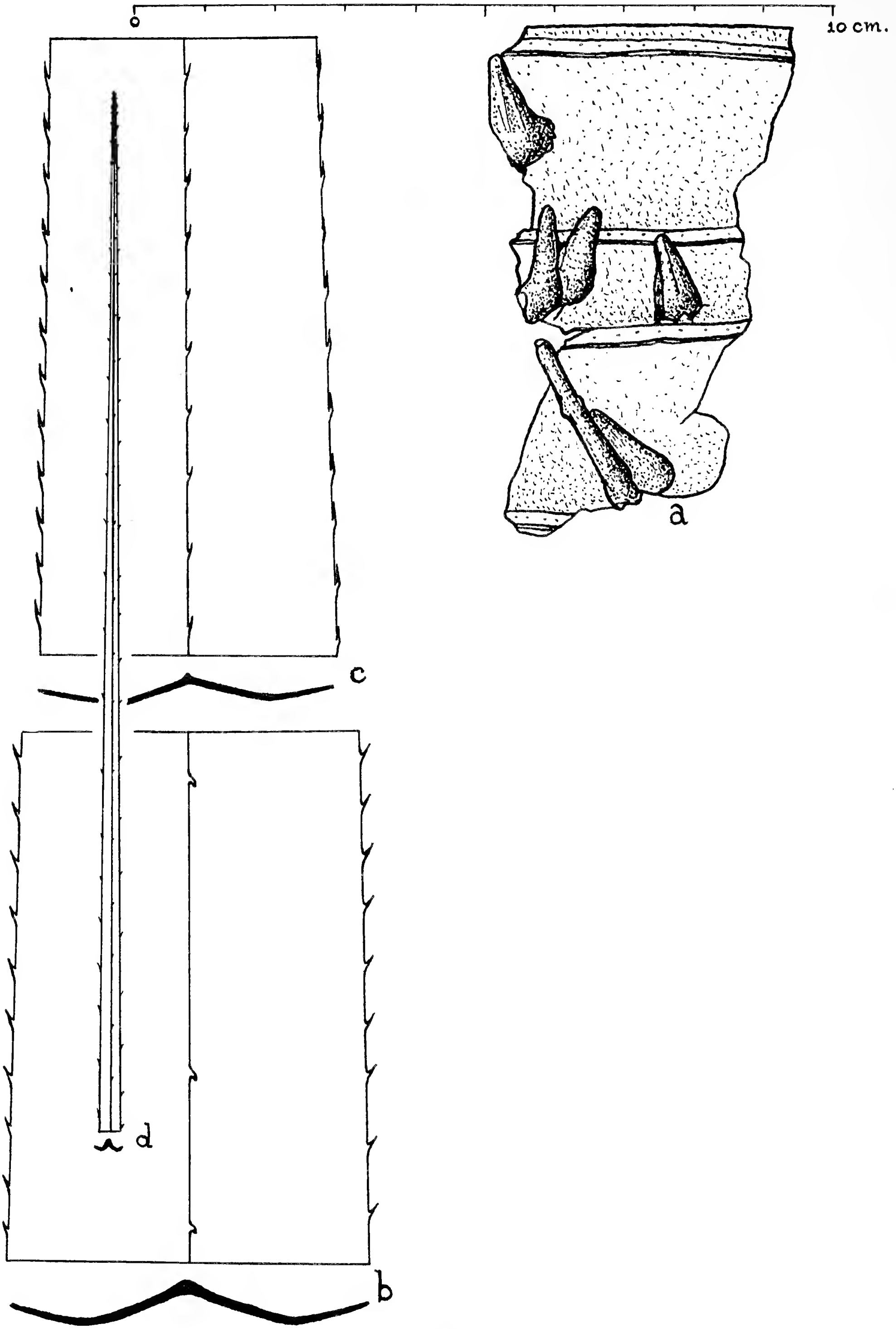

FIG. 61. *Pandanus hueensis,* from holotype. *a,* Bark with ascending rootlets, × 1; *b,* leaf base, lower side, × 1; *c,* leaf middle, lower side, × 1; *d,* leaf apex, lower side, × 1.

FIG. 62. *Pandanus hueensis,* from holotype. With figure of Mrs. H. St. John.

28 cm. long, 20 cm. in diameter, broadly elliptic-ovoid, distinctly 3-sided, the core ellipsoid, 5 cm. in diameter, with 143 phalanges, these 7.4–8 cm. long, 3–4.6 cm. wide, 2.8–3.6 cm. thick, narrowly oblong-oblanceoloid, not quite ripe, but yellow below and turning orange at apex, sides smooth, shining, plane or gently curved, 4–7-angled, upper ⅓ free, apex low convex, lateral sutures none; apical central sinuses 3.5–5 mm. deep, the lower half V-shaped; carpels 4–9, mostly 6–7, the apices pyramidal, but on the narrower, smaller phalanges the apices narrow pyramidal and the summit almost rostrate, while on the larger ones the apices oblate pyramidal; stigmas 2.5–3.5 mm. long, suborbicular to reniform, dark brown, creased, apical, centripetal, inclined; proximal crease wide and running ½–⅔ way to valley bottom; endocarp in upper third, 2 cm. long, bony, brown, the inner surfaces polished, the lateral margins 2 mm. thick; seeds 14–15 mm. long, 5 mm. in diameter, ellipsoid; apical mesocarp cavernous in each carpel, 10–18 mm. long, with a few fibers and many white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Vietnam, Thai Duong Ha, Hue, thicket at edge of brackish marsh by inner beach, sandy soil, 2 m. alt., April 3, 1960, *H. St. John 26,343* (BISH).

DISCUSSION: *P. hueensis* is a member of the section *Pandanus* and finds its closest relationship in *P. tutuilaensis* Martelli of Samoa, which has the syncarp oblong; phalanges 7 cm. long, 3.5 cm. wide, 2.5–3 cm. thick; carpel apices conic; central apical sinuses 3–9, mostly 5–7 mm. deep. On the other hand, *P. hueensis* has the syncarp broadly elliptic-ovoid, 3-sided; phalanges 7.4–8 cm. long, 3–4.6 cm. wide, 2.8–3.6 cm. thick; carpel apices pyramidal to oblate pyramidal; and the central apical sinuses 3.5–5 mm. deep.

The new epithet refers to the type locality, Hue, to which is added *–ensis,* making it a Latin place adjective.

Pandanus integriapicis sp. nov. (sect. *Pandanus*)

Figs. 64, 66

DIAGNOSIS HOLOTYPI: Trunco 50 cm. alto 7 cm. diametro, radicibus fulturosis nullis, foliis 78–87 cm. longis 4.2–4.5 cm. latis coriaceis viridibus glaucis in sectio M-formatis ligulatis ex medio sensim diminuentibus in apice longiter subulato eo in regione 10 cm. ex puncto 3 mm. lato, basi amplexicauli et integra sed ex 2 cm. marginibus cum spinis 4–7 mm. longis 5–15 mm. distantibus curvatis fortiter subulatis pallidis adscendentibus, midnervo ex 8–9 cm. supra basem cum spinis simulantibus sed reflexis, circa sectionem mediam marginibus cum spinis 3–4 mm. longis 7–12 mm. distantibus subulatis valde adpressis adscendentibus midnervo infra cum spinis 2–3 mm. longis simulantibus adscendentibus, circa apicem marginibus totis integris, midnervo infra cum spinis 0.5–1 mm. longis 6–11 mm. distantibus subulatis adpressi-adscendentibus, pedunculo 13 cm. longo vel ultra obtuse triangularibus foliosis, syncarpio solitario terminali 17 cm. longo 10–11 cm. diametro

FIG. 63. *Pandanus hueensis,* from holotype. Showing branch, foliage, and syncarp, lateral view.

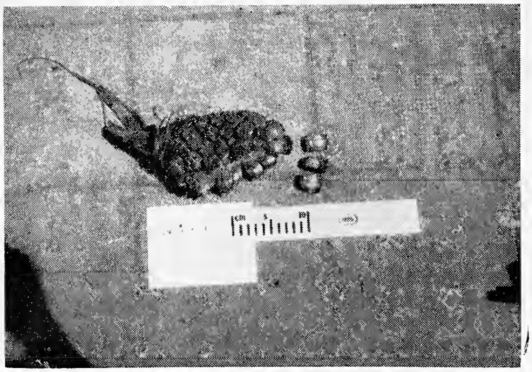

FIG. 64. *Pandanus integriapicis,* from holotype. Showing syncarp and phalanges, lateral view.

ellipsoideo minime trigono centro molliter carnoso et in post maturite in fibris paucis siccato, cum circa 74 phalangibus eis 2.7–3.1 cm. longis parte supera principali 2.1–3 cm. latis 1.8–2.6 cm. crassis oblongis viridibus sed pallide aurantescentibus, lateribus laevibus planis vel paene convexis sublucidis 4–7-angulosis parte ⅔ supera libera, apice depresso-convexo, suturis lateralibus nullis, sinibus centralibus apicalibus 2–4 mm. profundis, parte ⅓ infera carnosa distenta 2–4 mm. projecta lucida aurantiaca (Seguy, Code Univ. Couleurs pl. XIII no. 182), carpellis 7–9, apicibus centralibus conicis sed marginalibus oblique pyramidalibus et paene divergentibus, stigmatibus 2.5–3 mm. longis cordatis vel suborbicularibus vel oblatis sulcatis nigris terminalibus et prominentibus subhorizontalibus vel valde obliquis centripetalibus, sutura proxima profunda et lata ad fundam plerumque extentam, endocarpio submediali osseoso brunneo marginibus lateralibus 1 mm. latis, seminibus 7–8 mm. longis 2.5 mm. diametro fusiformibus, mesocarpio apicali cavernoso 8–13 mm. longo cum fibris longitudinalibus et membranis albis medullosis, mesocarpio basali luteo carnoso et fibroso.

DIAGNOSIS OF HOLOTYPE: Trunk 50 cm. tall, 7 cm. in diameter, prop roots none; leaves 78–87 cm. long, 4.2–4.5 cm. wide, coriaceous, green and glaucous, ligulate, in section M-shaped, gradually long tapering from the middle to a long subulate apex, this 10 cm. down only 3 mm. wide, the base amplexicaul and entire, but beginning 2 cm. up the margins with spines 4–7 mm. long, 5–15 mm. apart, curved, stout subulate, pale, ascending, the nearby midrib beginning 8–9 cm. up, with similar but reflexed spines; near the midsection the margins with spines 3–4 mm. long, 7–12 mm. apart, subulate, closely appressed ascending; the midrib below with similar ascending spines 2–3 mm. long; near the apex the margins entire, but the midrib below with appressed ascending, subulate spines 0.5–1 mm. long, 6–11 mm. apart; peduncle 13 or more cm. long, obtusely triangular, leafy bracted; syncarp solitary, terminal, 17 cm. long, 10–11 cm. in diameter, ellipsoid, slightly 3-sided, the core becoming soft fleshy and disintegrating to only a few fibers at maturity, bearing about 74 phalanges, these 2.7–3.1 cm. long, the main upper part 2.1–3 cm. wide (3.8 cm. in a double), 1.8–2.6 cm. thick, oblong, green, turning pale orange, the sides smooth, plane to gently convex, slightly shining, 4–7-angled, upper ⅔ free, apex low convex, lateral sutures none, apical central sinuses 2–4 mm. deep, lower ⅓ of phalange inflated fleshy at maturity, projecting 2–4 mm., shining, brilliantly colored, orange (Seguy, Code Universel Couleurs pl. XIII, no. 182); carpels 7–9, the apices conical on the central, but obliquely pyramidal and slightly divergent on the marginal ones; stigmas 2.5–3 mm. long, cordate or suborbicular or oblate, creased, black, prominent, terminal, subhorizontal to sharply oblique, centripetal; proximal crease deep and wide, extending to or nearly to the valley bottom; endocarp submedian, bony, brown, the lateral margins 1 mm. thick; seeds 7–8 mm. long, 2.5 mm. in diameter, fusiform; apical mesocarp in each carpel apex cavernous,

FIG. 65. *Pandanus Phamhoangii,* from holotype. Showing foliage and syncarp, lateral view.

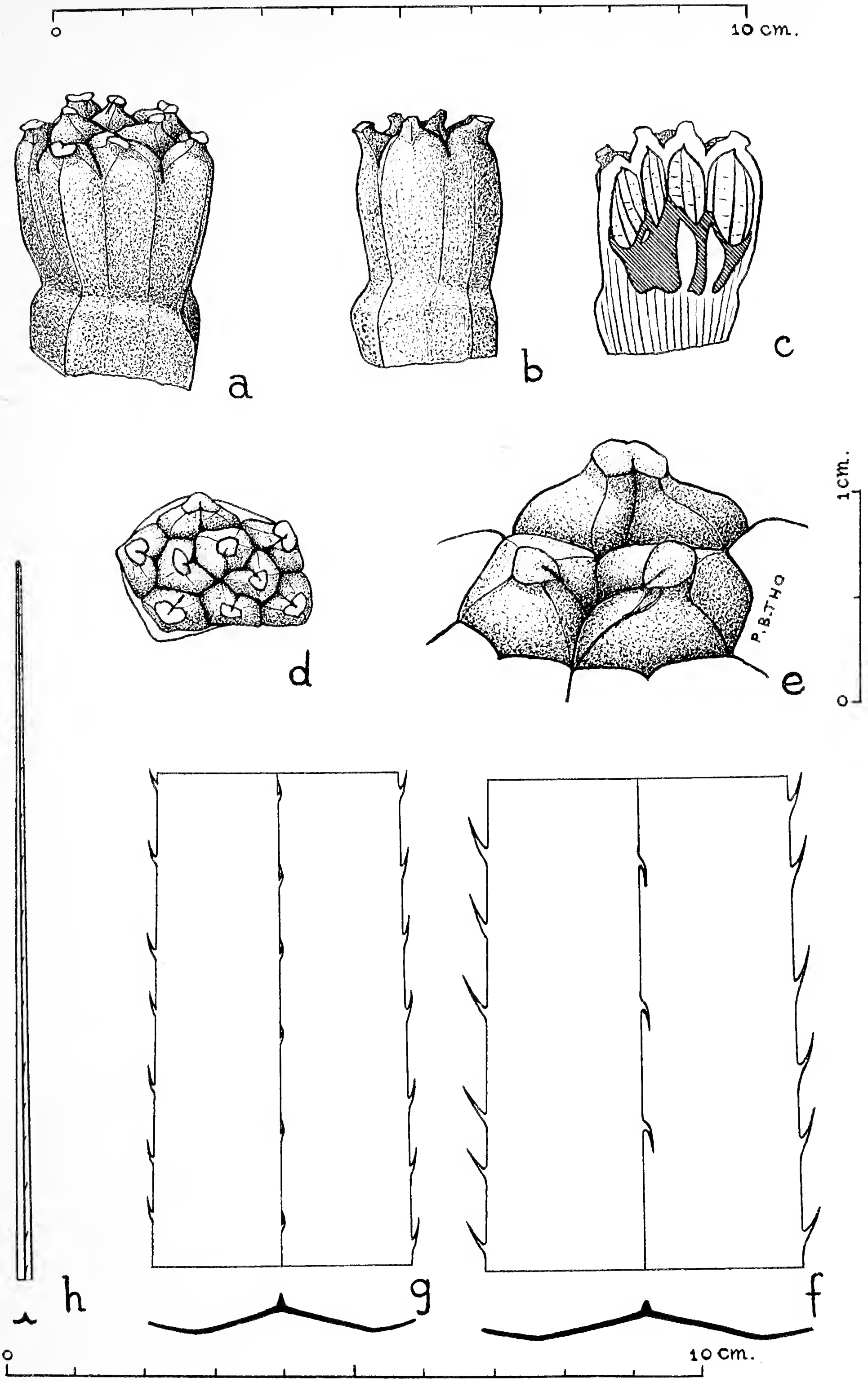

FIG. 66. *Pandanus integriapicis,* from holotype. *a,* Phalange, lateral view, × 1; *b,* smaller phalange, lateral view, × 1; *c, phalange,* longitudinal median section, × 1; *d,* phalange, apical view, × 1; *e,* carpel apices, oblique view, × 3; *f,* leaf base, lower side, × 1; *g,* leaf middle, lower side, × 1; *h,* leaf apex, lower side, × 1.

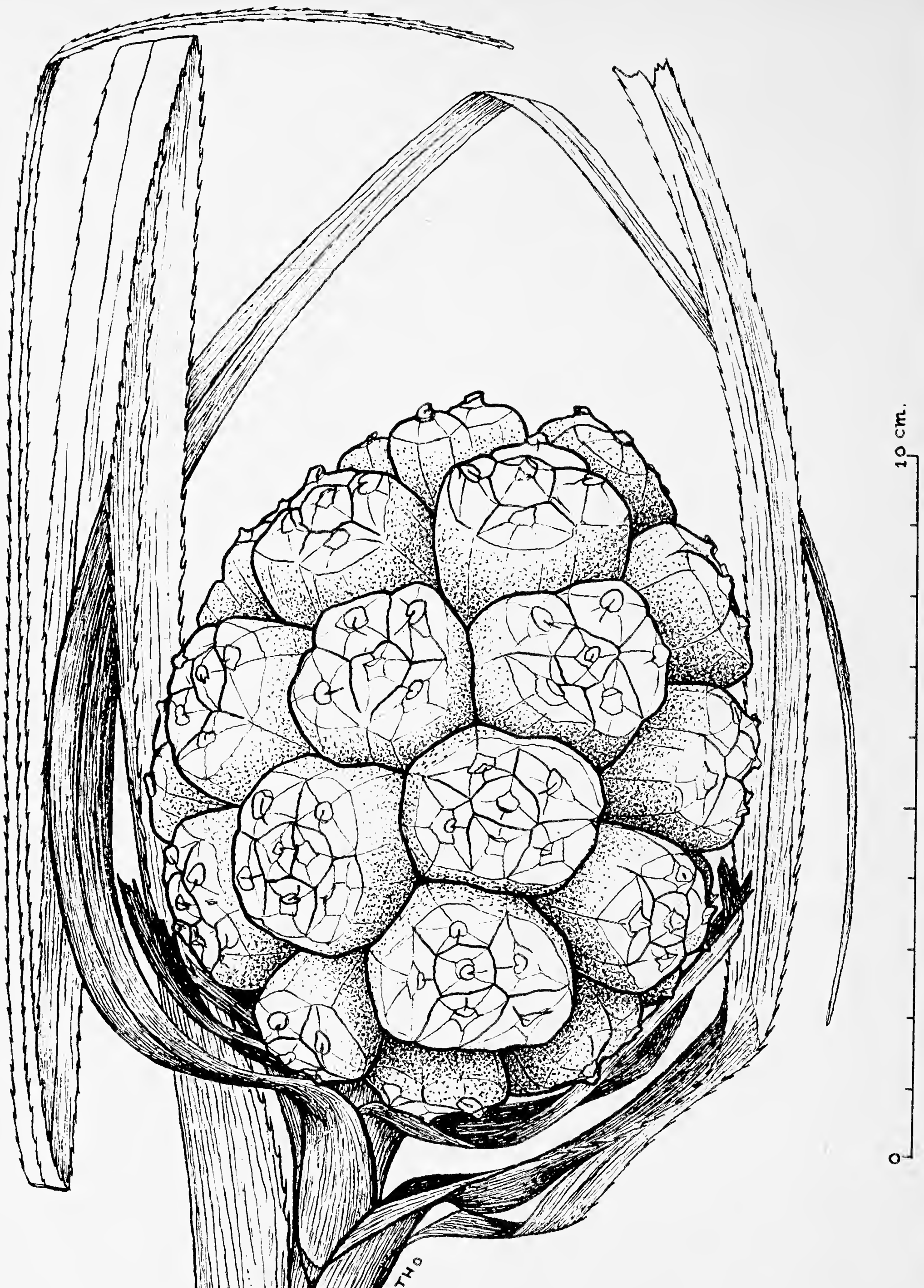

FIG. 67. *Pandanus Phamhoangii,* from holotype. Syncarp, lateral view, × 1.

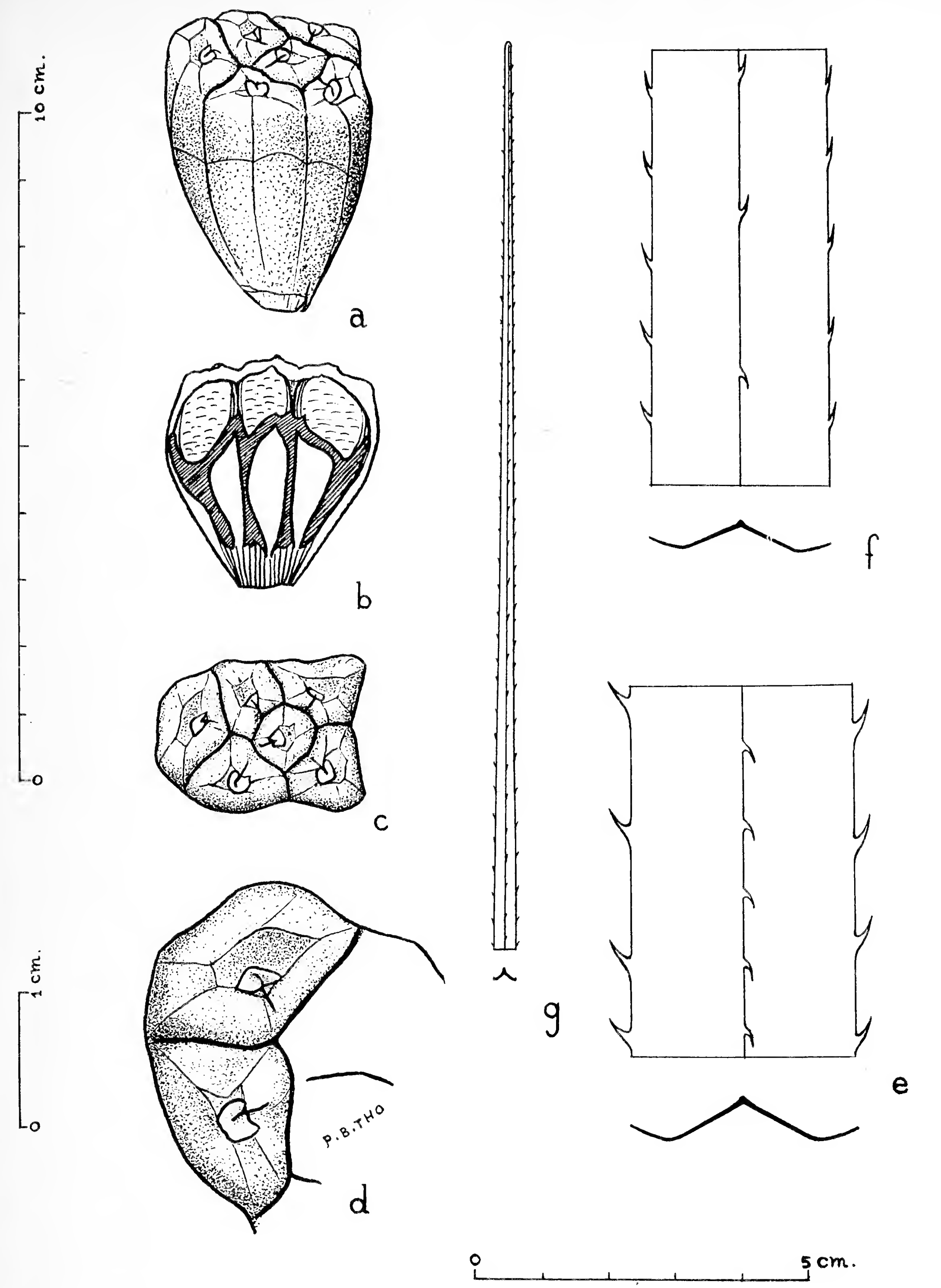

FIG. 68. *Pandanus Phamhoangii,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, apical view, × 2; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

8–13 mm. long, with longitudinal fibers and white, delicate, medullary membranes; basal mesocarp fibrous and fleshy, yellow.

HOLOTYPUS: Vietnam, plage de Phan thíêt, sur dunes de sable nues, avec peu de *Spinifex,* 19 Mars 1960, *Phung Trung Ngan 1* (BISH).

DISCUSSION: *P. integriapicis* is a member of the section *Pandanus.* The closest relative is *P. coronatus* Martelli of Mindanao I. It has the leaves 14 cm. wide; syncarp globose, almost 14 cm. in diameter; phalanges 3.5 cm. long; carpels 9–12, the apices diverging; endocarp slightly supramedian, and the lateral margins 2–3 mm. thick. On the contrary, *P. integriapicis* has the leaves 4.2–4.5 cm. wide; syncarp 10–11 cm. in diameter, ellipsoid; phalanges 2.7–3.1 cm. long; carpels 7–9, the apices often slightly diverging; endocarp slightly inframedian, and the lateral margins 1 mm. thick.

The new epithet is derived from the Latin, *integer,* entire, and *apex,* tip, in allusion to the unique characteristic of the spiny margined leaves which have the apical margins entire and unarmed.

Pandanus Phamhoangii sp. nov. (sect. *Pandanus*)

Figs. 65, 67–69

DIAGNOSIS HOLOTYPI: Arbor 2 m. alta 8–9 cm. diametro, cortice fusci breve tuberculosi, foliis 1.23–1.29 m. longis 3.4–3.6 cm. latis coriaceis olivaceis in initio glaucis in sectio V-formatis ligulatis sensim attenuatis midnervo prominenti apice graciliter subulato et in 10 cm. ex puncto olim 2 mm. lato, basi breviter amplexicauli et exarmata, marginibus ex 4–5 cm. ex basi cum dentibus 3–6 mm. longis 6–18 mm. distantibus graciliter subulatis curvatis in 45° adscendentibus albis vel apicibus brunneis in basi crassatis, midnervo infra 7 cm. ex basi cum spinis simulantibus sed reflexis armato, in medio marginibus cum dentibus simulantibus sed rectioribus 3 mm. longis 12–21 mm. distantibus adpressi-adscendentibus, midnervo infra cum aculeis 2–4.5 cm. longis 10–19 mm. distantibus reflexis, circa apicem spinis marginorum midnervique 0.3–0.5 mm. longis 3–9 mm. distantibus fortiter subulatis adpresse adscendentibus, quoque serie foliarum prima cum bractea 7 cm. longa 3 cm. lata naviculare cum duo carenis cucullata exarmata, secunda 9.5 cm. longa 3.5 cm. lata cuneata integra excarinata, tertia 20 cm. longa 3 cm. lata cum spinis adscendentibus, pedunculo 15 cm. longo obtuse trigono et bracteato, syncarpio 11 cm. longo 9.3 cm. diametro late ellipsoideo cum 34 phalangibus, eis 3.4–3.6 cm. longis 2.6–3.2 cm. latis 2.2–2.8 cm. crassis late cuneatis tertia supera libera viridibus sed probabiliter in maturitate aurantiacis, apice plano-truncato, lateribus laevibus paene curvatis 4–7-angulosis, suturis lateralibus nullis, suturis apicalibus centralibus 0.5–1 mm. profundis angustis tessellatis, carpellis 5–7, apicibus subplanis sed frequente minime subpyramidalibus et eis marginalibus cum depressione distali vadosa, stigmatibus 2–4.5 mm. longis breviter sulcatis suborbicularibus vel ovatis brunneis horizontalibus vel obliquis centripetalibus sinu profundo dimidia distantia ad fundum valleculae, endocarpio 2/5 distantia ex basi mahogani-colorato osseoso marginibus 2–3 mm. crassis, seminibus 11–14 mm. longis 4–5 mm. diametro oblique ellipsoideis, mesocarpio apicale cavernoso cum fibris paucis et membranis multis medullosis, mesocarpio basali aurantiaco-luteo carnoso fibrosoque.

DESCRIPTION OF SPECIMENS EXAMINED: Tree 2–4 m. tall, 8–10 cm. in diameter; prop roots few; bark buff-colored, with axillary, short, blunt tubercles; leaves 0.66–1.29 m. long, 3.4–4.6 cm. wide, olive green, coriaceous, at first slightly glaucous above and below, ligulate, gradually long attenuate, in section broad V-shaped but the sides arcuate, the midrib thickened, sharp and projecting below; the apex slender subulate and 10 cm. down only 2–3 mm. wide, base short amplexicaul and unarmed, but the margins with teeth beginning within 2–5 cm. of the base, the lowest teeth 3–7 mm. long 6–18 mm. apart, white or with small brown tips, slender subulate, upward curved, ascending at 45° from a thickened base, the midrib below beginning 3–7 cm. up with similar spines but reflexed at 45°, at the midsection the margins with teeth 3–6 mm. long, 12–21 mm. apart, similar but straighter and appressed ascending; the midrib below with spines 2–4.5 mm. long, 10–19 mm. apart, reflexed; near the apex the spines of margins and lower

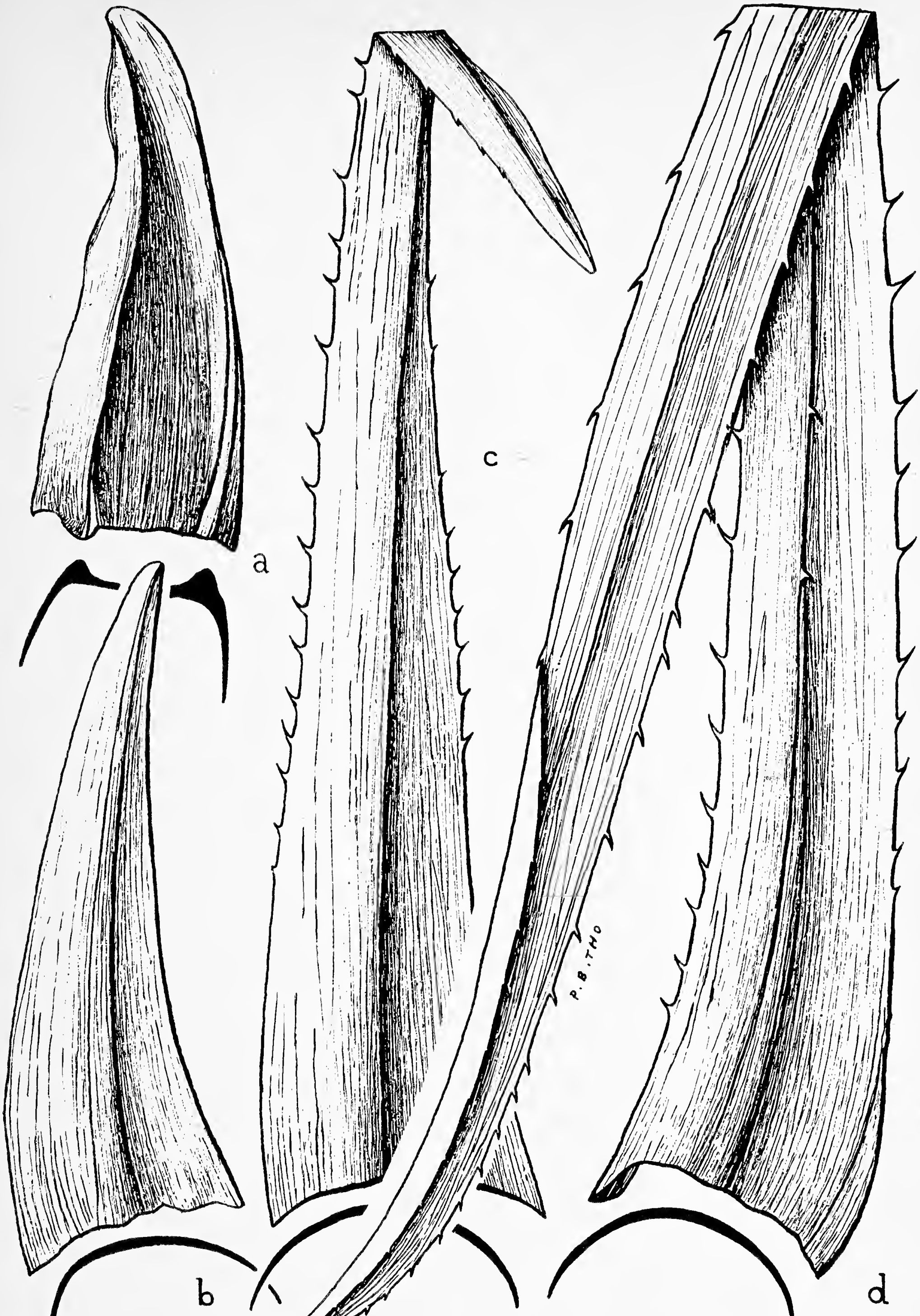

FIG. 69. *Pandanus Phamhoangii,* from holotype. Leaf series, beginning with, *a,* boat-shaped bract; *b,* lanceolate bract; *c,* foliaceous bract; *d,* larger foliaceous bract, all × 1.

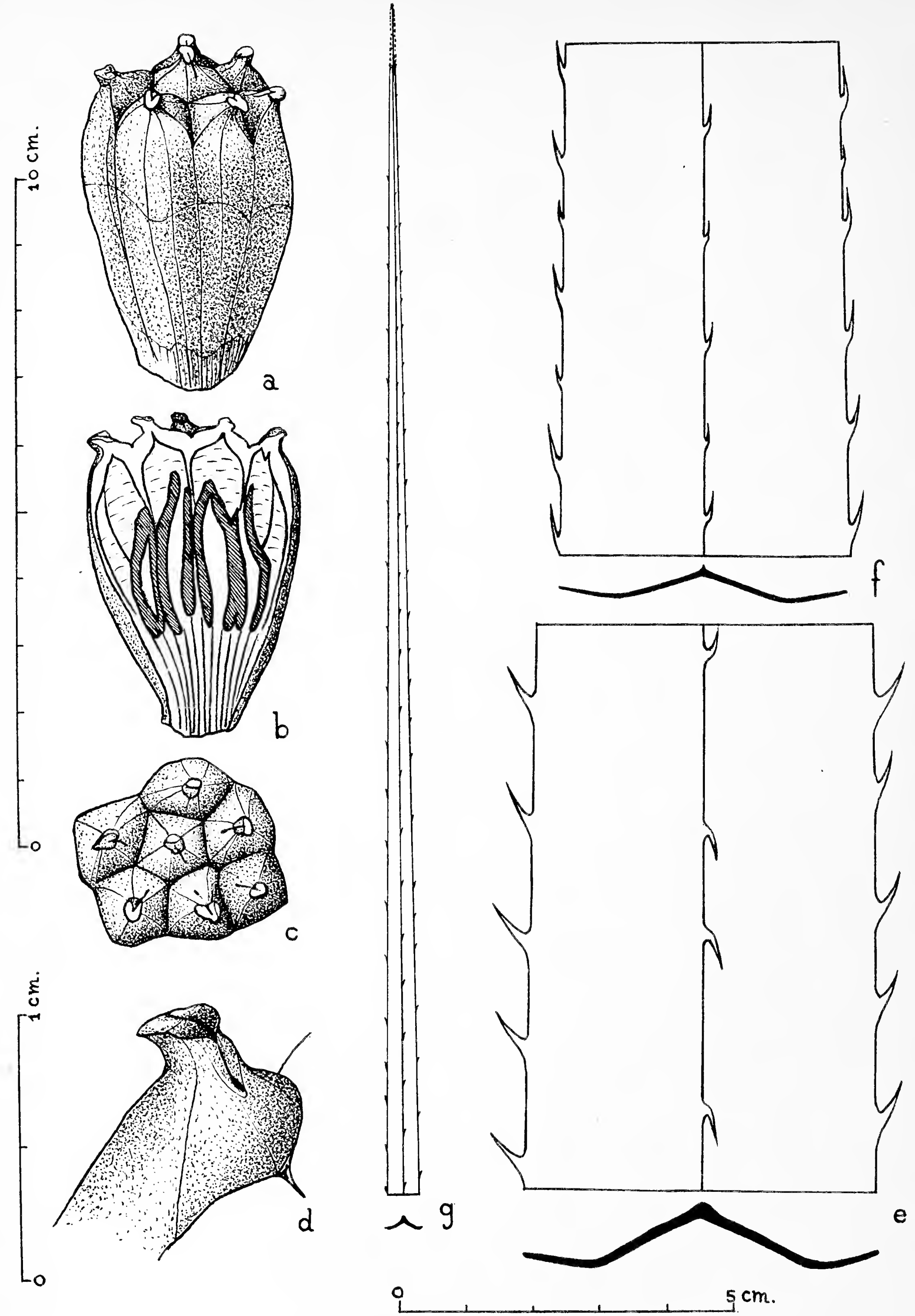

FIG. 70. *Pandanus projectens,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

midrib 0.3–1 mm. long, 3–9 mm. apart, stout subulate, appressed ascending; the foliar bracts that begin each series of normal leaves having the first 7 cm. long, 3 cm. wide, navicular but with only two strong keels and hence semiquadrate in section, cucullate, unarmed; the second bract 9.5 cm. long, 3.5 cm. wide, cuneate, unarmed, not keeled; the third 20 cm. long, 3 cm. wide, ascending spiny on both margins; the fifth 49 cm. long, 3–5 cm. wide, shaped like a normal leaf but acute and 10 cm. down from the apex 14 mm. wide, with spines of margin and midrib like those of a normal leaf; peduncle 15 cm. long, obtusely trigonous, leafy bracted; syncarp 11–12.5 cm. long, 9.3–10.5 cm. in diameter, broadly ellipsoid, of 34 phalanges, these 3.4–3.8 cm. long, 2.6–4 cm. wide, 2.2–3.1 cm. thick, broad cuneate, upper ⅓ free, apex flat truncate, green but probably turning orange-yellow, sides smooth, gently curving, 4–7-angled, lateral sutures none; apical central sinuses 0.5–2 mm. deep, narrow, impressed tessellate; carpels 5–8, the apices appearing flat, but usually with a slight central, subpyramidal elevation and at least the marginal ones with a shallow distal concavity; stigmas 2–4.5 mm. long, short creased, suborbicular to ovate, brown, horizontal or inclined, centripetal; the proximal crease deep, extending half way to the valley bottom; endocarp in lower 2/5, mahogany brown, bony, the lateral margins 2–3 mm. thick; seeds 11–14 mm. long, 4–5 mm. in diameter, obliquely ellipsoid; apical mesocarp cavernous above each seed, with a few fibers and many white medullary membranes; basal mesocarp fibrous and fleshy, orange yellow.

Fig. 71. *Pandanus reversispiralis,* from holotype. Habit, with figure of Prof. Pham Hoang Ho.

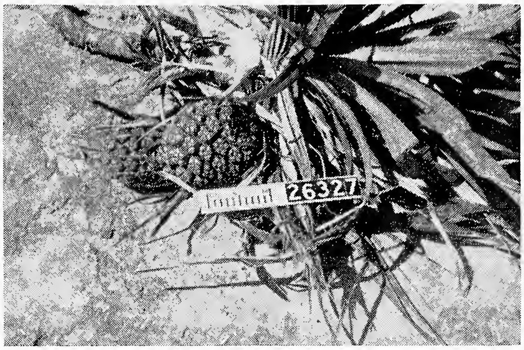

Fig. 72. *Pandanus reversispiralis,* from holotype. Showing branch, foliage, and syncarps.

HOLOTYPUS: Vietnam, Phu' ó' ctuy (formerly Baria), sources chauds de Cu-my, avec *Melaleuca leucadendron,* 2 m. alt., 15 janvier 1960, *Pham Hoang Ho 2,462* (BISH); isotype (Saigon).

SPECIMENS EXAMINED: Vietnam: Phan thîêt, bord de la mer, sur sable fin légèrement rouge, 19 mars 1960, *Phung Trung Ngan 2* (BISH). The collector recorded that the phalange bases are slightly sweet and are eaten by children.

Indonesia: Riouw Archipel, P. Toekoelai, strand, 16/9/1919, "pandan laoet," *H. A. B. Bunnemeijer 6,311* (BO). Anambas Is., 3/4/1928, *van Steemis 983* (BO); Natoena Eil., 13/4/1928, *van Steemis 1,309* (BO).

DISCUSSION: *P. Phamhoangii* is a member of the section *Pandanus.* Somewhat similar specimens have been determined by certain later authors as *P. tectorius* Soland. var. *sinensis* Warb. They came from countries other than China, and there is no indication that they are the same as the var. *sinensis* Warb. There are no published taxa so similar to this new one that it is of value to give comparative differences.

The new species is named in compliment to its collector, Pham Hoang Ho, Professeur de Botanique, Université de Saigon.

Pandanus projectens sp. nov. (sect. *Pandanus*)
Fig. 70, 91A

DIAGNOSIS HOLOTYPI: Arboriforma, trunco 1.5 m. alto 6–7 cm. diametro, foliis 1.26 m. longis 5 cm. latis ligulatis coriaceis in sectio M-formatis ex basi sensim in apice longo subulato diminuentibus eo in puncto 10 cm. ex apice 3 mm. lato, in regione basali marginibus cum aculeis 6–9 mm. longis 10–20 mm. distantibus arcuato-subulatis adscendentibus in tota stramineis vel apicibus brunneis, midnervo infra cum aculeis simulantibus 4–6 mm. longis 13–27 mm. distantibus reflexis, in sectio medialis marginibus et midnervo infra cum aculeis 4–5 mm. longis 7–15 mm. distantibus subulatis adpresse adscendentibus, circa apicem marginibus et midnervo infra cum subulato-serris 0.5–0.7 mm. longis 3–10 mm. distantibus, pedunculo 10 cm. vel ultra longo 12 mm. diametro deltoideo bracteoso, syncarpio solitario terminali 18.5 cm. longo 14.5 cm. diametro elliptico-ovoideo cum 82 phalangibus eis 4.2–4.6 cm. longis 2.2–4 cm. latis 2.3–3.5 cm. crassis cuneato-obovoideis 5–6-angulosis lateribus subconvexis sublucidis verisimiliter luteis parte ⅓ supera libera apice convexo, suturis lateralibus nullis, sinibus apicalibus centralibus 3–5 mm. profundis, carpellis 6–9 apicibus pyramidalibus sed quibusdam marginalibus divergentibus, stigmatibus 3–4 mm. longis obliquis projectentibus ovatis vel ellipticis brunneis papillosis sulcatis centripetalibus, sutura proximali ½ ad fondam extenta, endocarpio mediali brunneo osseoso marginibus lateralibus 1.5–2 mm. crassis, seminibus 8–11 mm. longis 3–4 mm. diametro fusiformibus, mesocarpio terminali in apice quaque carpella cavernam cum medulla alba formanti, mesocarpio basali fibroso et carnoso.

FIG. 73. *Pandanus semiorbicularis,* from paratype. Staminate inflorescence.

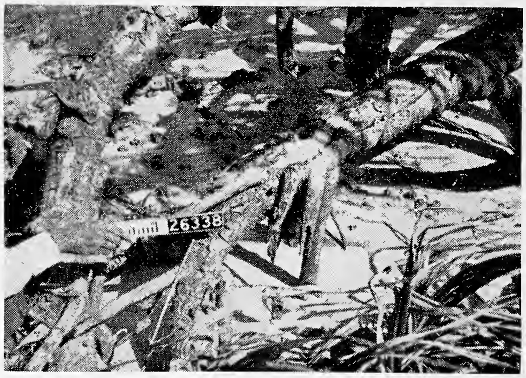

FIG. 74. *Pandanus semiorbicularis,* from holotype. Showing lower trunk and prop roots.

DIAGNOSIS OF HOLOTYPE: Treelike; trunk 1.5 m. tall, 6–7 cm. in diameter; leaves 1.26 m. long, 5 cm. wide, ligulate, coriaceous, in section M-shaped, gradually tapering from the base to the long subulate apex which about 10 cm. down is 3 mm. wide, near the base the margins with prickles 6–9 mm. long, 10–20 mm. apart, arcuate-subulate, ascending stramineous throughout or with the tip brownish; the nearby midrib below with similar prickles 4–6 mm. long 13–27 mm. apart but reflexed; at midsection the margins and midrib below with prickles 4–5 mm. long, 7–15 mm. apart, subulate, appressed ascending; near the tip the margins and midrib below subulate-serrate, the teeth 0.5–0.7 mm. long, 3–10 mm. apart; peduncle 10 or more cm. long, 12 mm. in diameter, triangular, leafy bracted; syncarp solitary, terminal, 18.5 cm. long, 14.5 cm. in diameter, elliptic-ovoid, with 82 phalanges, these 4.2–4.6 cm. long, 2.2–4 cm. wide, 2.3–3.5 cm. thick, cuneate-obovoid, 5–6-angled, the sides gently curved, almost smooth, somewhat shining, apparently becoming yellowish, upper ⅓ free, apex convex, lateral sutures none, apical central sinuses 3–5 mm. deep; carpels 6–9, the apices pyramidal but some of the marginal ones divergent; stigmas 3–4 mm. long, oblique, projecting and prominent, ovate or elliptic, brown, papillose, centripetal, creased; proximal crease mostly extending about ½ way to valley bottom; endocarp median, brown, bony, the lateral margins 1.5–2 mm. thick; seeds 8–11 mm. long, 3–4 mm. in diameter, fusiform; apical mesocarp forming in each carpel an apical cavern filled with white membranous pith; basal mesocarp fibrous and fleshy.

SPECIMEN EXAMINED: Vietnam: Phan Thíêt, à mi-chemin de la route allant vers Mui-Né, bord de la mer, 14 août 1960, *Pham Hoang Ho 5,345* (BISH).

DISCUSSION: *P. projectens* is a member of the section *Pandanus,* and there it seems most closely related to *P. odoratissimus* L. f. which has the phalange with the upper half free; the carpel apices conic-semiorbicular and with the peak erect. In contrast, *P. projectens* has the phalange with the upper third free; carpel apices pyramidal, with the peak slender, projecting and mostly diverging.

The new epithet is the Latin participle, *projectens,* projecting, in allusion to the projecting or diverging apices of the carpels.

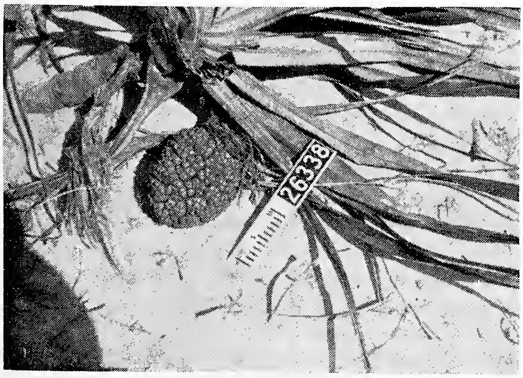

FIG. 75. *Pandanus semiorbicularis,* from holotype. Showing branch, foliage, and syncarp, lateral view.

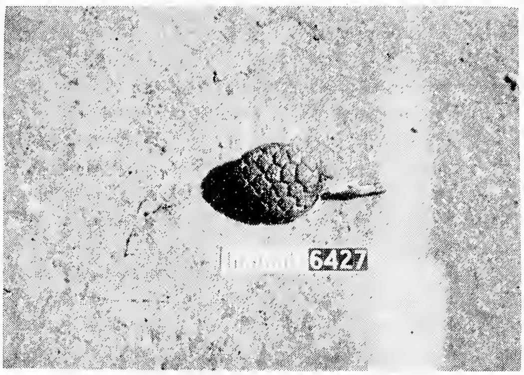

FIG. 76. *Pandanus Smitinandii,* from holotype. Showing syncarp, lateral view.

Pandanus reversispiralis, sp. nov. (sect. *Pandanus*)
Figs. 71–72, 79–80A

DIAGNOSIS HOLOTYPI: Arbor 7 m. alta 13 cm. diametro pauciter ramosa, cortice griseo sparse verrucoso ex alabastris axillaribus adventitiis in spiris tribus quibus post ascentionem gradorum 360° reversis sunt, radicibus fulturosis 30 cm. longis 2.5 cm. diametro muriculatis, foliis 70–88 cm. longis 4.8–5.2 cm. latis coriaceis viridibus in ambis lateribus sed subglaucis in sectio late U-formatis in basi amplexicaulibus apice gradatim longe attenuato et deltoideo-subulato, proxima basi marginibus cum dentibus 4–6.5 mm. longis 5–15 mm. distantibus albis sed apicibus brunneo-tinctis subulatis adscendentibus, midnervo cum aculeis 3–4 mm. longis 10–25 mm. distantibus fortibus subulatis reflexis, in sectio medialis marginibus cum aculeis 3–4 mm. longis 5–17 mm. distantibus subulatis subadpressi-adscendentibus, midnervo cum aculeis simulantibus sed 15–18 mm. distantibus in 45° adscendentibus, circa apicem marginibus midnervoque cum dentibus 1 mm. longis 3–5 mm. distantibus subulatis adscendentibus, pedunculis 20–25 cm. longis recurvatis minime triangularibus foliosis, syncarpiis 12–16 cm. longis 11–14 cm. diametro ovali-subglobosis cum 52–94 phalangibus eis immaturis viridibus et dense congregatis sed in maturite separatis namque amplificatio basorum carnosorum, centro albo molle carnoso, phalangibus 4.3–4.6 cm. longis 2.5–3.8 cm. latis 2.3–3.2 cm. crassis oblongis et paene cuneatis parte supera 3/5 libera, apice oblato-convexo vel in phalangibus paucicarpellatis truncatis, suturis lateralibus nullis, lateribus planis vel minime curvatis 5–8-angulatis, parte 2/5 infera carnosa incrassata aurantiaca, sinibus centralibus apicalibus 3.5–5 mm. profundis angustis, carpellis 5–7, apicibus eis marginalibus depresso-pyramidali—semiorbicularibus et cum concavite parvo distali obliquo, stigmatibus 2–3 mm. longis sulcatis ellipticis vel transverse ellipticis obliquis centripetalibus nigris, sinu proximali forti et ad fondam vallis extensam, endocarpio centrali 2 cm. longo osseoso brunneo lateribus 2–3 mm. crassis, seminibus 10–15 mm. longis 3 mm. diametro obliquiter ellipsoideis, mesocarpio apicali medulloso, mesocarpio basali fibroso et carnoso luteo.

DESCRIPTION OF ALL SPECIMENS: Tree 7 m. tall, 13–18 cm. in diameter, loosely branched; bark gray, sparsely warty from axillary adventitious buds in three ascending spirals which reverse direction after each circuit of 360°; prop roots 30 cm. long, 2.5 cm. in diameter, muriculate; leaves 70–130 cm. long, 4.8–6 cm. wide, coriaceous, green but slightly glaucous on both sides, broad M-shaped in cross section, clasping at base, the apex gradually long attenuate and triangular subulate, and 5 mm. wide 10 cm. down from the apex; near the base the margins with stout white, but brown-tipped, subulate, ascending teeth 4–6.5 mm. long, 5–15 mm. apart, the midrib with strong subulate reflexed prickles 3–4 mm. long, 10–25 mm. apart; at the middle the margins with the teeth 3–4 mm. long, 5–17 mm. apart, subulate, subappressed ascending; the midrib below with similar teeth 15–18 mm. apart, ascending at 45°; near the tip the margins and midrib below with ascending subulate teeth 1 mm. long, 3–5 mm. apart; peduncles 20–25 cm. long, recurving, perceptibly 3-sided, leafy bracted; syncarps 12–16 cm. long, 11–14 cm. in diameter, oval-subglobose, of 52–94 phalanges, these when green well crowded but when ripe becoming distant due to the swelling of the fleshy bases; the axis of the syncarp white, soft, fleshy, doubtless shrinking to a very small remnant; phalanges 4.3–4.6 cm. long, 2.5–3.8 cm. wide, 2.3–3.2 cm. thick, in outline oblong, but slightly cuneate, upper 3/5 free, apex low convex or in those with fewer carpels truncate, lateral sutures none, sides plane or gently curving, 5–8-angled, distinctly fleshy and swollen up to 2/5 way from base, this swelling orange (orange, planche XIV, no. 196, Seguy, E., Code Universel des Couleurs, 1936, Paris, P. Lechevalier), while the upper 3/5 are orange no. 181, pl. XIII; central apical sinuses 3.5–5 mm. deep, narrow; carpels 5–7, the apices of the marginal ones depressed pyramidal-semiorbicular and just distal of the apex with a small oblique concavity; stigmas 2–3 mm. long, creased, elliptic or transversely so, oblique, centripetal, black; the proximal crease strong and extending fully to the bottom of the valley; endocarp central, 2 cm. long, bony, brown, the lateral walls 2–3 mm. thick; seeds 10–15 mm. long, 3 mm. in diameter, oblique ellipsoid; apical mesocarp with a section in each carpel tip, filled solid with white pith; basal mesocarp with fibers and a yellow flesh of bland taste at first, but after a minute irritating. Staminate plant (from Ho 2,532): staminate inflorescence 50 cm. long, terminal, pendent, bearing numerous white bracts; lowest

FIG. 77. *Pandanus subcarnosus,* from holotype. Habit view.

FIG. 78. *Pandanus subcarnosus,* from holotype. Showing foliage and syncarp.

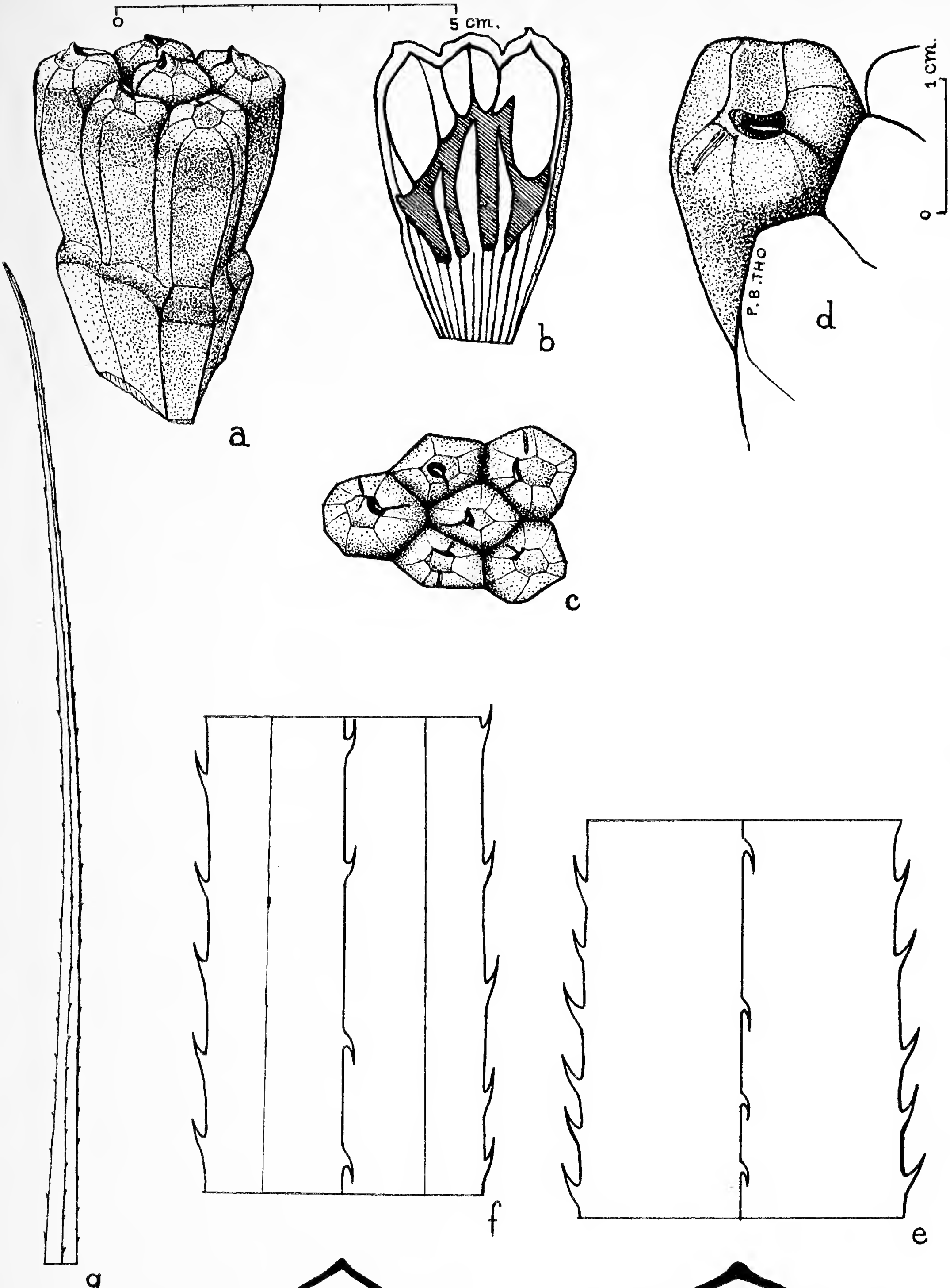

FIG. 79. *Pandanus reversispiralis,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, oblique view, × 2; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

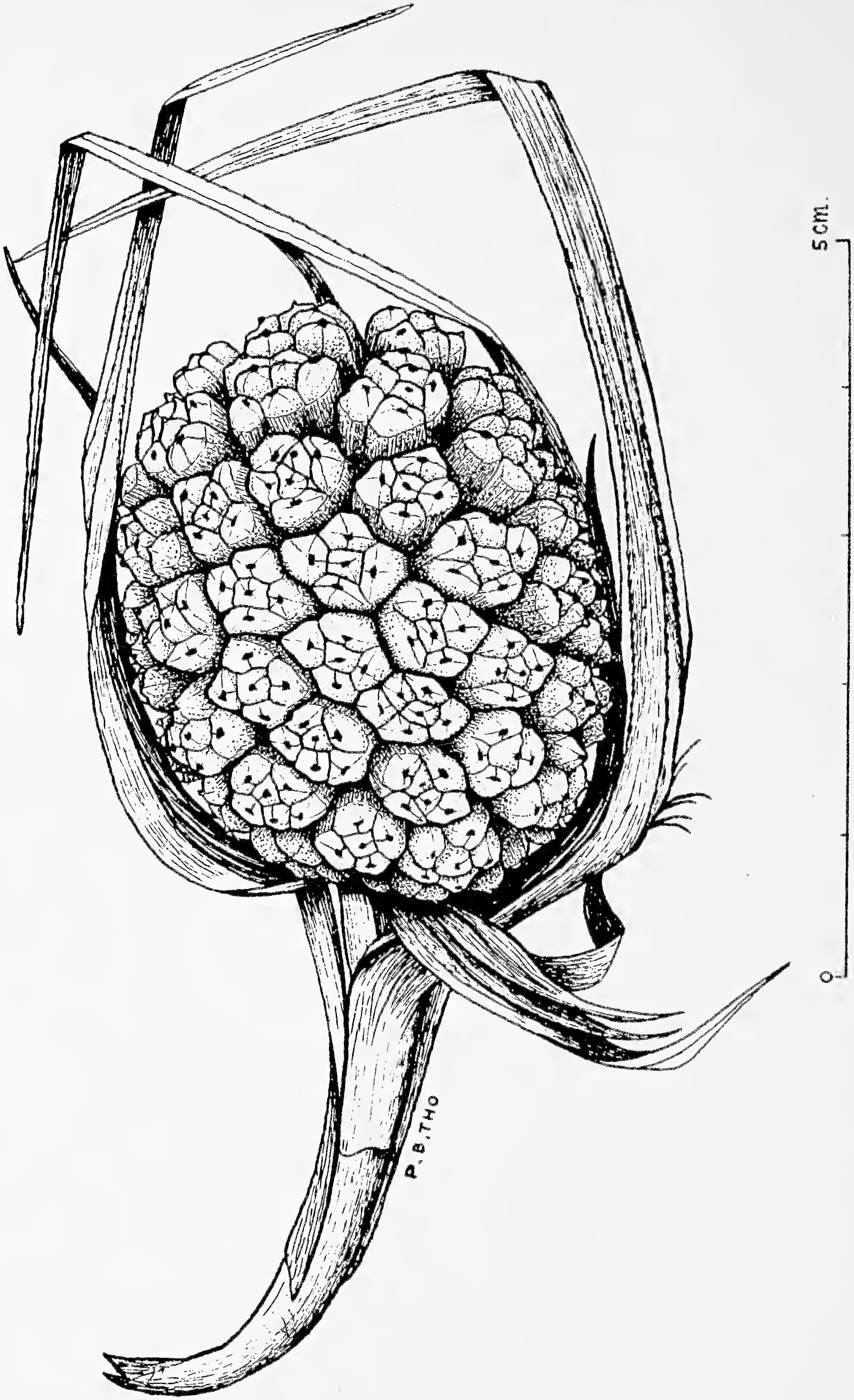

FIG. 80. *Pandanus reversispiralis,* from holotype. Syncarp, lateral view, × ½.

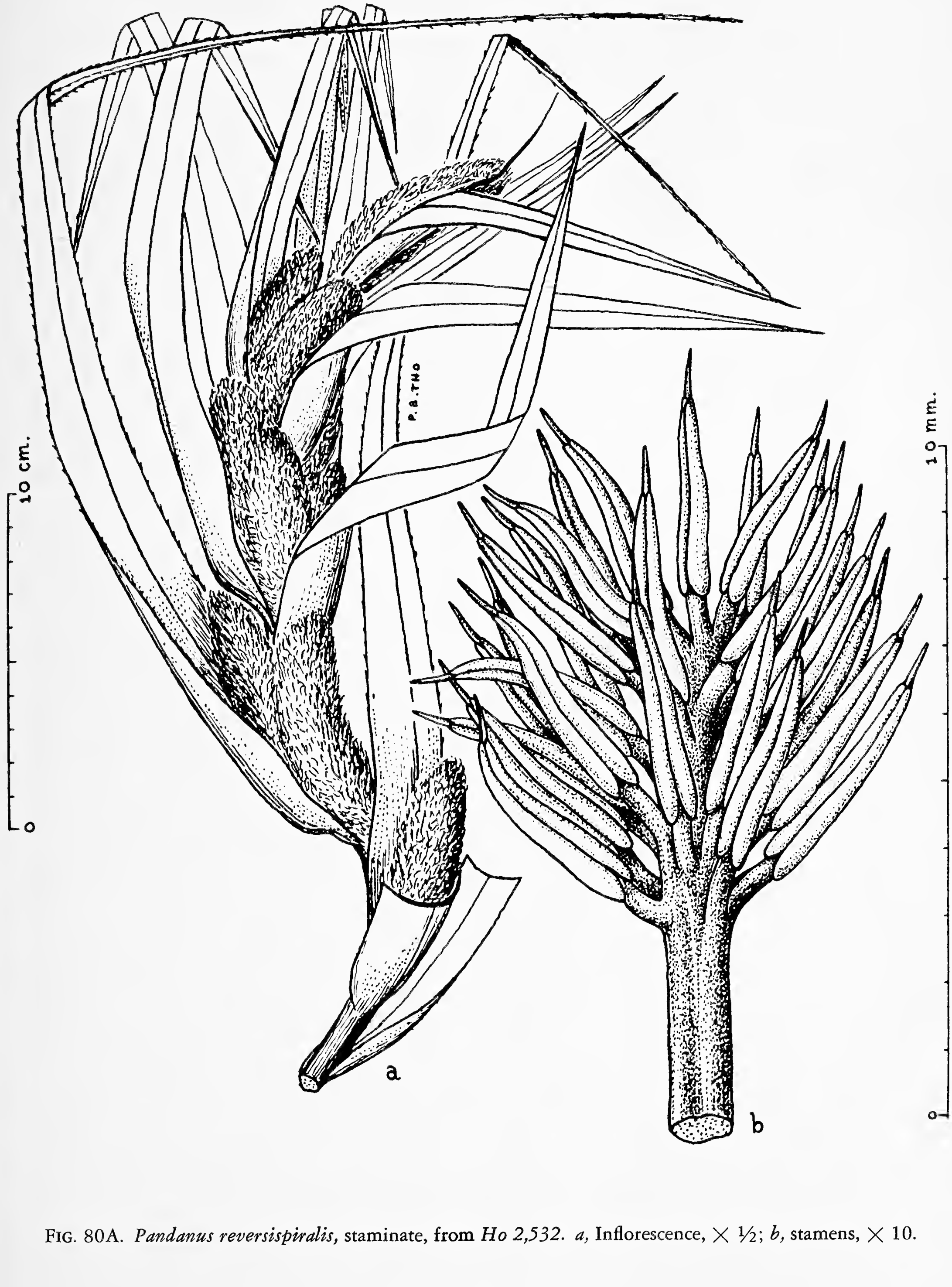

FIG. 80A. *Pandanus reversispiralis,* staminate, from *Ho 2,532. a,* Inflorescence, × ½; *b,* stamens, × 10.

floral bract 50 cm. long, 4.2 cm. wide, the lower half narrowly elliptic, of this its lower half narrowly elliptic, unarmed, its upper half with the margins with prickles 1.5–1.8 mm. long, 3–6 mm. apart, acicular, appressed ascending, white; the upper half long slender subulate, towards the apex the margins unarmed but the midrib below minutely subulate serrulate; median floral bract 25 cm. long, 28 mm. wide, narrowly oblong-lanceolate, the margins with prickles 0.7–1.3 mm. long, 1–2 mm. apart, acicular, ascending, white; at midsection the midrib below with subulate serrulations 0.2–0.3 mm. long, 0.3–1 mm. apart; spikes about 15, fragrant, 5–7 cm. long, 2–2.5 cm. in diameter, dense; staminal fascicles 14–16 mm. long, with about 25 anthers, the naked common column 6–7 mm. long; free filament tips 0.8–1.5 mm. long; anthers 2.5–4 mm. long, 0.5 mm. wide, subulate, at base slender auriculate, at apex bearing a subulate projection of the connective 0.7–0.9 mm. long.

HOLOTYPUS: Vietnam, Cap St. Jacques, Corniche d'Oguăn, granite ledges above beach, Jan. 3, 1960, *H. St. John 26,327* (BISH).

SPECIMENS EXAMINED: Vietnam, Cap St. Jacques, Báisau, moist dune hollow, Jan. 3, 1960, *H. St. John 26,326* (BISH); Hòn Tho'm, ile s. de Phu Qu'ôc, plage, bord de la mer, 7 avril 1961, *Pham Hoang Ho 2,531,* fruit (BISH); same data, *Ho 2,532,* staminate, (BISH); Phu Qu'ôc Ile, village Du'o'ng dtông, 6 avril 1961, *Pham Hoang Ho 2,533,* staminate, (BISH). The latter staminate specimen shows branch, leaves, and inflorescence. It matches the specimen of this species from the nearby islet Hòn Tho'm, but is more complete, having a stem 25 cm. long, 4 cm. in diameter which clearly shows by the axillary buds the reversal of phyllotaxy at each peduncle scar.

DISCUSSION: *P. reversispiralis* is a member of the section *Pandanus,* but none of the described species seem to be close relatives to it.

The new epithet is from the Latin, *reversus,* reversed; *spira,* a spiral, in allusion to the reversing spirals in its phyllotaxy. This phenomenon has recently been described and illustrated by the author (Univ. de Saigon, Fac. de Sci., Ann. 1960: 279, figs. 1–2, 1961).

Pandanus semiorbicularis sp. nov. (sect. *Pandanus*)

Figs. 73–75, 81–82

DIAGNOSIS HOLOTYPI: Arbor 6 m. alta 10 cm. diametro, cortice laeviore, radicibus fulturosis nullis vel paucis et ad 40 cm. longis 4 cm. diametro, foliis 85–94 cm. longis 4.5–5 cm. latis coriaceis glaucis in sectio M-formatis ligulatis sensim ad apicem subulatum diminuentibus eo in 10 cm. ex puncto 8 mm. lato, basi amplexicauli inermi sed ex 2.5–3 cm. marginibus cum spinis 2–4 mm. longis 5–14 mm. distantibus subulatis pallidis adscendentibus, midnervo cum spinis 2–2.5 mm. longis subulatis eis tribus inferioribus valde reflexis superioribus adscendentibus, in sectio medialis marginibus cum spinis 2–3 mm. longis 8–12 mm. distantibus graciliter subulatis valde adpressi-adscendentibus, midnervo cum spinis 2.5–3 mm. longis 12–18 mm. distantibus subulatis adscendentibus, circa apicem marginibus et midnervo infra acute serratis, dentibus 0.2–0.3 mm. longis 3–5 mm. distantibus brunneis, pedunculo 31 cm. longo obtuse trigono folioso, syncarpio solitario terminali 17 cm. longo 14.5 cm. diametro 86 phalangibus ferrentibus eis 4.5–5 cm. longis 2.5–4.3 cm. latis 2.4–3.5 cm. crassis late obovoideo-cuneatis viridibus aurantescentibus, lateribus infra laevibus supra rugulosis planis vel subcurvatis, 7–13-angulosis, parte tertia supera libera, apice subconvexo, suturis lateralibus angustis sed in parte ⅔ supera distinctis sinis apicalibus centralibus 5–9 mm. profundis angustis, carpellis 5–10, plerumque 7–8, apicibus semiorbiculari- vel oblato-pyramidalibus, stigmatibus 2–3 mm. longis cordatis vel suborbicularibus brunneis sulcatis inclinatis centripetalibus, sutura proximali profunda ad basem ¼–½ extenta, endocarpio paene supramediali osseoso pallide brunneo intra lucido mahogani-brunneo marginibus 3 mm. crassis, seminibus 12–16 mm. longis 5 mm. diametro ellipsoideis, mesocarpio apicali in quaque carpella 8–17 mm. longo cavernoso et solum cum membranis albis medullosis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 6 m. tall, 10 cm. in diameter; bark very smooth; prop roots none or few up to 40 cm. long, and 4 cm. in diameter; leaves 85–94 cm. long, 4.5–5 cm. wide, coriaceous, glaucous, ligulate, in section

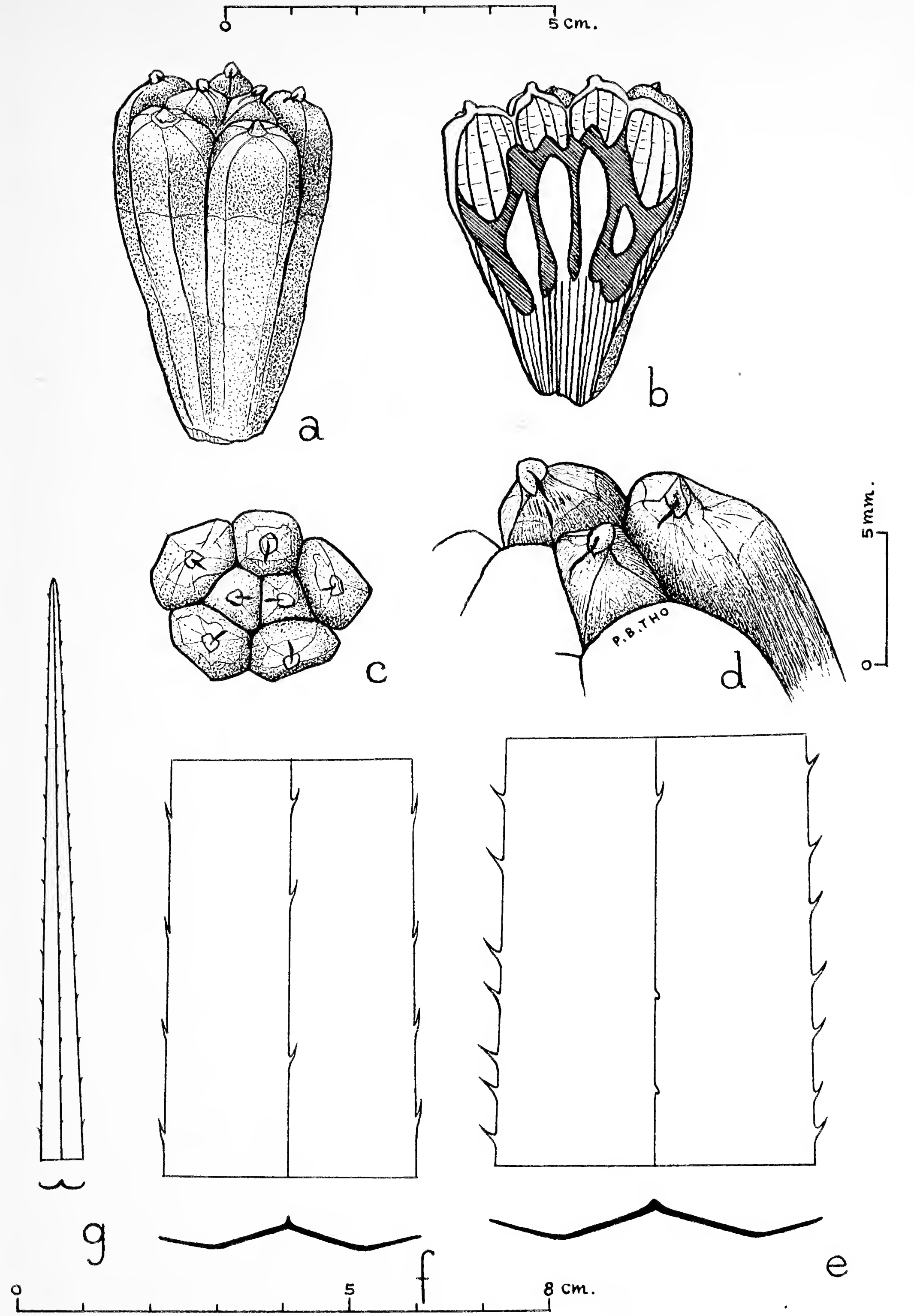

FIG. 81. *Pandanus semiorbicularis,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, oblique view, × 2; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

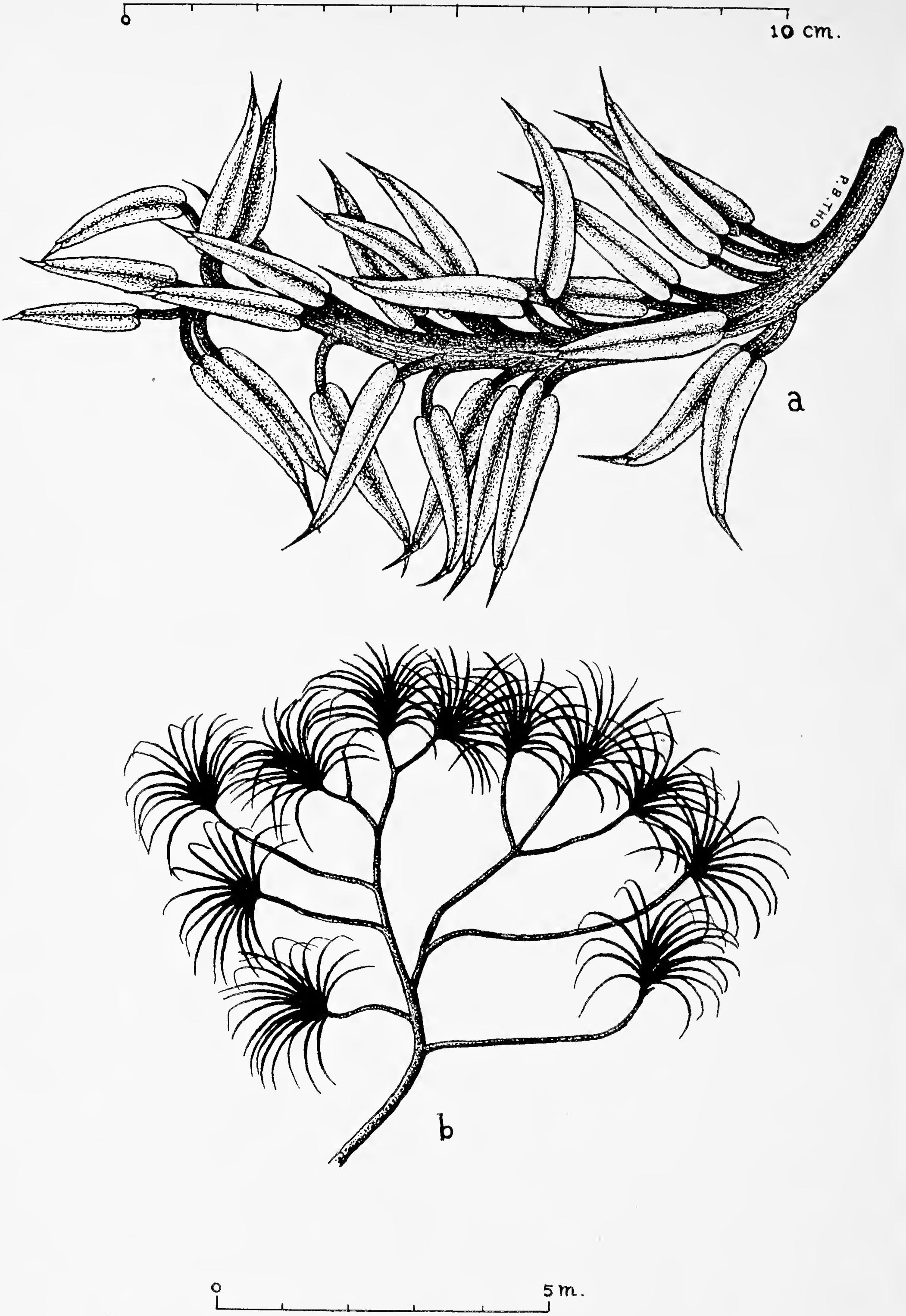

FIG. 82. *Pandanus semiorbicularis,* from paratype. *a,* Staminal column, × 10; *b,* profile of tree, × $\frac{1}{10}$.

M-shaped, gradually tapering to the subulate apex, this 10 cm. down only 8 mm. wide, the enclosed base amplexicaul and unarmed, but beginning 2.5–3 cm. up the margins with spines 2–4 mm. long, 5–14 mm. apart, subulate, pale, ascending, the nearby midrib with spines 2–2.5 mm. long, subulate, broader based, the three lowest sharply reflexed, the upper ascending; near the midsection the margins with spines 2–3 mm. long, 8–12 mm. apart, slender subulate, closely appressed ascending; the midrib with spines 2.5–3 mm. long, 12–18 mm. apart, subulate, ascending; near the apex the margins and midrib below sharply serrate, the teeth 0.2–0.3 mm. long, 3–5 mm. apart, brown; peduncle 31 cm. long, in section obtusely triangular, leafy bracted; syncarps solitary, terminal, 17 cm. long, 14.5 cm. in diameter, of 86 phalanges, these 4.5–5 cm. long, 2.5–4.3 cm. wide, 2.4–3.5 cm. thick, broadly obovoid-cuneate, green, turning orange, sides smooth below, rugulose above, plane or gently curving, 7–13-angled, upper ⅓ free, apex low convex, lateral sutures narrow but distinct in upper ⅔; apical central sinuses 5–9 mm. deep, narrow; carpels 5–10, mostly 7–8, the apices semiorbicular- or oblate-pyramidal; stigmas 2–3 mm. long, suborbicular or cordate, brown, creased, inclined, centripetal; proximal crease deep, extending ¼–½ way to valley bottom; endocarp slightly supramedian, bony, light brown, the inner surfaces shining mahogany brown, the lateral margins 3 mm. thick; seeds 12–16 mm. long, 5 mm. in diameter, ellipsoid; apical mesocarp with a cavern 8–17 mm. long in each carpel, empty except for white medullar membranes; basal mesocarp fibrous and fleshy. Staminate trees (no. 26,337) of similar stature and herbage; inflorescence 30 cm. long, with many bracts, these white, the lowest 26 cm. long, long acuminate, the upper ones 5–9 cm. long, lanceolate, acute; staminate spikes 4–6 cm. long, 15–20 mm. in diameter, numerous; staminal columns many, 8–10 mm. long, tree-like, anther-bearing except at base; free filament tips 0.8–1 mm. long; anthers 2–3.3 mm. long, yellowish, linear lanceolate, the connective produced into a prominent apical acumen.

HOLOTYPUS: Vietnam, Cap Varella, Province of Khanh Hoa, coastal sand dunes, top of beach, with *Scaevola Taccada, Euphorbia* sp., *Thuarea involuta,* and *Spinifex* sp., Feb. 7, 1960, *H. St. John 26,338* (BISH).

SPECIMENS EXAMINED: Vietnam, Cap Varella, same locality and data, staminate tree, *H. St. John 26,337* (BISH).

DISCUSSION: *P. semiorbicularis* is a member of the section *Pandanus.* Its closest relative is *P. tectorius* Soland. var. *Loureiri* (Gaud.) Martelli, from Tourane, Vietnam, but this is incompletely known only on the basis of a single phalange collected by Gaudichaud. It has the phalange 3.7 cm. long, short pyriform; carpel apices low convex, the central apical sinuses apparently 2–3 mm. deep. In contrast, *P. semiorbicularis* has the phalanges 4.5–5 cm. long, broadly obovoid-cuneate; carpel apices semiorbicular or oblate-pyramidal; and the central apical sinuses 5–9 mm. deep.

The new epithet is the Latin adjective, *semiorbicularis,* half orbicular, in reference to the shape of the carpel apices.

Pandanus Smitinandii sp. nov. (sect. *Pandanus*)

Figs. 76, 83

DIAGNOSIS HOLOTYPI: Arbor 2–3 m. alta 10 cm. diametro, trunco furcato distorto cum aculeis paucis quibusdam adpressi-adscendentibus, radicibus fulturosis ad 1 m. longis, foliis 1–1.15 m. longis 4.3–4.8 cm. latis coriaceis ligulatis gradatim diminuentibus in apice longe subulato eo in 10 cm. ex apice 2–2.5 mm. lato, basi inermi et amplexicauli sed ex 3.5–7 cm. marginibus cum spinis 3–4.5 mm. longis 5–15 mm. distantibus crassiter subulatis arcuatis adscendentibus stramineis, midnervo infra cum spinis reflexis 3 mm. longis 11–25 mm. distantibus, in sectio medialis marginibus cum spinis 2–3 mm. longis 3–12 mm. distantibus subulatis adscendenti-subadpressis, midnervo infra cum spinis simulantibus adscendentibus 14–20 mm. distantibus, circa apicem marginibus cum spinis 0.2–0.3 mm. longis 3–5 mm. distantibus valide subulatis divergentibus, eis midnervo infra simulantibus sed 2–5 mm. distantibus, pedunculo 17 cm. longo obtuse triangulari folioso, syncarpio 14 cm. longo 11.5 cm. diametro late ovoideo solitario terminali pendenti cum 72 phalangibus, eis adhuc viridibus sed amplitudinibus plenis et basi lutescenti 4–4.3 cm. longis

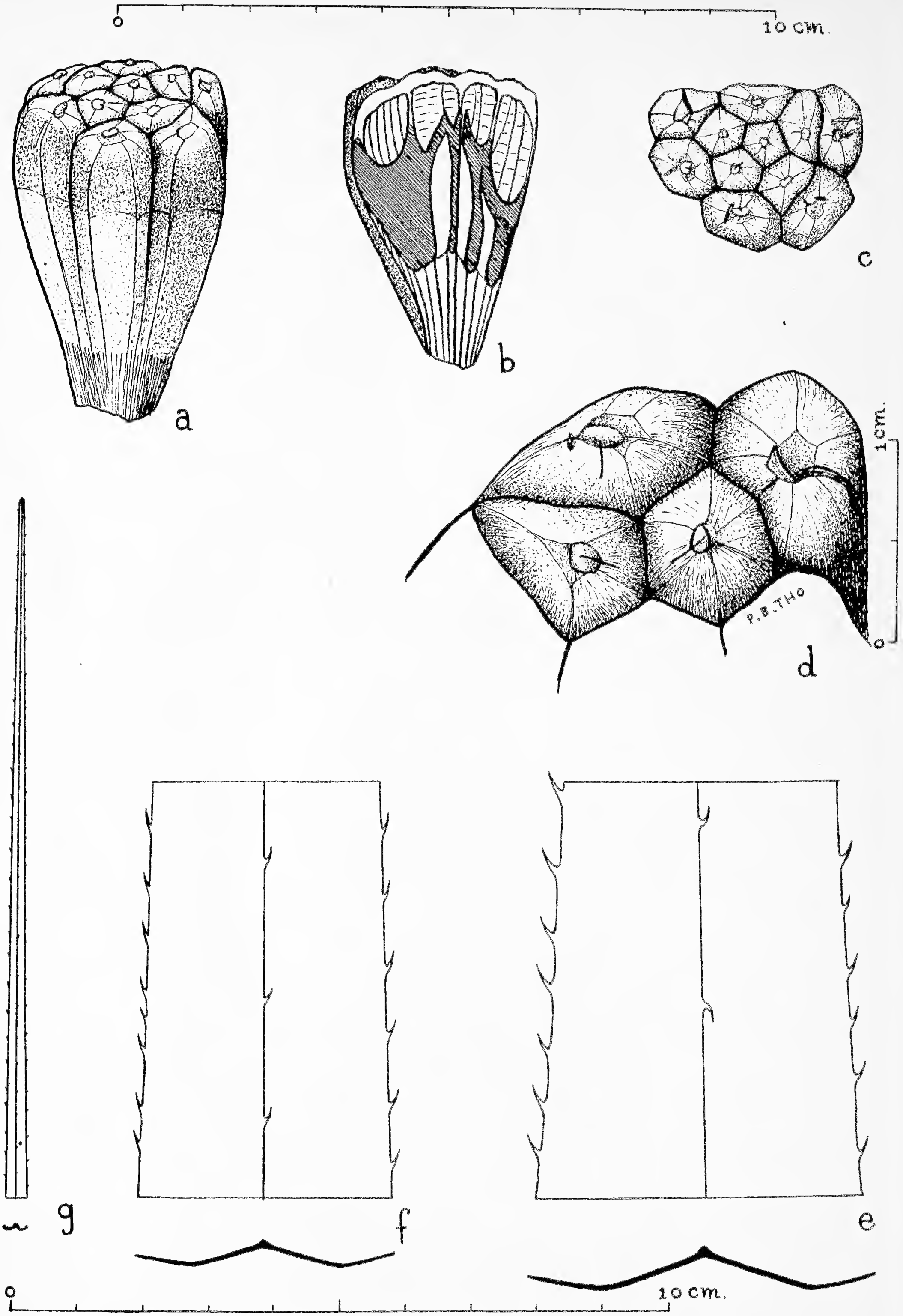

FIG. 83. *Pandanus Smitinandii,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, oblique view, × 3; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

2.5–3 cm. latis 2.1–3.1 cm. crassis late cuneatis parte ¼ supera libera apice depresso convexo lateribus laevibus sublucidis planatis vel subcurvatis 7–10-angulatis suturis lateralibus nullis vel paucis in media supera, sinibus centralibus apicalibus 2–3 mm. profundis V-formatis, carpelis 6–12, plerumque 8–9, apicibus depresso-pyramidalibus, stigmatibus 1–2 mm. longis suborbicularibus ad cordatis obliquis centripetalibus, sutura proxima profunda dimidia distanciae ad fondam extenta, endocarpio paene supramediali osseoso pallide brunneo pagina interiori lucida brunnea marginibus lateralibus 2–3 mm. crassis, seminibus 14–16 mm. longis 2–3 mm. diametro anguste ellipsoideis, mesocarpio apicali in carpella quaque cavernoso 10–15 mm. longo cum fibris longitudinalibus paucis sed cum membranis medullosis albis multis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 2–3 m. tall, 10 cm. in diameter; trunk forked, crooked, with sparse prickles, some of them appressed ascending; prop roots up to 1 m. long; leaves 1–1.15 m. long, 4.3–4.8 cm. wide, coriaceous, ligulate, gradually tapering to a long subulate apex which 10 cm. back from the tip is 2–2.5 mm. wide, the base unarmed and amplexicaul, but from a point 3.5–7 cm. up, the margins with spines 3–4.5 mm. long, 5–15 mm. apart, stout subulate, arcuate ascending, stramineous, the nearby midrib below with reflexed spines 3 mm. long, 11–25 mm. apart; at the midsection the margins with spines 2–3 mm. long, 3–12 mm. apart, subulate ascending-subappressed; the midrib below with similar, ascending spines 14–20 mm. apart; near the apex the margins with spines 0.2–0.3 mm. long, 3–5 mm. apart, stout subulate, divergent; those of the midrib below similar but 2-5 mm. apart; peduncles 17 cm. long, obtusely triangular in cross section, leafy bracted; syncarp 14 cm. long, 11.5 cm. in diameter, broadly ovoid, solitary, terminal, pendent, of 72 phalanges, these still green, but apparently full sized and the lower part turning yellowish, 4–4.3 cm. long, 2.5–3.3 cm. wide, 2.1–3.1 cm. thick, broad cuneate, upper ¼ free, apex low convex, sides smooth, somewhat shiny, plane or gently curved, 7–10-angled, lateral sutures none or few in upper half; apical central sinuses 2–3 mm. deep, V-shaped; carpels 6–12, mostly 8–9, the apices much flattened pyramidal; stigmas 1–2 mm. long, suborbicular to cordate, oblique, centripetal; the proximal crease deep, extending ½ way to the valley bottom; endocarp slightly supramedian, bony, light brown, but the inner surface shining brown, the lateral margins 2–3 mm. thick; seeds 14–16 mm. long, 2–3 mm. in diameter, narrowly ellipsoid; apical mesocarp cavernous in each carpel, 10–15 mm. long, with a few longitudinal fibers but many white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Vietnam, near Qua'ng Ngãi, 94 km. s. of Touranne (Da Nang), common on dunes and sandy soil along the road, 2 m. alt., 12 Feb. 1960, *Tem Smitinand 6,427* (BISH).

DISCUSSION: *P. Smitinandii* is a member of the section *Pandanus* and finds there as its closest relative *P. subulatus* St. John of Vietnam, which species has the bark with a few appressed ascending adventitious rootlets; leaves 70–74 cm. long, 4 cm. wide and with the marginal spines near the base 5–6 mm. long; phalanges 3.5–4.1 cm. long, the sides 5–7-angled; carpels 5-6; and the seeds 8–11 mm. long, 4.5 mm. in diameter. In contrast *P. Smitinandii* has the bark only with sparse prickles; leaves 100–115 cm. long, 4.3–4.8 cm. wide, the marginal spines near the base 3–4.5 mm. long; phalanges 4–4.3 cm. long, the sides 7–10-angled; carpels 6–12; and the seeds 14–16 mm. long, 2–3 mm. in diameter.

The new epithet is given in honor of Mr. Tem Smitinand, chief of the section of Botany and Zoology, Royal Forest Department, Thailand.

Pandanus subcarnosus sp. nov. (sect. *Pandanus*)

Figs. 77–78, 84

NOM. VERN.: "dua".

DIAGNOSIS HOLOTYPI: Arbor 2–3 m. alta 15 cm. diametro, cortice laeve, radicibus fulturosis nullis, foliis 99–113 cm. longis 3.7–4 cm. latis subcoriaceis ligulatis sed sensim ad apicem longam subulatam diminuentibus eo 10 cm. ex puncto 3 mm. lato, 3–6 cm. ex basi marginibus armatis spinis 2–3.5 mm. longis 4–10 mm. distantibus albis subulatis adscendentibus, midnervo infra cum spinis 2–3 mm. longis 15–20 mm. distantibus subulatis, eis tribus reflexis alteris adscendentibus, circa mediam marginibus cum spinis 2–3 mm. longis 6–12 mm. distantibus

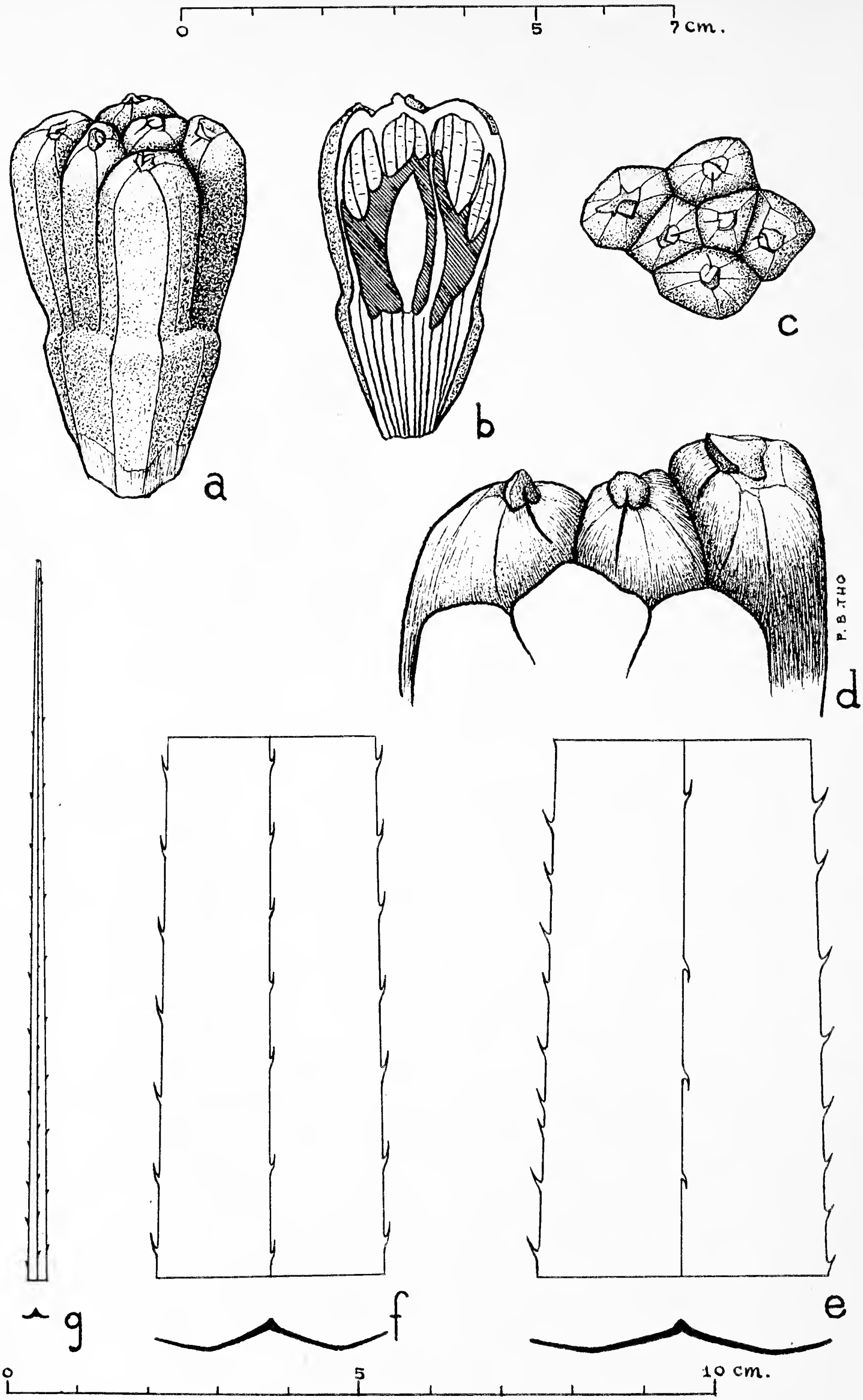

FIG. 84. *Pandanus subcarnosus,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, oblique view, × 3; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

subulatis adpressi-adscendentibus, midnervo infra cum spinis 2 mm. longis gracilibus subulatis albis adpressi-adscendentibus, ad apicem marginibus midnervoque infra cum subulato-serris 0.3–0.5 mm. longis 5–15 mm. distantibus, pedunculo 20 cm. longo obtuse deltoideo folioso, syncarpio terminale solitario 16 cm. longo 14 cm. diametro late ovoideo aurantiaco (colore 196, tab. XIV, Seguy, E., Code Univ. Couleurs, 1936) 84 phalangibus ferrentibus, eis 4.5–4.9 cm. longis 2.6–4.2 cm. latis 2.2–2.9 cm. crassis, oblongis vel ad formam cuneato-oblongam variantibus, parte supera 3/5 libera, parte 2/5 infera carnosa incrassata, apice plerumque paene convexo sed rariter truncato, lateribus laevibus lucidis planis sed ad apicem subcurvatis 5–9-angulosis, suturis lateralibus nullis, sinibus apicalibus centralibus 3–5.5 mm. profundis angustis, carpellis 6–10, plerumque 7–8, apicibus oblato-pyramidalibus exterioribus plerumque cum concavito parvo obliquo subterminali distali, stigmatibus 1.5–2.5 mm. longis obliquis centripetalibus breve sulcatis suborbicularibus, eis marginalibus cum galea cartilaginea inflexa semitectis, sinu proximo profundo ½–¾ distancia ad fondam extento, endocarpio paene supramediale osseoso lucido mahogani-brunneo lateribus 2–3 mm. latis, seminibus 16 mm. longis 5–6 mm. diametro ellipsoideo, mesocarpio apicali cavernoso pauce fibroso et cum membranis albis medullosis repleto, endocarpio basali fibroso et carnoso luteo.


FIG. 85. *Pandanus subulatus.* Habit of holotype.

FIG. 86. *Pandanus vietnamensis,* from holotype. Foliage and branches with syncarps.

DIAGNOSIS OF HOLOTYPE: Tree 2–3 m. tall, 15 cm. in diameter, but the clumps apparently repeatedly cut back by the people of the vicinity; bark smooth; prop roots none; leaves 99–113 cm. long, 3.7–4 cm. wide, subcoriaceous, ligulate, but tapering gradually to the long subulate tip, this at 10 cm. back from the apex 3 mm. wide, near the base the margins spiny beginning 3–6 cm. from the base, the spines 2–3.5 mm. long, 4–10 mm. apart, white, stout subulate, ascending, the nearby midrib below with spines 2–3 mm. long, 15–20 mm. apart, subulate, the first three reflexed, the others ascending; near the middle the margins with spines 2–3 mm. long, 6–12 mm. apart, subulate, appressed ascending, the midrib below with spines 2 mm. long, slender subulate, white, appressed ascending, near the apex the margins and midrib below with subulate serrations 0.3–0.5 mm. long, 5–15 mm. apart; peduncle 20 cm. long, obtusely triangular in cross section, leafy bracted; syncarps terminal, solitary, 16 cm. long, 14 cm. in diameter, broadly ovoid, orange (color no. 196, pl. XIV, Seguy, E., Code Universel de Couleurs, 1936, Paris, Paul Lechevalier), of 84 phalanges, these 4.5–4.9 cm. long, 2.6–4.2 cm. wide, 2.2–2.9 cm. thick, oblong to cuneate-oblong, upper 3/5 free due to the fleshy enlargement of the lower 2/5, the apex mostly slightly convex but on a few truncate, the sides smooth, shining, plane except where gently curved near the apex, 5–9-angled, lateral sutures none; apical central sinuses 3–5.5 mm. deep, narrow; carpels 6–10, mostly 7–8, the apices oblate pyramidal, the outer mostly with a small, oblique, distal, subterminal concavity; stigmas 1.5–2.5 mm. long, oblique, centripetal, short creased, suborbicular, the marginal ones partly covered by a cartilaginous inflexed visor; the proximal crease deep and extending ½–¾ way to the valley bottom; endocarp placed slightly above the middle, bony, shining mahogany brown, the lateral margins 2–3 mm. thick; seeds 16 mm. long, 5–6 mm. in diameter, ellipsoid; apical mesocarp cavernous in each carpel, traversed by a few strong, longitudinal fibers and filled with white medullary, membranous partitions; basal mesocarp fibrous and fleshy, yellowish.

HOLOTYPUS: Vietnam, Nha Trang, on sand dunes back of the beach, common, forming clumps, growing with *Calotropis gigantea, Randia prostrata, Dodonaea viscosa,* and *Zoisia pungens,* Feb. 8, 1960, *H. St. John 26,341* (BISH).

DISCUSSION: This new *P. subcarnosus* is a member of the section *Pandanus,* and there its closest relative is the Philippine *P. coronatus* Merr. which is characterized by having the leaves 14 cm. wide (juvenile); syncarps globose, of about 50 phalanges; phalanges 3.5 cm. long, 2.5–3 cm. wide, the base with a fleshy enlargement 5 mm. or more wide on each side; carpels 9–12, the apices conic; and the stigmas erect or some of them oblique, 0.5 mm. long. In contrast, *P. subcarnosus* has the leaves 3.7–4 cm. wide; syncarps broadly ovoid, of 84 phalanges, phalanges 4.5–4.9 cm. long, 2.6–4.2 cm. wide, the basal fleshy enlargement only 1–2 mm. wide on each side; carpels 6–10, mostly 7–8, the apices oblate-pyramidal; and the stigmas oblique, 1.5–2.5 mm. long.

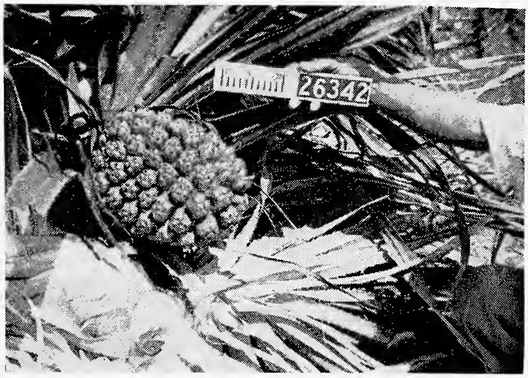

FIG. 87. *Pandanus vietnamensis,* from holotype. Foliage and syncarp, lateral view.

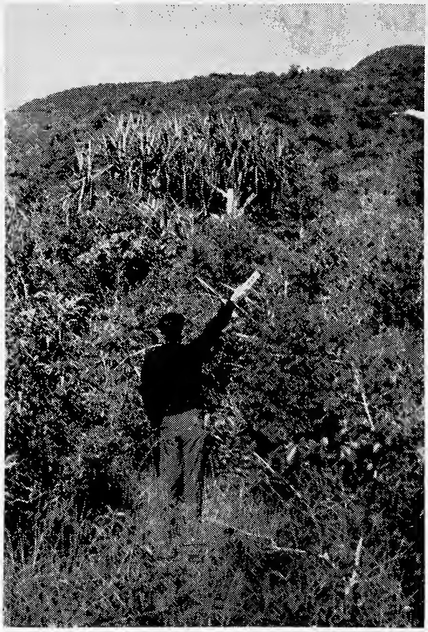

FIG. 88. *Pandanus corniferus,* from holotype. Habit view of tree.

Pandanus subulatus sp. nov. (sect. *Pandanus*)
Figs. 85, 92

DIAGNOSIS HOLOTYPI: Arbor 2–4 m. alta 12–15 cm. diametro, cortice cum radicibus paucis adventiviis adpressi-adscendentibus, radicibus fulturosis 30–50 cm. longis 15–20 cm. diametro, series foliarum supra quidque pedunculam cum serie bractearum, bractea prima 9 cm. longa 5 cm. lata, bracteis in foliis mergentibus, foliis 70–74 cm. longis 4 cm. latis coriaceis minime glaucis olivaceis V-formatis ligulatis sed ex tertia parte infera ad apicem longe subulatam diminuentibus in puncto 10 cm. ex apice 3.5 mm. latis, marginibus ad basem cum spinis 5–6 mm. longis 6–12 mm. distantibus subulatis albis in 45° adscendentibus, midnervo infra cum spinis 3–4 mm. longis 12–20 mm. distantibus albis crassiter subulatis reflexis, circa mediam marginibus cum spinis omnibus longis vel in uno latere longis brevibusque alternatis 2–5 mm.

longis 6–10 mm. distantibus subulatis adpressi-adscendentibus, spinis in midnervo 2–3.5 mm. longis 7–15 mm. distantibus adscendentibus, circa apicem marginibus et midnervo infra cum spinis 0.5–0.8 mm. longis 3–5 mm. distantibus subulato-serratis, pedunculo foemineo 15–20 cm. longo obtuse triangularibus bracteatis, syncarpiis 10–12 cm. longis 10–10.5 cm. diametro solitariis terminalibus pendentibus aurantescentibus suborbiculari-ellipticis cum 47–73 phalangibus eis 3.5–4.1 cm. longis 2.2–3.3 cm. latis 1.8–2.3 cm. crassis obovoideo-cuneatis vel anguste ita, lateribus laevibus planis vel minime curvatis parte supera pauce rugulosa et cum fissuris longitudinalibus brevibus brunneis multis, 5–7-angulatis, suturis lateralibus nullis, apice truncato, sinibus apicalibus centralibus 2–3.5 mm. profundis V-formatis, carpellis 5–6, plerumque 5, apicibus pyramidalibus vel oblato-pyramidalibus quando marginalibus et cum angulo forte tum stigmate terminale cum concavo distali minimo, sed carpella marginali cum latere plano grandi stigmate marginali, stigmatibus 1.5–2 mm. longis nigris suborbicularibus vel cordatis sulcatis obliquis et centripetalibus, sinu proximali profundo et ⅓–⅔ distancia ad fundam extenso, endocarpio paene supramediale 13–15 mm. longo osseoso brunneo marginibus 1.5–2 mm. latis, seminibus 8–11 mm. longis 4–5 mm. diametro obliquiter ellipsoideis, mesocarpio apicale cavernoso 8–13 mm. longo exfibroso sed cum membranis albis medullosis multis, mesocarpio basali fibroso et carnoso.

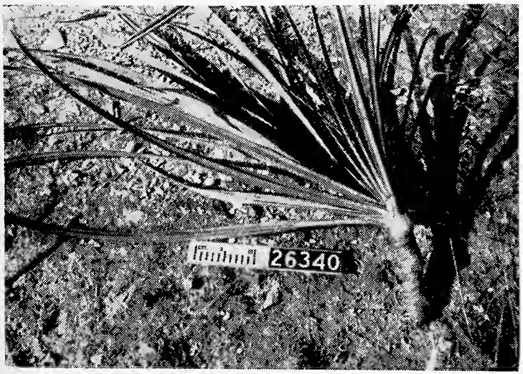

Fig. 89. *Pandanus corniferus,* from holotype. Lateral view of branch and foliage.

Fig. 90. *Pandanus corniferus,* from holotype. Young vigorous shoot showing foliage.

DIAGNOSIS OF HOLOTYPE: Tree 2–4 m. tall, 12–15 cm. in diameter; bark with a few, appressed-ascending, adventitious roots; prop roots 30–50 cm. long, 15–20 mm. in diameter; leaf series beginning above each peduncle with an entire deltoid bract 9 cm. long, 5 cm. wide, the successive several bracts each larger and the later ones spiny, merging in series to the foliage leaves, these 70–74 cm. long, 4 cm. wide, coriaceous, somewhat glaucous on both sides, especially towards the base, olive green, at base wide V-shaped in section, ligulate, but gradually narrowing from the lower third to a long subulate apex which 10 cm. back from the tip is 3.5 mm. wide, the margins spiny beginning 4 cm. from the base, the spines near the base 5–6 mm. long, 6–12 mm. apart, white, subulate, ascending at 45°, the midrib below with spines 3–4 mm. long, 12–20 mm. apart, white, stout subulate, reflexed; at the middle the marginal spines all long, or on one margin alternately long and short, 2–5 mm. long, 6–10 mm. apart, subulate, appressed ascending, those of the midrib 2-3.5 mm. long, 7–15 mm. apart, ascending; near the apex the margins and midrib below with spines 0.5–0.8 mm. long, 3–5 mm. apart, subulate-serrate; pistillate peduncle 15–20 cm. long, in cross section obtusely triangular, leafy bracted;

syncarps solitary, terminal, pendent, becoming orange, 10–12 cm. long, 10–10.5 cm. in diameter, suborbicular-elliptic, of 47–73 phalanges, these 3.5–4.1 cm. long, 2.2–3.3 cm. wide, 1.8–2.3 cm. thick, obovoid-cuneate or narrowly so, turning orange, sides smooth, plane or gently curving, upper part slightly rugulose, and with numerous short, brown, longitudinal cracks, 5–7-angled; lateral sutures none, apex truncate; apical central sinuses 2–3.5 mm. deep, the valley V-shaped; carpels 5–6, usually 5; the apices pyramidal or oblate-pyramidal, if the carpel is marginal and including a strong lateral angle, then the stigma is terminal and central and outside it is a tiny concavity, but if the carpel centers by a flat side, the stigma is marginal and there is no concavity; stigmas 1.5–2 mm. long, black, suborbicular to widely cordate, creased, oblique and centripetal; the proximal crease deep, extending ⅓–⅔ way to the valley bottom; endocarp slightly supramedian 13–15 mm. long, bony, brown, the lateral margins 1.5–2 mm. thick; seeds 8–11 mm. long, 4–5 mm. in diameter, obliquely ellipsoid; apical mesocarp with a cavern in each carpel, 8–13 mm. long, free of fibers but with numerous white medullary membranous partitions; basal mesocarp fibrous and fleshy.

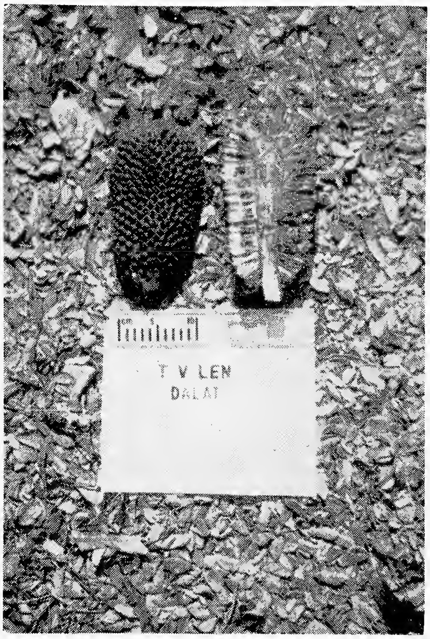

FIG. 91. *Pandanus multidrupaceus,* from holotype. Lateral view of syncarp.

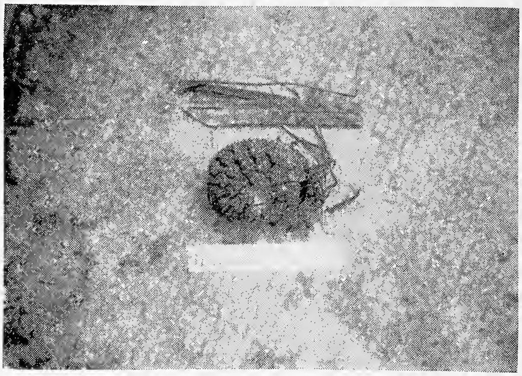

FIG. 91A. *Pandanus projectens,* from holotype. Lateral view of syncarp and leaf.

HOLOTYPUS: Vietnam, n. side of Hon Mieu I., Baie de Nha Trang, top of rocky beach, growing with *Scaevola Taccada,* and *Thespesia populnea,* Feb. 6, 1960, *H. St. John 26,331* (BISH).

DISCUSSION: *P. subulatus* is a member of the section *Pandanus.* Its closest relative seems to be *P. odoratissimus* L. f. var. *savaiiensis* (Martelli) Martelli of Samoa which has the leaves 60 cm. long, 1.5 cm. wide (juvenile?), the midrib below near the base with one or two or no spines; carpels 5–8, the apices pyramidal-subrotund; and the endocarp convex below. *P. subulatus* has, in contrast, the leaves 70–74 cm. long, 4 cm. wide, the midrib below near the base with spines 3–4 mm. long, 12–20 mm. apart, white, stout subulate, reflexed; carpels 5–6, usually 5, the apices pyramidal or oblate-pyramidal; and the endocarp concave below.

The new epithet is the Latin adjective, *subulatus,* awl-shaped, in allusion to the shape of the leaf apex.

Pandanus vietnamensis sp. nov. (sect. *Pandanus*)

Figs. 86, 87, 93

DIAGNOSIS HOLOTYPI: Arbor 3–5 m. alta 15 cm. diametro, radicibus fulturosis nullis, foliis 99.5–149 cm. longis 5–6 cm. latis olivaceis infra minime glaucis coriaceis ligulatis ex medio sensim ad apicem deltoideum longe subulatum diminuentibus eo in 10 cm. ex apice 1.5 mm. lato, basi amplexicaule inerme sed marginibus ex 5–11 cm. cum spinis 4–11 mm. longis 7–22

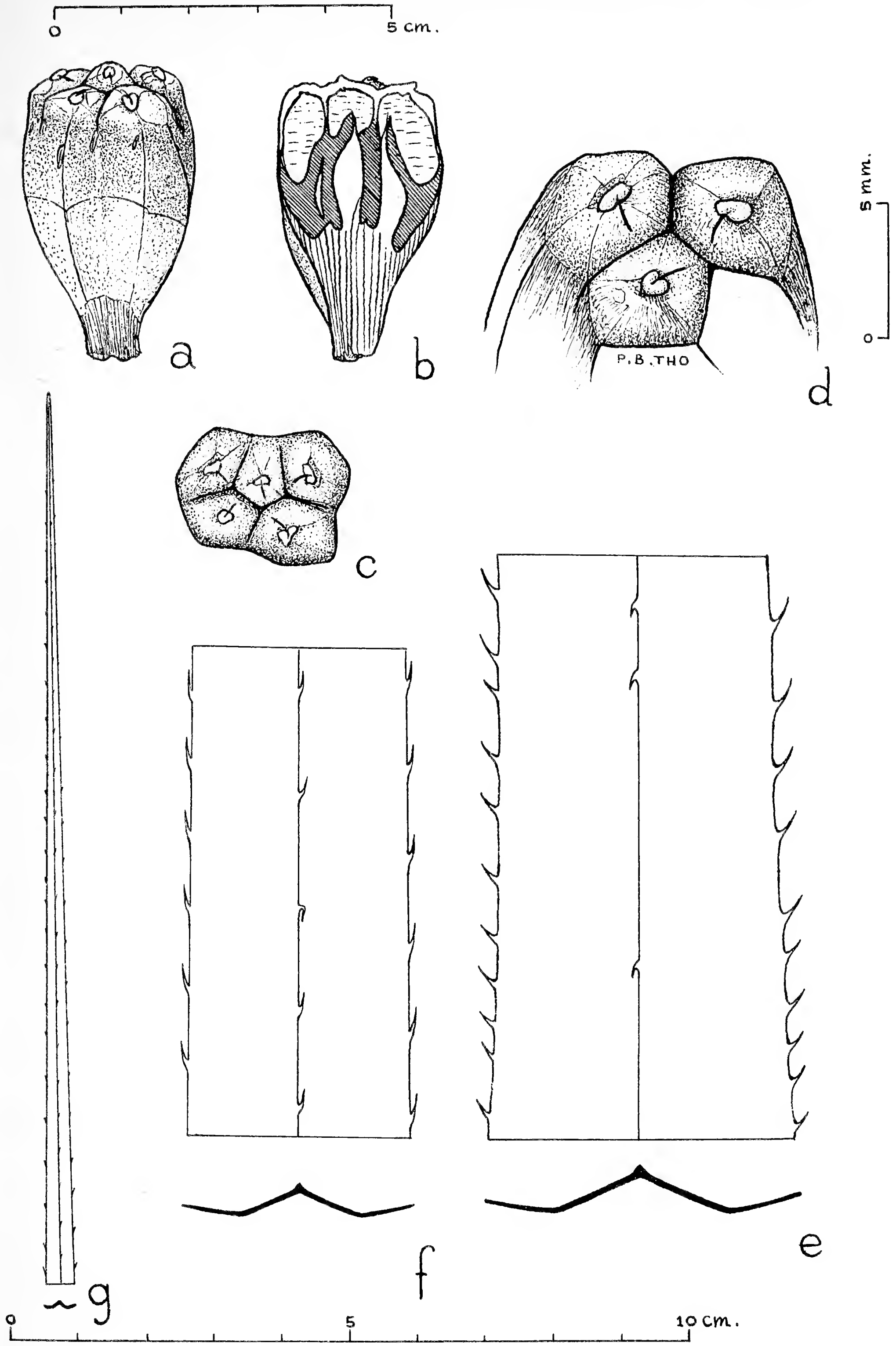

FIG. 92. *Pandanus subulatus,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, oblique view, × 2; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

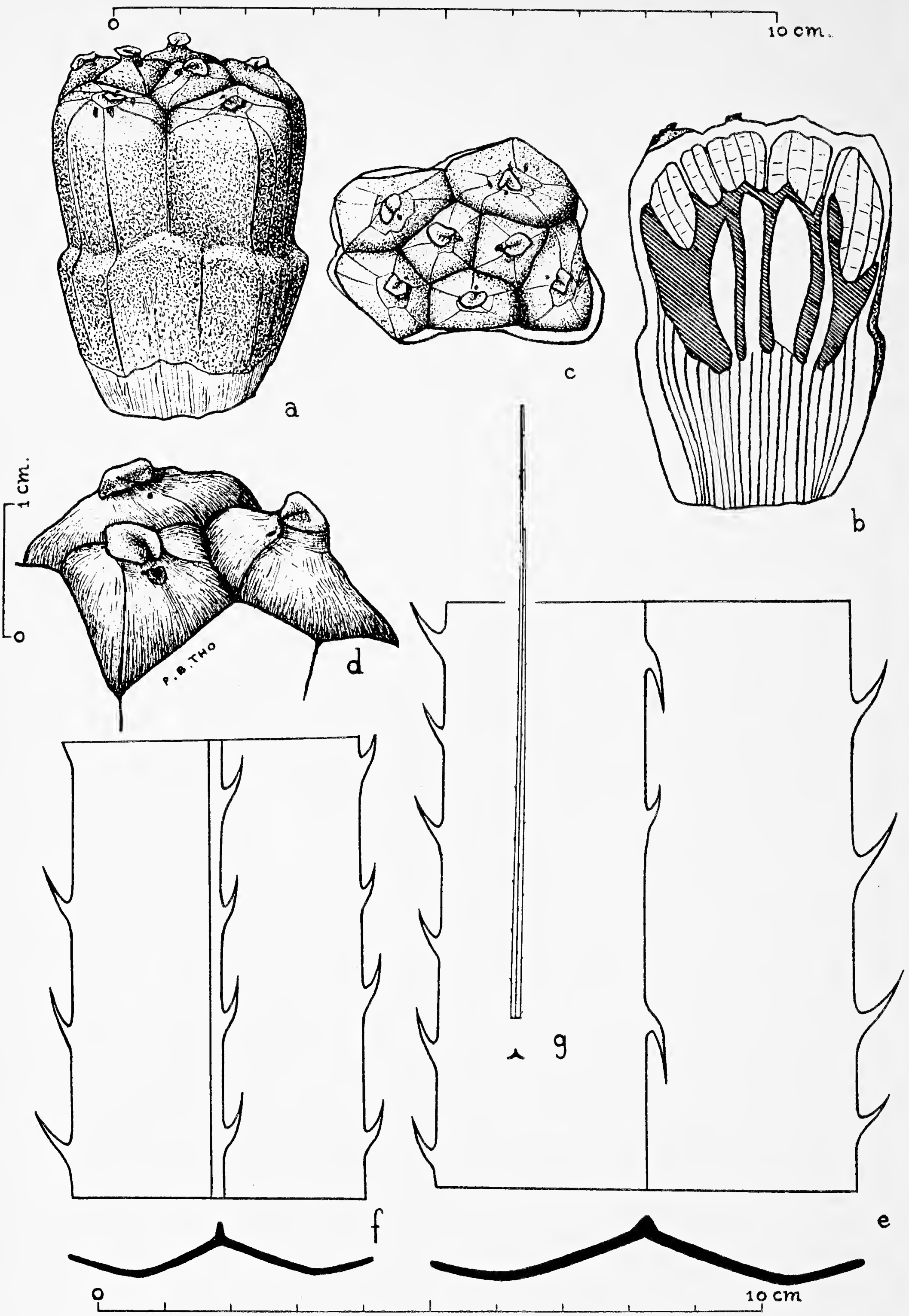

FIG. 93. *Pandanus vietnamensis,* from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, oblique view, × 2; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

mm. distantibus arcuatis subulatis albis adscendentibus, midnervo infra cum spinis 6–8 mm. longis 20–42 mm. distantibus subulatis reflexis basibus fortioribus, circa mediam marginibus sum spinis 6–8 mm. longis 12–25 mm. distantibus, midnervo infra cum spinis 6–8 mm. longis 12–25 mm. distantibus subulatis curvatis adscendentibus in nervo angusto elevato affixis, circa apicem marginibus cum spinis 0.5–0.9 mm. longis 5–11 mm. distantibus subulatis valde adpressis adscendentibus, midnervo subulato-serratis dentibus 0.3–0.5 mm. longis 5–8 mm. distantibus, pedunculo 30 cm. longo obtuse deltoideo folioso, syncarpio solitario terminali 27 cm. longo 19 cm. diametro coccineo (rouge no. 152, Seguy, E., Code Univ. Couleurs 1936) late ellipsoideo cum 106 phalangibus, eis 5.8–6 cm. longis, parte supera libera 3–4.2 cm. latis, 2.5–3.7 cm. crassis, parte infera 4–10 mm. latioribus et carnosa incrassata, suturis lateralibus nullis, lateribus dimidiae superae plerumque planis vel in parte subconcavis 7–9-angulosis, suturis centralibus apicalibus 1.5–3 mm. profundis angustis, carpelis 5–9 plerumque 6–7 apicibus plano-pyramidalibus, stigmatibus nigris 3.5–5 mm. longis vel latis ovalibus vel suborbicularibus vel ceteris lateralibus truncatis et latioribus quam longis sulcatis obliquis prominentibus centripetalibus, sinu proximo solum punctato vicino stigmati, endocarpio paene supramediali 2.7–3 cm. longo osseoso rubro-brunneo lateribus 1.5–2 mm. crassis, seminibus 20 mm. longis 6 mm. diametro ellipsoideis vel obliquiter ellipsoideis, mesocarpio apicali in carpela quaque cavernoso cum fibris fortibus paucis et cum membranis albis medullosis completis, mesocarpio basali fibroso carnosoque.

DIAGNOSIS OF HOLOTYPE: Trees 3–5 m. tall, 15 cm. in diameter; prop roots none; leaves 99.5–149 cm. long, 5–6 cm. wide, olive green, below slightly glaucous, coriaceous, ligulate, from the middle gradually tapering to the long acuminate, subulate, deltoid apex which 10 cm. down is only 1.5 mm. wide, the base amplexicaul, unarmed, but the margins beginning 5–11 cm. from the base with spines 4–11 mm. long, 7–22 mm. apart, arcuate, ascending, subulate, white; the nearby midrib below with spines 6–8 mm. long, 20–42 mm. apart, subulate, reflexed, heavier based; near the midsection the margins with similar spines 6–8 mm. long, 12–25 mm. apart, the sharp, raised midrib below with spines 6–8 mm. long, 12–25 mm. apart, subulate, curved, ascending; near the apex the margins with spines 0.5–0.9 mm. long, 5–11 mm. apart, subulate, ascending, closely appressed; the midrib subulate-serrate, the teeth 0.3–0.5 mm. long, 5–8 mm. apart; peduncle 30 cm. long, obtusely triangular in section, leafy bracted; syncarps terminal, solitary, 27 cm. long, 19 cm. in diameter, scarlet (or more exactly Rouge no. 152, pl. XI, Seguy, E., Code Universel des Couleurs, 1936, Paris, Paul Lechevalier), broad ellipsoid, of 106 phalanges, these 5.8–6 cm. long, the upper half 3–4.2 cm. wide, and 2.5–3.7 cm. thick, the lower half from 4–10 mm. wider and thicker due to its fleshy enlargement (which is color no. 152, shading down to yellow, or orange, no. 213, pl. XV), the upper half, or slightly more than half, free, apex low convex; lateral sutures none; sides of upper half mostly plane or in part gently concave, 7–9-angled, central apical sinuses 1.5–3 mm. deep, narrow; carpels 5–9, mostly 6–7, the apices flattened pyramidal; stigmas black, 3.5–5 mm. long or wide, oval to suborbicular, or some of the lateral ones truncate and wider than long, all creased, obliquely inclined and centripetal, prominent; proximal crease represented by a mere point or cut a short distance below the stigma; endocarp placed slightly above the center, 2.7–3 cm. long, bony, reddish brown, the lateral walls 1.5–2 mm. thick; seeds 20 mm. long, 6 mm. in diameter, ellipsoid or obliquely so; apical mesocarp of a cavern in the apex of each carpel, these traversed by a few strong fibers and filled with white medullary membranes forming an aerenchyma; basal mesocarp with many longitudian fibers and a white, tasteless flesh.

HOLOTYPUS: Vietnam, 6 km. e. of Mũí Nê, Phan Thiêt Province, clumps at top of beach, Feb. 9, 1960, *H. St. John 26,342* (BISH).

DISCUSSION: *P. vietnamensis* is a member of the section *Pandanus* and there finds its closest relative, *P. coronatus* Martelli of the Philippines, which species has its leaves 14 cm. wide and near midsection the marginal teeth 0.5–1 mm. long; syncarp globose, almost 14 cm. in diameter, with about 50 phalanges; phalanges 3.5 cm. long, 2.5–3 cm. wide; carpels 9–12 and

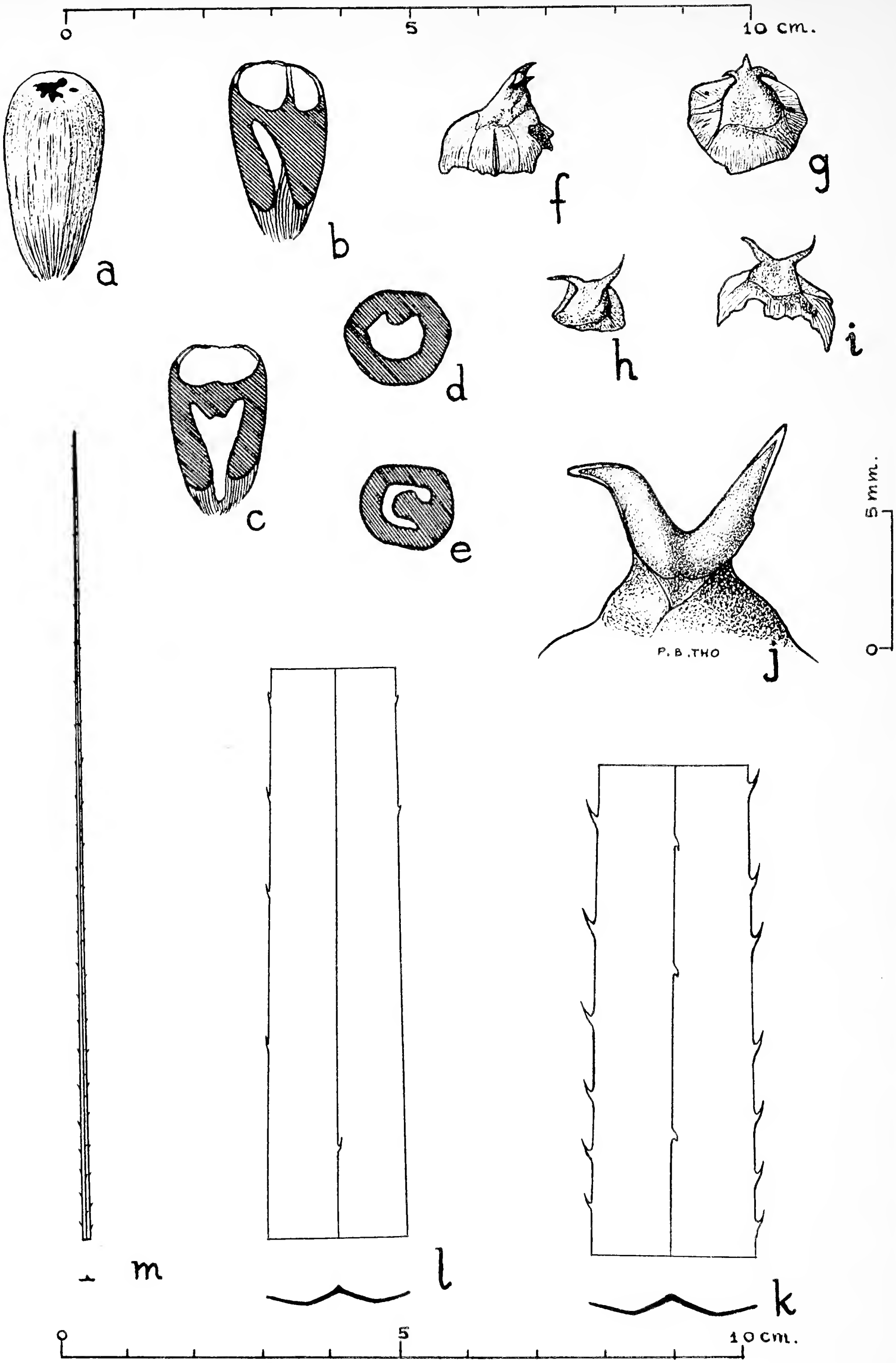

FIG. 94. *Pandanus corniferus,* from holotype. *a,* Drupe, minus the pileus, lateral view, × 1; *b, c,* drupe, longitudinal median section, × 1; *d,* drupe, median transverse section, × 1; *e,* supramedian transverse section of drupe, × 1; *f, g, h, i,* pileus with stigma, oblique view, × 1; *j,* stigma, lateral view, × 4; *k,* leaf base, lower side, × 1; *l,* leaf middle, lower side, × 1; *m,* leaf apex, lower side, × 1.

their apices obliquely conic; and the stigmas 2 mm. long. In contrast, *P. vietnamensis* has its leaves 5–6 cm. wide and near the midsection the marginal teeth 6–8 mm. long; syncarp broad ellipsoid, 27 cm. long, 19 cm. in diameter, of 106 phalanges; phalanges 5.8–6 cm. long, 3–4.2 cm. wide; carpels 5–9 and their apices flattened pyramidal; and the stigmas 3.5–5 mm. long.

The new epithet is formed of the name of the native country, Vietnam, plus *-ensis,* the Latin, adjectival, place ending.

Pandanus corniferus sp. nov. (sect. *Rykia*)
Figs. 88–90, 94

DIAGNOSIS HOLOTYPI: Arbor 5–8 m. alta 15 cm. diametro, cortice brunneo laevi, radicibus fulturosis multis ad 3 m. longis 1–2 cm. diametro pallide griseis laevibus sed cum radicibus spinis simulantibus verticillatis, foliis 1.81–1.87 m. longis 2.4–2.7 cm. latis obscure olivaceis crassis sed fragilibus supra late sulcatis ligulatis sed longiter diminuentibus in apice subulato deltoideo ad 10 cm. solum 0.9 mm. lato, marginibus cum spinis ex 45 mm. ex basi incipiendis eis 3–4 mm. longis 7–15 mm. distantibus subulatis adscendentibus pallidis, midnervo infra ex 9.5 cm. spinoso spinis 3.5–4 mm. longis 25–35 mm. distantibus subulatis basi distenta subiter reflexis, circa mediam marginibus subintegris, midnervo infra cum spinis paucis remotis 1.3 mm. longis subulatis adscendentibus apice brunneo, circa apicem marginibus et midnervo infra cum serris 0.2–0.3 mm. longis adpressis, foliis plantae juvenalis 1.81–1.87 m. longis 4 cm. latis cum apice longiori et spinis pauciter majori, syncarpiis quam dicunt "solitariis 20 cm. diametro (?) globoso rubro, drupis saccharosis edulibus sed celeriter irritantibus," drupis manifesto 32–35 mm. longis teretibus 14–16 mm. diametro ellipsoideis vel cuneato-ellipsoideis, pileo 15–20 mm. alto 15–19 mm. diametro semiorbiculari in apice ferrenti instrumentum stigmatalis 13–17 mm. longum in 45° obliquum parte libera 7–9 mm. longa dimidia bipartita, stylis 3–6 mm. longis subulatis divergentibus recurvatis, corpore druparum in sicco 20–29 mm. longo 12–17 mm. diametro stramineo vel pallide brunneo, endocarpio 14–16 mm. longo solido osseoso brunneo pauciter inframediali in media supera invaginata lateribus 3–4 mm. latis, seminibus 7–10 mm. longis 7 mm. diametro subteretibus, mesocarpio apicali unico cavernoso 6–7 mm. longo fibris nullis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Trees 5–8 m. tall, 15 cm. in diameter; bark brown, smooth; prop roots numerous, as much as 3 m. long from the trunk, 1–2 cm. in diameter, the bark light gray, smooth except for small, spine-like rootlets in remote whorls; leaves 1.8–1.87 m. long, 2.4–2.7 cm. wide, dark olive green, thick but the tissue weak and easily torn across, above with a wide central furrow, the margins reflexing, ligulate but long tapering to a slender subulate tip, deltoid in cross section and 10 cm. back from the tip only 0.9 mm. wide, the margins with spines commencing 45 mm. from the base, these 3–4 mm. long, 7–15 mm. apart, subulate, ascending, pale, the adjacent midrib below spiny beginning at 9.5 cm. from the base, the spines 3.5–4 mm. long, 25–35 mm. apart, subulate, broad based, sharply reflexed; near the middle the margins subentire, the midrib with a few remote spines 1.3 mm. long, subulate, ascending, brown-tipped; near the apex the margins and midrib below with appressed serrulations 0.2–0.3 mm. long; leaves of juvenile plants 1.81–1.87 m. long, 4 cm. wide, the subulate apex much longer and the spines a little larger; syncarps reported to be "solitary, 20 cm. in diameter (which size I doubt and think much too large), globose, red, the drupes sweet, with the flesh edible but soon irritating"; no attached or complete fruits were found on the scores of trees, only fallen drupe bodies and many detached, dried examples of the pileus; drupes apparently 32–35 mm. long, terete and 14–16 mm. in diameter, or slightly compressed and 12–15 mm. thick, ellipsoid or cuneate-ellipsoid; pileus 15–20 mm. high, 15–19 mm. in diameter, semiorbicular, bearing on the apex a dark brown, shining, stigmatic apparatus, the whole 13–17 mm. long, oblique at 45°, but the free part 7–9 mm. long, this parted about ½ way into two styles 3–6 mm. long, subulate, widely diverging and recurving; body of the drupes when dried 20–29 mm. long, 12–17 mm. in diameter, stramineous or pale brown; endocarp 14–16 mm. long, massive, placed slightly below the middle, bony, brown, the upper half of the

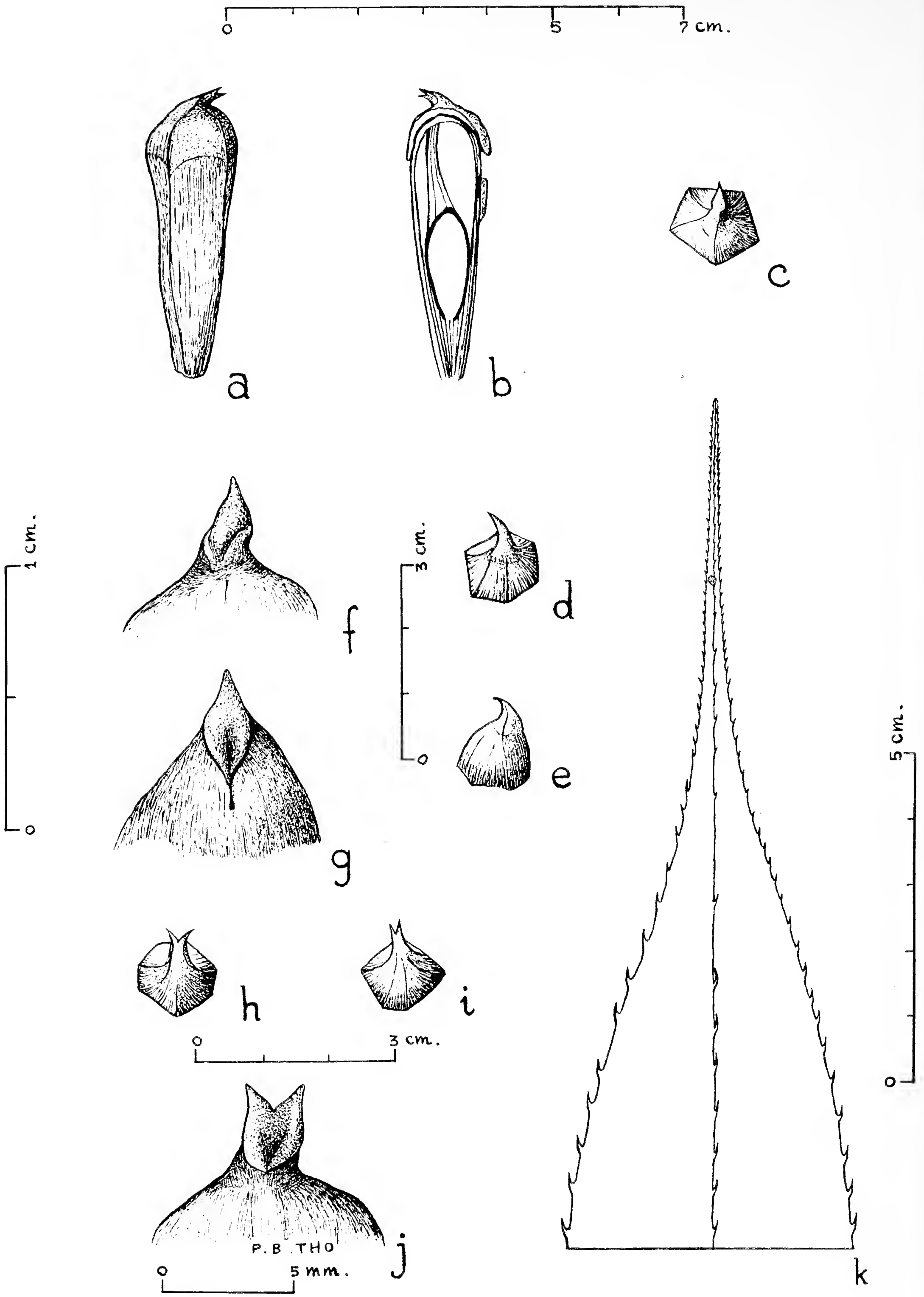

FIG. 95. *Pandanus multidrupaceus,* from holotype. *a,* Drupe, lateral view, × 1; *b,* drupe, longitudinal median section, × 1; *c,* drupe, apical view, × 1; *d,* pileus, lateral view, × 1; *e,* pileus, lateral view, × 1; *f, g,* stigma, lateral view, ×4, this and *a–f* from median drupes; *h, i,* apical view of pileus of subbasal drupes, × 1; *j,* lateral view of stigma of subbasal drupe, × 4; *k,* apex of floral bract, lower side, × 1.

cavity partly filled by a broad invagination from one side, the lateral walls 3–4 mm. thick; seed cavity 7–10 mm. long, 7 mm. in diameter, terete except for the invagination; apical mesocarp a single cavern 6–7 mm. long, free of fibers except for those making a central shaft; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Vietnam, Ile Tre (Hon-Mieu), Baie de Nha Trang, lower wooded slopes on s. side, common at 30–200 m. alt., in brush and forest of *Randia* and other spiny or thorny species, Feb. 7, 1960, *H. St. John 26,340* (BISH).

DISCUSSION: The new *P. corniferus* is a member of the section *Rykia.* Its closest relative there is *P. furcatus* Roxb., described from northeast India and later found growing also in Burma and in Vietnam. It is distinguished by its drupes 3–4 cm. long, 8–9 mm. in diameter; pileus 1 cm. long, 12–13 mm. in diameter, broad cylindric; style 3–4 mm. long, bifurcate less than ½ way, slightly curved; and the apical mesocarp 1 cm. long. *P. corniferus* differs in having the drupes 32–35 mm. long, 13–18 mm. in diameter; pileus and stigma 15–20 mm. long, 15–19 mm. in diameter; styles 2–3-forked, 3–6 mm. long, cleft ½ way, the subulate forks widely diverging and recurving.

Pandanus multidrupaceus sp. nov. (sect. *Rykia*)

Figs. 91, 95, 96

DIAGNOSIS HOLOTYPI: Arbor 3.5–5 m. alta 8 cm. diametro, radicibus fulturosis 1.5–2.5 cm. diametro laevibus excepta tuberculis paucis remotis, foliis 2–2.95 m. longis 6.3–6.8 cm. latis coriaceis ligulatis apice longe acuminato subulato in puncto 10 cm. ex apice 3.5 mm. latis basi inerme vix majore sed in uno latere ex 14 cm. dum in alter ex 29 cm. marginibus cum spinis 6–8 mm. longis 14–33 mm. distantibus subrectis subulatis adscendentibus basi incrassata, midnervo cum spinis 7–9 mm. longis simulantibus sed crassioribus reflexisque, in regione mediali marginibus cum spinis 3–4 mm. longis 28–40 mm. distantibus crassiter subulatis adscendentibus, midnervo infra cum spinis crassissimis 4–5 mm. longis reflexis, proxima apice subulato-serrato dentibus 1–1.5 mm. longis 6–27 mm. distantibus, midnervo inerme, pedunculo 15 cm. et ultra longo obtuse deltoideis folioso, bracteis inferis 11 cm. latis superioribus 60 cm. longis 10 cm. latis lanceolatis acuminatis marginibus medialis inferique cum spinis 1–1.5 mm. longis sed ad apicem in marginibus midnervoque majoribus 2–2.5 mm. longis 4–11 mm. distantibus valde subulatis curvatis, syncarpio 22 cm. longo 12 cm. diametro anguste obovoideo-cylindraceo cum 752 drupis luteis, nucleo 2.5–3 cm. diametro albido molle carnoso et fibroso, drupis immaturis rubrescenti-viridibus apice glauco, eis medialis et superis 4.2–4.5 cm. longis 10–13 mm. latis 9–13 mm. crassis illis inferis et subbasalibus 3.3–4.2 cm. longis 9–12 mm. latis 12–15 mm. crassis cuneatis 5–6-angulosis lateribus planatis parte 1/5 supera libera, pileo glauco conico-pyramidali sed parte proxima obliqua et supra curvata decidua, stylo 5–7 mm. longo osseoso lucido ad basem obscure brunneo ad apicem pallide brunneo irregulariter bifido (vel paucis apicalibus integris), stigmatibus brunneis papillosis infra confluentis sed in ramis separatis, endocarpio in tertia infera 14–16 mm. longo 4–6 mm. diametro osseoso marginibus lateralibus 0.5 mm. crassis, superficie interiori straminea lucida in stylo cum fibris connectis, seminibus late ellipsoideis, mesocarpio apicali quam parte tertia grandiori albo molle exfibroso, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 3.5–5 m. tall, 8 cm. in diameter; prop roots 1.5–2.5 cm. in diameter, smooth except for a few remote tubercles; leaves 1.58–2.95 m. long, 6.3–6.8 cm. wide, coriaceous, ligulate, the apex long acuminate, the tip subulate, and 10 cm. down only 3.5 mm. wide, the very base unarmed, scarcely widened, beginning at 14 cm. on one side, at 29 cm. on the other the margins with spines 6–8 mm. long, 14–33 mm. apart, nearly straight subulate, heavy based, and ascending, the midrib below with spines 7–9 mm. long, similar but even thicker and reflexed; at the middle the margins with spines 3–4 mm. long, 28–40 mm. apart, stout subulate, ascending, the midrib below with very stout ones 4–5 mm. long, reflexed; near the apex the margins subulate serrate, the teeth 1–1.5 mm. long, 6–27 mm. apart, the midrib unarmed; peduncle 15 or more cm. long, bluntly triangular in cross section, leafy bracted, the lower bracts 11 cm.

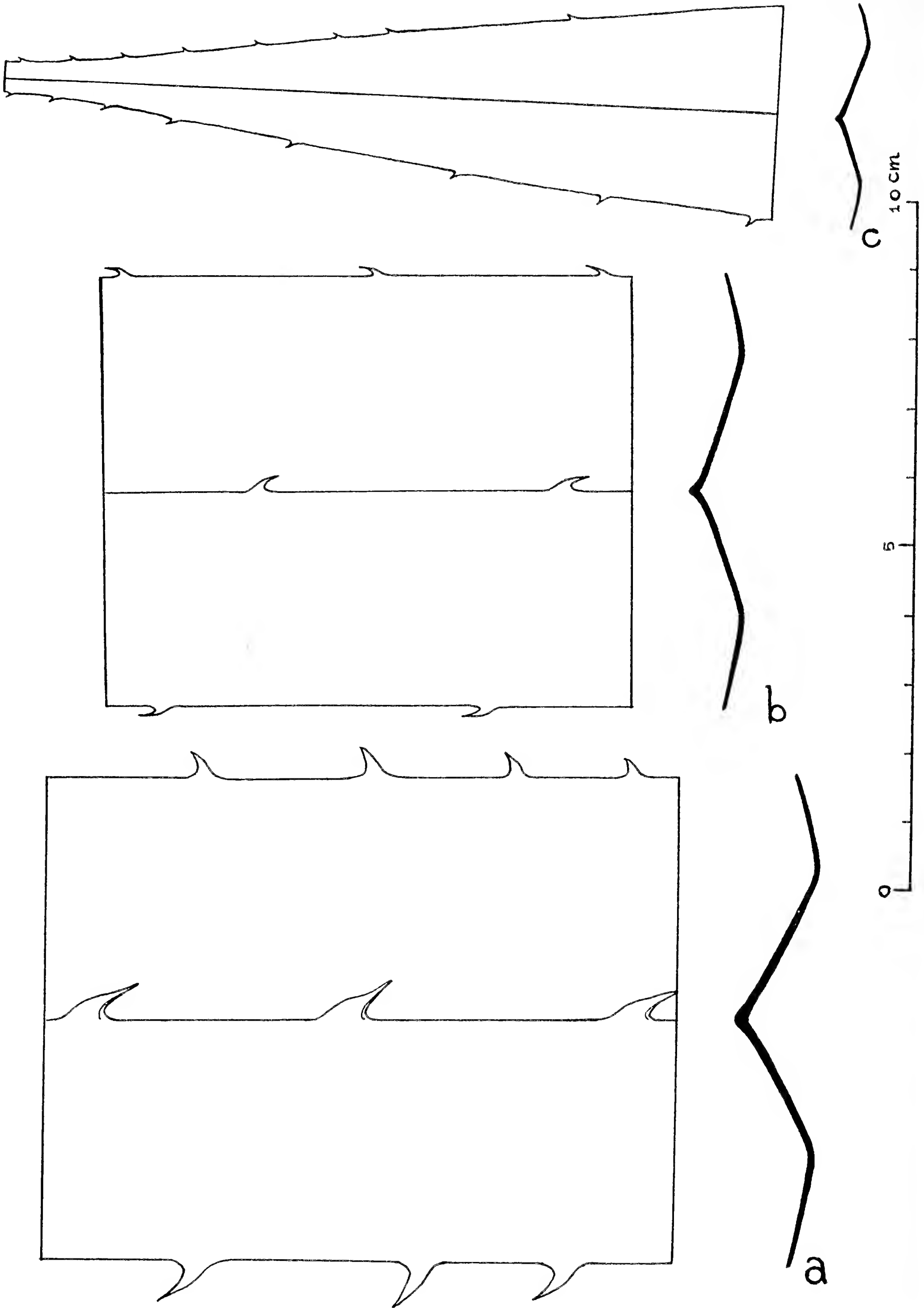

FIG. 96. *Pandanus multidrupaceus,* from holotype. *a,* Leaf base, lower side, × 1; *b,* leaf middle, lower side, × 1; *c,* leaf apex, lower side, × 1.

wide, the upper bracts 60 cm. long, 10 cm. wide, lanceolate, acuminate, the middle and lower margins with spines 1–1.5 mm. long but increasing upwards, and near the tip on margins and midrib below the spines 2–2.5 mm. long, 4–11 mm. apart, stout subulate, upcurved; syncarp 22 cm. long, 12 cm. in diameter, narrowly obovoid-cylindric, of 752 drupes; the core 2.5–3 cm. in diameter, white, soft fleshy and fibrous; drupes reddish green, but still unripe and the apex glaucous, the middle and upper drupes 4.2–4.5 cm. long, 10–13 mm. wide, 9–13 mm. thick, the lower and subbasal ones 3.3–4.2 cm. long, 9–12 mm. wide, 12–15 mm. thick, cuneate, 5–6-angled, the sides plane, upper 1/5 free; pileus glaucous, conic-pyramidal, but the upper part oblique and curved towards the apex of the syncarp, deciduous; style 5–7 mm. long, bony, shining, towards the base dark brown, towards the apex pale brown, irregularly bifid (or on a few apical drupes entire); stigmas brown, papillose, confluent below but separating on the forks; endocarp in lower ⅓, 14–16 mm. long, 4–6 mm. in diameter, bony, the lateral walls 0.5 mm. thick, the inner surface stramineous, shining, produced upwards by a broad subulate, fibrous, oblique connection to the style; seeds broadly ellipsoid; apical mesocarp extensive, filling more than the upper ⅓ with a white, soft, continuous, non-fibrous tissue; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Vietnam, 8 km s. w. de Pampei, Teurnoum, Dalat, frequent, le long des ruisseaux, forêt dense, 9 Fev. 1960, Trung Van Lén (BISH).

SPECIMENS EXAMINED: Vietnam, forest of Manglinh, near Dalat, 25 mars, 1960, Trung Van Lén.

DISCUSSION: *P. multidrupaceus* is in the section *Rykia* and is most closely related to *P. tonkinensis* Martelli, of Tonkin and Annam, which species has the plant 1–2 m. tall; leaves 70–80 cm. long, 4 cm. wide, the basal marginal prickles 8–15 mm. long; pistillate inflorescence bracts 7 cm. long, 2.5 cm. wide; syncarp broadly ellipsoid (very young); drupes about 80. *P. multidrupaceus* has the tree 3.5–5 m. tall; leaves 2–2.95 m. long, 6.3–6.8 cm. wide, the basal marginal prickles 6–8 mm. long; pistillate inflorescence bracts 55 cm. long, 9.5 cm. wide; syncarp cylindric-obovoid; and the drupes 752.

The new epithet is composed from the Latin *multus,* many; *drupaceus,* bearing drupes, in reference to the 752 drupes of the syncarp.

Trematolobelia: Seed Dispersal; Anatomy of Fruit and Seeds

SHERWIN CARLQUIST[1]

THE ENDEMIC HAWAIIAN GENUS *Trematolobelia* (Lobeliaceae, or Campanulaceae, subfamily Lobelioideae) was erected on the basis of its distinctive fruit. This fruit has a seed-dispersal mechanism unique in the family. Assertions have been made by some workers that holes in the fruit wall are the work of insects, and are not related to the dispersal mechanism. This contention has been adequately disproved by other investigators, but, in fact, the precise nature of the dispersal mechanism and the anatomical structure responsible for its action have never been adequately described. In addition, the present study reveals the potential taxonomic use of capsular anatomy, a feature of importance because various authors recognize one, two, or three species in the genus. These species are based largely on floral features or foliar characteristics, and not on those of the fruit. Unusually good material of *Trematolobelia* collected by the writer during the summer of 1958 provides a sufficient basis for presenting the features mentioned above in some detail.

MATERIALS AND METHODS

The following specimens were utilized for this study: *Trematolobelia macrostachys* var. *macrostachys* Zahlbruckner: Carlquist 563 (Puu Kukui, Maui); Carlquist 612 (Huumulu Rd., Hawaii); Flavious Peter April 21, 1958 (Molokai). *T. macrostachys* var. *kauaiensis* Rock: Carlquist 508 (Pihea, Kauai). *T. macrostachys* var. *grandifolia* Rock: Carlquist 612A (Cultivated at Volcano, Hawaii; plant brought from Kehena Ditch Trail, Kohala Mts., Hawaii, by Mrs. Ella Stephens).

All of these specimens were collected in the field; portions of each were preserved in formalin-propiono-alcohol (Johansen, 1940). Other portions were dried. Herbarium specimens of all of these collections are located in the Rancho Santa Ana Botanic Garden Herbarium.

The flowers and fruits which were studied (see figure legends for specimens used) were embedded in paraffin according to the tertiary-butyl alcohol technique of Johansen (1940: 130–131), sectioned, and stained with a safranin-fast green combination corresponding to Northen's modification of Foster's tannic acid–ferric chloride method (Johansen, 1940: 92–93).

ANATOMICAL DESCRIPTIONS

The mature fruit prior to parenchyma decomposition is green and appears fleshy, much

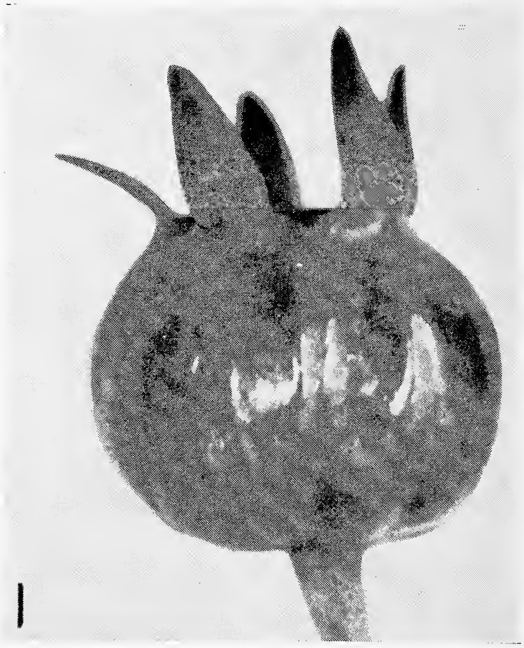

FIG. 1. *Trematolobelia macrostachys,* Carlquist 612. Mature fruit before decomposition of parenchyma.

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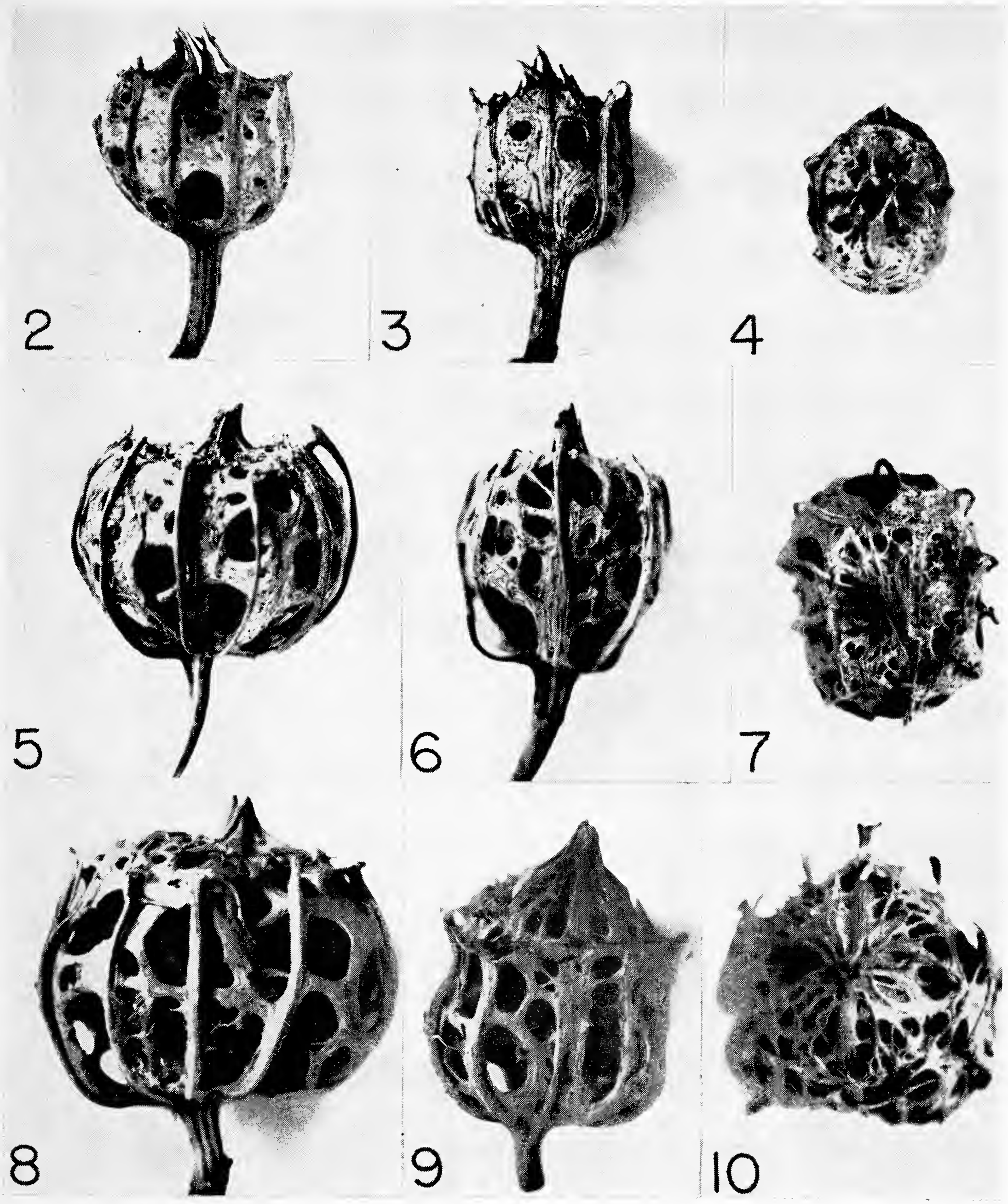
[1] Claremont Graduate School, Rancho Santa Ana Botanic Garden, Claremont, California. Manuscript received February 24, 1961.

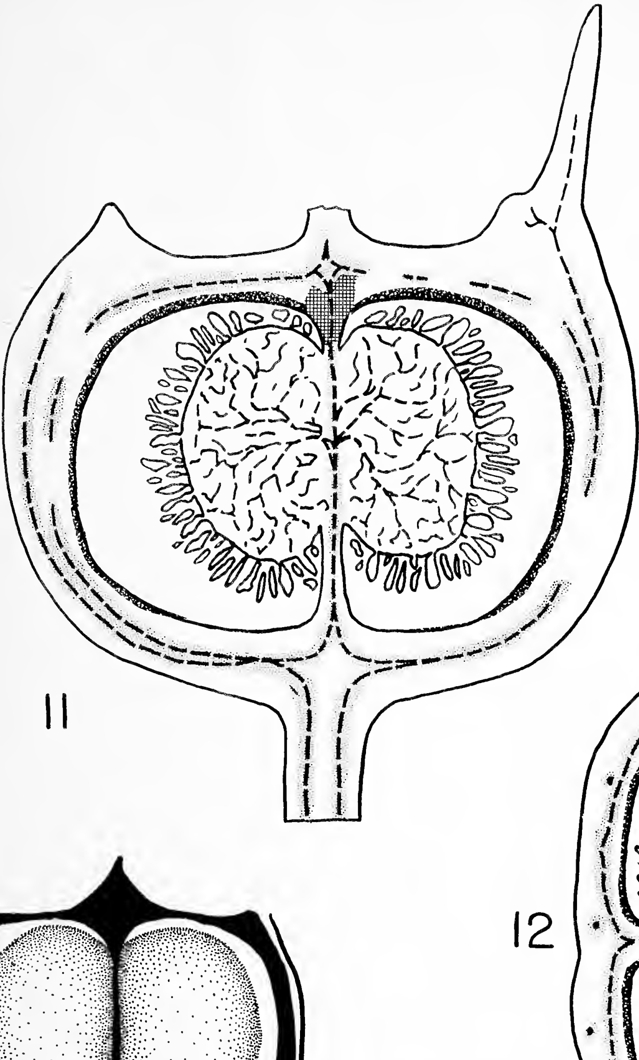


FIGS. 2–10. *Trematolobelia macrostachys* fruits after decomposition of parenchyma. In each row, view at left represents lateral view (with regard to carpels), middle view represents dorsiventral view (center is median line of carpel), and view at right represents top of capsule. 2–4, *T. macrostachys* var. *kauaiensis,* Carlquist 508. 5–7, *T. macrostachys* var. *macrostachys,* Carlquist 563. 8–10, *T. macrostachys* var. *grandifolia,* Carlquist 612A. For comparisons, see text. All × 3.6.

like the baccate fruits of the other endemic Hawaiian lobeliads, such as *Cyanea* and *Clermontia* (Fig. 1). Sections of this fruit (Figs. 11, 12, 15) reveal three distinctive tissues: ground-tissue parenchyma, endocarp sclerenchyma, and fibrous vascular bundles. The ground tissue of the fruit wall is composed of thin-walled parenchyma cells which are large in diameter (decreasing in size toward interior and exterior of the fruit wall). These parenchyma cells are rich in chloroplasts. Although the inner epidermis of the fruit wall is thin-walled, there are two to four layers of thick-walled sclereids internal to the epidermis (Fig. 15). As shown in Figures 11 and 12, this endocarp sclerenchyma is present around the inner surface of the carpels with the exception of the basal portion of the carpels and the portion lying between the two placentas. The apical portion of the carpels is not coated with endocarp sclerenchyma, but possesses instead a spongy sclerenchyma (Fig. 11; Fig. 17) which connects endocarp sclerenchyma with the vascular bundles which form a pointed terminus, as seen in a dry fruit (e.g., Fig. 5, above). The vascular tissue is composed of two sorts of bundles: the 10 main bundles which extend upwardly into the calyx, corolla, and stamens of the flower, and the carpellary bundles, internal to the 10 main bundles. The carpellary bundles form a dense mesh, in which large pores are present. The distinctions between the two sorts of bundles can be seen especially well in Figs. 5–7, where they are adnate only to a limited extent. The drawing in Fig. 11 shows the carpellary bundles united to the 10 vertical bundles only in the basal portion of the fruit. Thus, they appear largely separate in Fig. 12. The 10 main bundles represent the fusion of bundles from the three outermost whorls of the flower. They separate into calyx, corolla, and stamen traces only at the top of the ovary (Fig. 11, upper right). The carpellary bundles form a network-like system which encloses the carpels. This network, seen in Figs. 2–10, is composed of bundles which run in all directions, and are absent where pores are formed. These pores are preformed in the fruit (e.g., the space between bundles at left and right, below, in Fig. 15, will be such a pore). The carpellary bundles not only form a network on the outside of the carpels, but between them (Fig. 12) as well. These central carpellary bundles supply the two placentas. In their upward extent, carpellary bundles supply the style.

The vascular bundles, both inner carpellary and outer calyx-corolla-stamen bundles, show a peculiar feature of construction. The prominence and persistence of these bundles, as seen following the decomposition of the parenchymatous portion of the fruit, is due to abundance of fibers present in these bundles. Only the basal portion of calyx-traces and style-traces possess such fibers, and entire traces are thus absent in the dry fruit. Such thick-walled fibers may be seen in Fig. 15. One might suppose that these fibers have the same origin as the fibers in most bundles, that is to say, from a bundle-cap, or protophloem region. This is, however, not the case. Sections of the ovary wall from flowers at anthesis (Fig. 16) reveal clearly that the bundles are amphicribral in construction. The periphery of the bundle consists of phloem, in which many articulated non-anastomosing laticifers are embedded. These laticifers, although present with particular prominence at the periphery of the bundles, also extend into the ground tissue of the ovary wall (Fig. 15, above left). This close association between laticifers and phloem is frequent in dicotyledons. The center of the bundle, as shown in Fig. 16, contains mature tracheary elements. Longitudinal sections of bundles reveal that these are mostly vessel elements. Between the phloem and the tracheary elements is a zone which consists

FIGS. 11–14. *Trematolobelia macrostachys* var. *macrostachys*. 11, 12, sections of fruits from the collection Carlquist 612. 11, Median longitudinal (sagittal) section of mature fruit before decomposition of parenchyma. 12, Transverse section. Conventions as follows: broken lines = tracheary elements of vascular bundles; stippled = xylary fibers; cross-hatched = spongy sclerenchyma (see Fig. 17); spatter pattern = endocarp sclerenchyma; phloem, laticifers, parenchyma, and seeds are left white. 13, 14, Fruits, following decomposition of parenchyma, dissected to show the endocarp sclerenchyma sacs; sclerenchymatous vascular tissue black, endocarp sacs stippled; from the collection Carlquist 563. 13, Lateral view, showing sacs shrunken away from base, slits below. 14, View from below, vascular tissue cut away; note slits in sacs, which permit escape of seeds. 11–12, × 5.4. 13–14, × 4.



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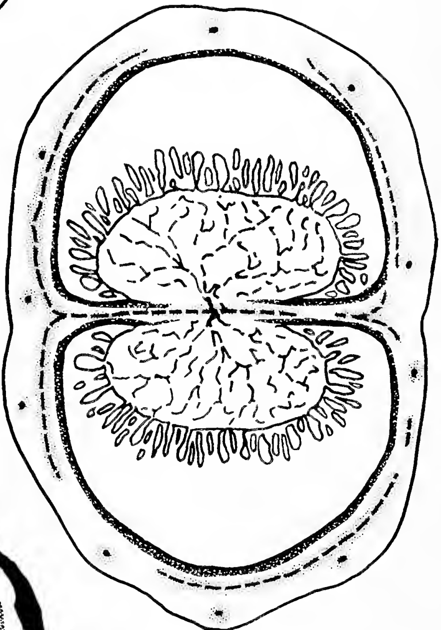

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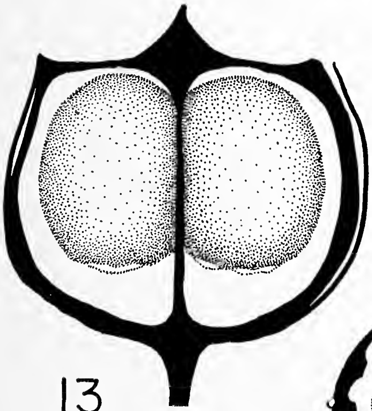

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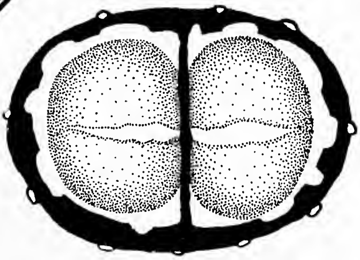

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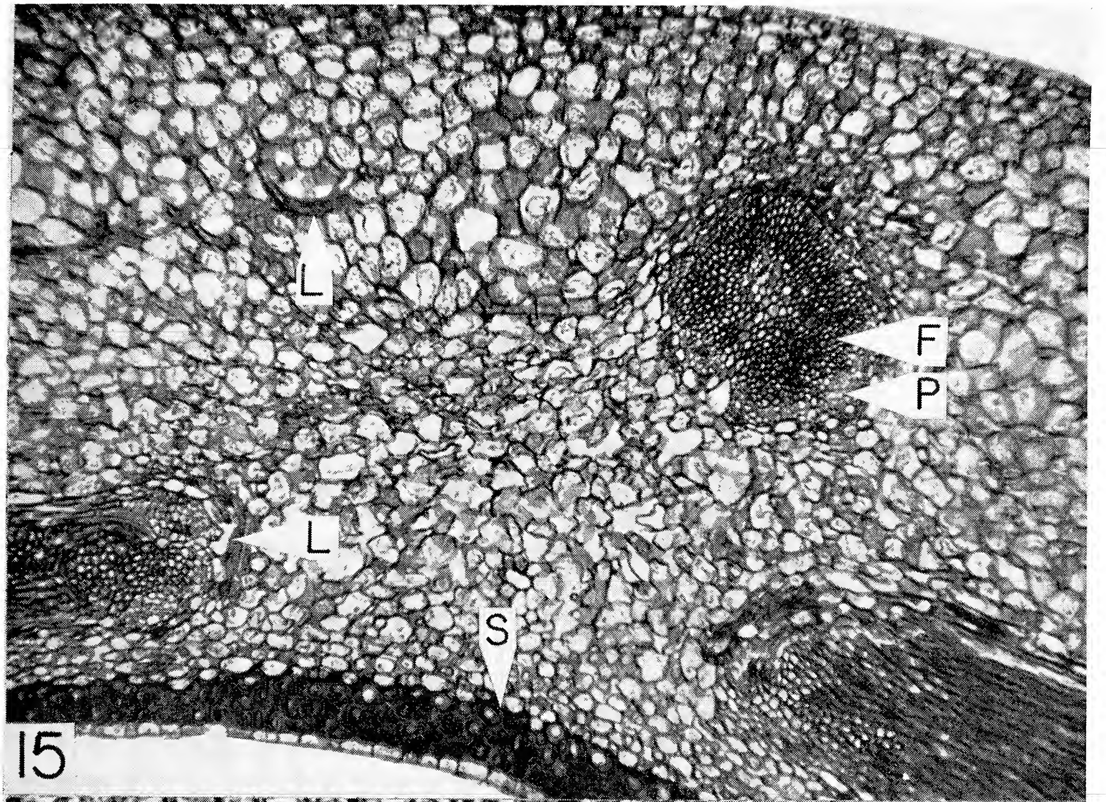
wholly of fiber initials. Thus, the fiber initials occur internal to the phloem, and must be regarded as *xylary* fibers. As seen in Fig. 16, vessels are actually scattered among these xylary fibers. Xylary fibers are not infrequent in primary bundles, but the prominent representation of them in the vasculature of *Trematolobelia* fruits is truly exceptional. Moreover, by greatly widening the bundles, these fibers are responsible for the alteration of the carpellary vasculature from a reticulate pattern (like that in a leaf) to a sheet-like conformation, interrupted by the pores.

Trematolobelia is also distinctive among lobeliads in the prominent wings which are present on seeds. Because of the importance of winged seeds to the dispersal mechanism, these have been studied anatomically (Figs. 18–20). The central portion of the seed (Figs. 18, 19) consists of endosperm in which the embryo is embedded. At either end of the endosperm there is a haustorium. These haustoria are termed micropylar and chalazal, respectively. In details of embryo, endosperm, and haustoria, seeds of *Trematolobelia macrostachys* appear to agree with the descriptions given by Hewitt (1939) for *Lobelia amoena.* Earlier stages in embryo-sac development were not studied. The micropylar portion of the ovule is much more prominent than in *Lobelia amoena,* however. This is probably due to the formation of a wing in the seed of *Trematolobelia.* The chalazal portion likewise forms a prominent thin wing (Fig. 18, right), which is widened somewhat at the margin. This widened portion contains the ovule trace. The epidermis contains prominent thickenings worthy of description. As seen in Fig. 20, these thickenings occur on radial walls of the epidermis, and are particularly conspicuous near the outside of the epidermis. Thus, a heart-shaped outline is formed by the thickenings of adjacent cells. These thickenings do not correspond to those in the epidermis of *Lobelia amoena* seeds. The figures of Hewitt (1939) for that species show an ellipsoid thickening in the center of radial walls of the epidermis. Rather, thickenings in *Trematolobelia* are like those figured for *Campanula sarmatica* (Campanulaceae), *Linaria vulgaris* (Scrophulariaceae), and especially *Gentiana lutea* (Gentianaceae) by Guttenberg (1926: 204–205). Portions of epidermal walls which are not prominently thickened are nevertheless thicker than walls of internal ovular cells (except for the outer epidermal wall), and bear prominent pits, both in the genera listed above (Guttenberg, 1926) and in *Trematolobelia.* Thus, anatomy of the seed-wing in *Trematolobelia* shows more similarity to that of winged seeds in unrelated genera than to that of seeds of *Lobelia,* or even non-winged species of *Campanula* (Netolitzky, 1926: 305). These thickenings undoubtedly offer mechanical strength necessary for increasing rigidity, without greatly increasing weight, in the otherwise delicate wings.

DISPERSAL MECHANISM

The controversy over the distinctness of the dispersal mechanism in *Trematolobelia,* although presumably now resolved, suggests that an accurate description of the mechanism, with comparisons with accounts of earlier authors, is desirable. Zahlbruckner's (1891) erection of *Trematocarpus,* a name later changed by him to *Trematolobelia* for reasons of nomenclatural necessity, was questioned by Hemsley (1892). Hemsley claimed that the true pores in the sclerenchymatous (carpellary) system were irregular, and caused by insects. Although Zahlbruckner reaffirmed his position in a letter, quoted by Hemsley (1893), Hemsley claimed that this could not be a true dispersal mechanism at all, and was therefore an inadequate basis for erection of a new genus. Stapf (1893) maintained that the pores in the sclerenchyma are

FIGS. 15–17. 15, *Trematolobelia macrostachys* var. *macrostachys,* Carlquist 612; portion of mature fruit wall, outer surface above; *F* = xylary fibers; *L* = laticifers; *P* = phloem; *S* = endocarp sclerenchyma. 16, *T. macrostachys* var. *macrostachys,* Flavious Peter IV–21–1958; portion of ovary wall, inner surface below, from flower at anthesis; the vascular bundle corresponds to the bundle shown, above right, in Fig. 16; *(F)* = future xylary fibers; *L* = laticifer; *P* = phloem; *T* = tracheary elements (mostly vessels). 17, *T. macrostachys* var. *macrostachys,* Carlquist 612; spongy sclerenchyma from near apex of fruit (see Fig. 11), from longitudinal section. 15, × 62. 16, × 132. 17, × 155.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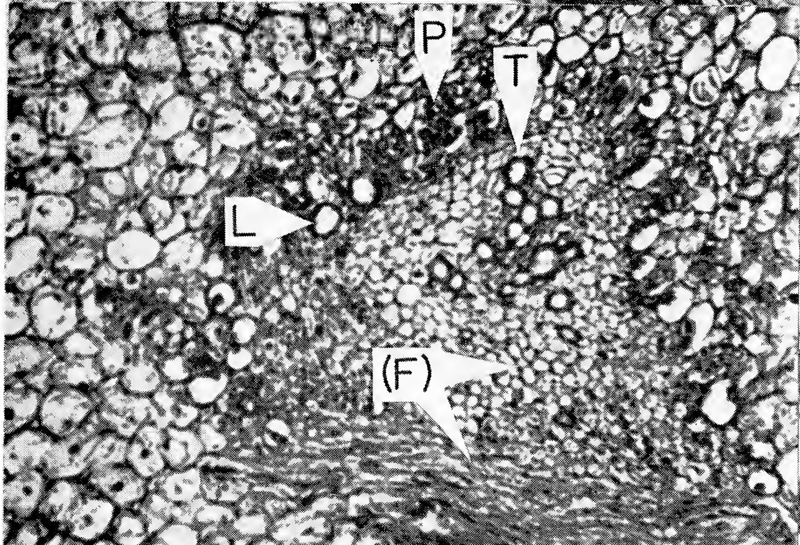
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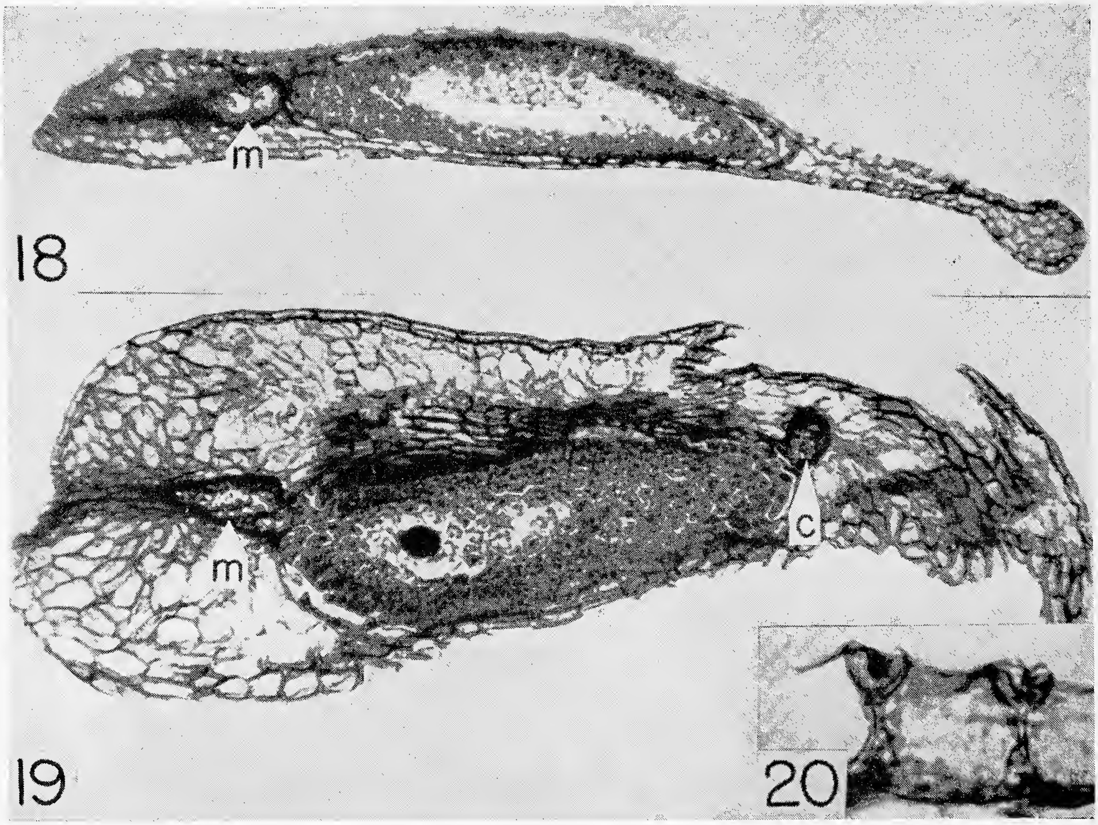
caused by insect action, but claims that similar mechanisms of dispersal in *Lobelia* (where such a sclerenchyma network is not present) negate the necessity of a separate genus for *T. macrostachys.* Rock (1919: 141) denied that insects produced holes in the capsule, and cited his own field experience in this regard. The controversy mentioned above would not have arisen if field observation had, from the beginning, been undertaken. Fortunately, I was able to study dispersal in the field and relate it to anatomy of liquid-preserved specimens.

The fully-formed capsules (Fig. 1) are borne upright on the plant. This upright position is achieved by curvature in pedicels. Such curvature takes place above the point where reduced bract-leaves are borne. This portion of the pedicel is thinner than that below the bract leaves, and at the time of curvature, the fibers in the pedicel vasculature have not yet formed rigid, thick walls. In July and August, the mature green capsule yellows, and the parenchymatous portion decomposes. This is not a decay caused by fungi or other microorganisms (which may, of course, occur secondarily), but rather is the result of a natural maceration. The parenchyma does not separate from the sclerenchyma by drying, as suggested by Zahlbruckner (1891) and Stapf (1893). Had these writers seen the plants in the field, they would have seen that the frequent rains in locations where *Trematolobelia* grows virtually prevent drying of the capsule; these rains, in fact, wash the decomposing sclerenchyma away, revealing the porous



FIGS. 18–20. *Trematolobelia macrostachys* var. *macrostachys,* Carlquist 612. Views of seeds. 18, Near-median section (embryo not shown) in a plane at right angles to wing; m = micropylar haustorium; chalazal edge at right. 19, Near-median section of seed, parallel to wing; m = micropylar haustorium; c = chalazal haustorium; black in center of endosperm = embryo. 20, Epidermis of seed, from chalazal end of seed sectioned as in Fig. 18; note prominent thickenings near outer surface (above). 18–19, × 90. 20, × 633.

sclerenchyma. Pores are not formed during disappearance of the parenchyma, as claimed by Zahlbruckner (1891). Rather, they are preformed, and loss of the parenchyma exocarp merely exposes these patterns. Views of the sclerenchyma network are shown in Figs. 2–10 for three collections of *Trematolobelia.*

The porous sclerenchyma varies in number and size of pores. The collection shown in Figs. 2–4 has fewer, smaller pores than those of the collection shown in Figs. 5–7; the largest pores, however, are shown by capsules of the collection illustrated in Figs. 8–10. The apex of the capsule may be composed of tooth-like structures, separate at their tips, as shown in Figs. 2–4, or as illustrated in *T. macrostachys* var. *kaalae* by Degener (1936). Other collections (Figs. 5–10), however, show that the apical portion of the capsule consists of a closed network of bundles. The pores are smaller than those in the lateral portions of the capsule.

Within the sclerenchymatous network, parenchyma around the endocarp sclerenchyma decomposes at the same time as that external to the network. The endocarp thus exposed does not have slits or pores at its apex, which is connected with the network above by the persistent spongy sclerenchyma. During occasional dry periods in the rain forest where *Trematolobelia* grows, the thin, papery endocarp can dry. Drying of the endocarp results in shrinkage, so that the sacs shrink upward from the base of the capsule (Fig. 13), and the splits in the basal and placental regions (Fig. 14) become prominent. Through these slits, the winged seeds escape. This escape is not rapid, and a few seeds may be found in capsules which are a year old. The endocarp, which does not have splits above, is apparently functional in preventing wetting of the undispersed seeds. Alternate wetting and drying can result in successive dispersals of seeds over a longer period of time, so that the entire contents of the capsule may be slowly lost. Because capsules are borne upright, and because splits occur in the basal and central portions of the endocarp, seeds are probably scattered mostly through the most basal pores in the sclerenchyma network, and the upper holes do not function appreciably in the dispersal process. I was able to demonstrate this experimentally with the capsules illustrated in Figs. 8–10, which were full of seeds when collected. Presumably the sclerenchyma network can, or does, slow seed dispersal somewhat, especially if the pores are relatively small. Undoubtedly the shaking afforded by winds, as actually observed in the field, does promote escape of seeds through the pores.

The winged nature of seeds undoubtedly is probably effective in permitting more widespread distribution (presumably by wind) of seeds. Thus, of the Hawaiian species of lobeliads studied by Rock (1919), only one, *Trematolobelia macrostachys* (the only species of the genus in Rock's treatment), occurs on all major islands. Within each island, *Trematolobelia* is present in many wetter areas of the rain forest, and although it is never abundant in a particular locality, few suitable areas seem to lack it altogether.

TAXONOMIC CONCLUSIONS

Rock (1919: 141–148) recognizes one species of *Trematolobelia* with three varieties. Degener (1934, 1936) recognizes three species, one of which is considered to have two varieties. Wimmer (1953) reduces one of these species to a variety, but otherwise follows Degener's treatment. More information obviously is needed before a clear-cut designation can be made as to the rank of entities involved. For this reason, the conservative treatment of Rock (1919) is used here. However, morphology of the dry capsules seems to be singularly neglected. Capsules are, in fact, not often collected. The taxa which have been named depend for their recognition primarily on floral characteristics, and secondarily on those of leaves. The three collections for which capsules are illustrated here represent the three major taxa: *T. macrostachys* var. *kauaiensis* (Figs. 2–4), *T. macrostachys* var. *macrostachys* (Figs. 5–7), and *T. macrostachys* var. *grandifolia* (Figs. 8–10). Distinctions among these include formation of an apical network (Figs. 7, 10) or separate teeth (Figs. 2–4), comparative size and frequency of holes in the sclerenchymatous network, total size of capsules, and relative union of the carpellary network to the 10 vertical bundles. These latter bundles are united with the network in var. *kauaiensis* (Figs. 2–4), are largely separate in var. *macrostachys* (Figs. 5–7), and are united, but with prominent free tips in var. *grandifolia* (Figs. 8–10). None of the differences mentioned may, when more collections have been made, prove to be entirely constant, but the fact that such prominent differences occur suggests that features potentially valuable to the taxonomy of this genus deserve further investigation.

Detailed anatomical studies on capsules of other genera of Lobeliaceae may also benefit systematics by demonstrating the relationships of *Trematolobelia.* Such studies can probably aid in assessing the relative merit of various hypotheses, such as that of Stapf (1893) that *Trematolobelia* is close to *Lobelia,* or that of Wimmer (1953: 754) that *Trematolobelia* should be grouped with *Sclerotheca.*

ACKNOWLEDGMENTS

Without aid of several individuals, the writer would have been unable to locate plants and obtain materials. Mrs. Ella Stephens of Volcano, Hawaii, was very helpful in locating living plants. Mr. Bruce Fleming, of Honokawai, Maui, aided investigations on Puu Kukui. The Bishop Museum supplied the liquid-preserved flowers collected by Mr. Peter. Appreciation is expressed to these individuals, and to Claremont College, which aided research with a research and publication funds grant.

REFERENCES

DEGENER, OTTO. 1934. *Trematolobelia.* In: The New Illustrated Flora of the Hawaiian Islands, Book 2. Privately published by the author.

——— 1936. *Trematolobelia sandwicensis* var. *kaalae* Degener. In: The New Illustrated Flora of the Hawaiian Islands, Book 3. Privately published by the author.

GUTTENBERG, HERMANN VON. 1926. Die Bewegungsgewebe. In: K. Linsbauer, ed., Handbuch der Pflanzenanatomie 5(1): 1–289. Gebrüder Borntraeger, Berlin.

HEMSLEY, WILLIAM B. 1892. *Trematocarpus.* Ann. Bot. 6: 154.

——— 1893. The genus *Trematocarpus.* Ann. Bot. 7: 289–290.

HEWITT, W. C. 1939. Seed development of *Lobelia amoena.* Jour. Elisha Mitchell Sci. Soc. 55: 63–82.

JOHANSEN, DONALD A. 1940. Plant Microtechnique. McGraw Hill, New York. xi + 523 pp.

NETOLITZKY, FRITZ. 1926. Anatomie der Angiospermen-Samen. In: K. Linsbauer, ed., Handbuch der Pflanzenanatomie 10(1): 1–364.

ROCK, JOSEPH F. 1919. A monographic study of the Hawaiian species of the tribe Lobelioideae, family Campanulaceae. Mem. Bernice P. Bishop Mus. 7(2): 1–394.

STAPF, OTTO. 1893. The genus *Trematocarpus.* Ann. Bot. 7: 396–398.

WIMMER, F. E. 1953. Campanulaceae-Lobelioideae, II Teil. In: R. Mansfeld, ed., Das Pflanzenreich 107(2): 261–813. Akademie-Verlag, Berlin.

ZAHLBRUCKNER, ALEXANDER. 1891. Ueber einige Lobeliaceen des Wiener Herbariums. Ann. Naturh. Hofmus. Wien 6: 430–445.

Contribution to the Marine Chlorophyta of Hawaii, I[1]

WILLIAM J. GILBERT[2]

WITH ONE EXCEPTION the annotated list which follows is comprised of new or previously unreported green algae from the Hawaiian Islands. The new records result from a partially completed survey of algae from several sources, chief of which are collections by Dr. Maxwell S. Doty[3] made during the past ten years, the Herbarium of the Bernice P. Bishop Museum in Honolulu, and my own collections made during March–June, 1959.

Type specimens are deposited at the University of Michigan Herbarium, Ann Arbor, Michigan.

1. *Bryopsis hypnoides* Lamouroux (prox.), 1809, p. 135, pl. 5, fig. 2.

COLLECTION: Gilbert 10060, in wash between Kawela and Kamaloo on S. shore of Molokai, June 5, 1959.

The material was present in abundance and shows many of the characteristics of *Bryopsis hypnoides,* including the production of pinnules on all sides of the axis and the gradual tapering of successive series of branches. The ultimate pinnules were 43–51 μ in diameter, the upper ones simple but with some of the lower and longer ones once or twice branched. In none of the Hawaiian material was I able to find a main axis over 180 μ in diameter. Because of the small diameter of the main axis and the relatively small diameter of the ultimate pinnules it is with hesitation that the material is assigned to *B. hypnoides.*

2. *Caulerpa ambigua* Okamura, 1897, p. 4, pl. 1, figs. 3–12.

Fig. 1, *A*

COLLECTION: *Doty 10224,* along edge of reef, Anahola, Kauai, Feb. 7, 1952.

Despite opinions to the contrary by Eubank (1946) and Børgesen (1949), I am inclined to agree with Dawson (1956) that *Caulerpa ambigua* Okamura and *C. vickersiae* Børgesen are distinct entities. I had examined many plants of what I now believe to be *C. vickersiae* (Fig. 1, *B*) in both my own collections and in those of others from Hawaii before I ran across the collection by Doty, cited above, which I have assigned to *C. ambigua.* While the plants are relatively the same size as those of *C. vickersiae,* they are so clearly distinct from that species on the basis of the "basally contracted, multifarious branchlets" (Dawson, 1956: 36) that I have no hesitation in making the separation. I have compared the Hawaiian plants with the material from Kwajalein Atoll of the southern Marshalls reported by Dawson and find them to be remarkably similar, with the exception that the Marshall material does not have as many of the ramuli twice-dichotomously branched as does the Hawaiian material.

On the basis of my observations it appears that *Caulerpa vickersiae* Børg. is by far the more common of the two species in Hawaii. I believe that most if not all of the material reported by Eubank from Hawaii as *C. ambigua* is in reality *C. vickersiae.* Among my own collections it would be in order to list the following as *C. vickersiae: Gilbert 9122,* Kahana, Maui, March 22, 1959; *9413,* Waikiki Beach, Oahu, April 9, 1959; *9581,* Kapaa, Kauai, April 26, 1959; *10115,* near Mapalehu, Molokai, June 7, 1959.

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3. *Caulerpa verticillata* J. Agardh, 1847, p. 6.

COLLECTIONS: *Gilbert 9797,* Mokuoloe (Coconut Island), Kaneohe Bay, Oahu, May 14, 1959; *Doty 8117,* forming a green "meadow" around and under the prow of the Seth Parker, beached on Mokuoloe Island, Kaneohe Bay, Oahu, Oct. 3, 1950; *10100,* ponds on wharf side of Mokuoloe, Kaneohe Bay, Oahu, May 9, 1953.

I have examined five different collections of this alga, all taken from a limited area at the Marine Biological Station on Mokuoloe Island in Kaneohe Bay, Oahu. It has not appeared in any of the other collections I have studied.

4. ***Cladophoropsis adhaerens*** sp. nov.
Fig. 2, *A–C*

Plantae 1–2 cm. alt., caespitem implexum patentemque, substrato umbroso saxi coraliive firme adhaerentem, efficientes; parce ad profuse ramosae; ramus plerumque sine septo ad basim effectus, infra septum filamenti, autem, ramiferi oriens; septa rara nisi ad ramos et prope basim rhizoideorum aliquorum et raro prope cacumina ramorum terminalium longorum; rhizoidea multa, ad plerosque ramos effecta; filamenta 160–290 μ diam.; membranae cellularum valde striatae, 10–54 μ crass.; cellulae in partibus parcius ramosis ad 120–140 plo longiores quam latae.

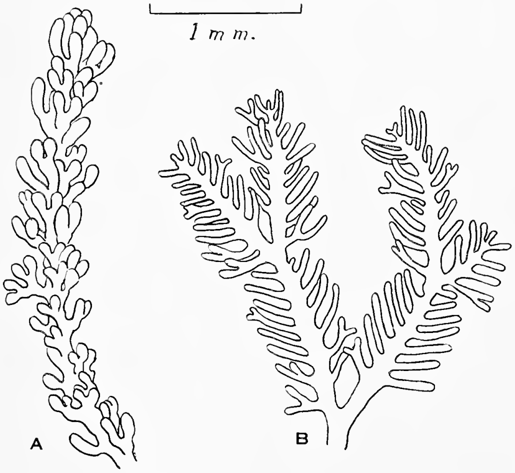

FIG. 1. *Caulerpa* spp. *A, Caulerpa ambigua* Okamura, a branch of a plant of *Doty 10224. B, C. vickersiae* Børgesen, part of a plant.

Planta typica, Gilbert num. 9410 nomine, a saxo et "concrete" ad partem molis prope litus collecta inter locos Natatorium et Societatem Alcium, Waikiki, Hawaii dictos, m. Apr. 9 an. 1959.

Plants turf-forming, spreading, matted, 1–2 cm. high, tightly adherent to rock or coral substratum, in shaded areas; sparingly to profusely branched; branch usually without a cross-wall at its base but arising beneath a cross-wall of the filament which bears it; cross-walls seldom forming except at branches, near the base of some rhizoids, and rarely near the tip of long terminal branches; rhizoids numerous, forming at most of the branches; filaments 160–290 μ diameter; cell walls strongly striated, varying from 10–54 μ in thickness; cells in the more sparsely branched portions to 120–140 diameters long.

TYPE: *Gilbert 9410,* from rock and concrete at shore end of pier between Natatorium and Elks Club, Waikiki, Honolulu, Oahu, April 9, 1959.

This species is characterized by its markedly striated thick cell walls which give the plant a tough, wiry feel which can be readily recognized on collecting. At times the cell walls appear to be so thick as to almost occlude the filaments, but careful observation frequently reveals this condition to be an artifact resulting from the strongly striated walls. However, the walls are unusually thick and I have demonstrated them to my satisfaction up to 54 μ thick. The formation of rhizoids at nearly all the branches is also characteristic of this species and results in the thallus becoming strongly adherent to the substratum and hence difficult to remove. Unlike most species of *Cladophoropsis* this one apparently prefers shaded areas and does not usually grow fully exposed to sunlight.

OTHER COLLECTIONS: *Gilbert 9712,* on basalt rocks at Kilauea Bay, near Kepuhi Point, Kauai, May 1, 1959; *10037,* Del Monte Park, ca. 3 miles east of Kaunakakai, Molokai, June 5, 1959.

5. ***Cladophoropsis luxurians*** sp. nov.
Fig. 3, *A, B*

Plantae pulvinatae patentes aliquot cm. lat., 1–2 cm. alt., in substrato saxi coraliique aprico umbrosove frequentes; thallus e filamentis cylin-

FIG. 2. *Cladophoropsis adhaerens* sp. nov. *A, B,* habit drawings from *Gilbert 9410. C,* A young plant.

dricis parce ad profuse ramosis constans, ramus sine septo ad basim effectus, infra septum filamenti, autem, ramiferi oriens; ramificatio plerumque secunda, versus substratum saepe curvata, thallo sic repente; septa inter ramos formata, in partibus plantae inferioribus frequentiora quam in superioribus nisi in ramis terminalibus qui haptera formant; haptera secondaria in partibus thalli decumbentibus, interdum ad cacumina ramorum facta; filamenta diametro variantia, usque ad 510 (770) μ, prope cacumina ramorum ad 240–350 μ, autem, gradatim attenuata; cacumina ramorum quae haptera formant plerumque paulo angustiora quam alia, membranae cellularum striatae, usque ad 9 μ crass., haptera septata aut non septata.

Planta typica, Gilbert num. 10077 nomine, in saxis et in lacubus minuente aestu relictis crescens, ad litus loci Molokai oppositi Mokuhooniki Is., Hawaii dicti, m. June 6 an. 1959.

Plants cushion-like, spreading, several centimeters wide, 1–2 cm. high, common on rock and coral substratum in full sunlight or shade; thallus of cylindrical, sparingly to profusely branched filaments, the branch formed without cross-wall at its base but arising beneath a cross-wall of the filament which bears it; branching usually secund and often curving toward the substratum giving the thallus a repent habit; cross-walls formed between branches, more frequent in lower portions of plant than in upper parts except in those terminal branches which form holdfasts; secondary holdfasts produced on decumbent parts of thallus and occasionally at the tips of branches; filaments variable in diameter, up to 510 (770) μ in diameter, but gradually tapering to 240–350 μ near tips of branches; branch tips forming holdfasts usually somewhat narrower than others; cell walls striated, to 9 μ thick; holdfasts may or may not be septate.

TYPE: *Gilbert 10077,* rocks and tide pools, shore of Molokai opposite Mokuhooniki Island, Hawaii, June 6, 1959.

This species of *Cladophoropsis* has been referred to heretofore in Hawaii as *C. membranacea* (C. Ag.) Børg., and is included by that name in Egerod's (1952: 356) excellent report on the siphonous Chlorophyta. However, the resemblance of this new species to *C. membranacea* is largely superficial. The Hawaiian plant is much coarser and darker green. I have not seen on the Hawaiian material any lateral tenaculae referred to by Børgesen as characteristic of *C. membranacea,* and the rather common formation of holdfasts from the tips of the decumbant filaments sets the Hawaiian plant apart from *C. membranacea. Cladophoropsis robusta* Setchell and Gardner (1924) has filaments as wide as *C. luxurians,* but the branching differs in that it is bilateral and frequent near the upper portion of the plant in *C. robusta,* rather than secund and less frequent, and in that terminal holdfasts on the branches do not occur. I have seen nothing of the annular constrictions at the base of the lower filaments, to which Egerod referred, in either my material or in the collections of Papenfuss which she cited.

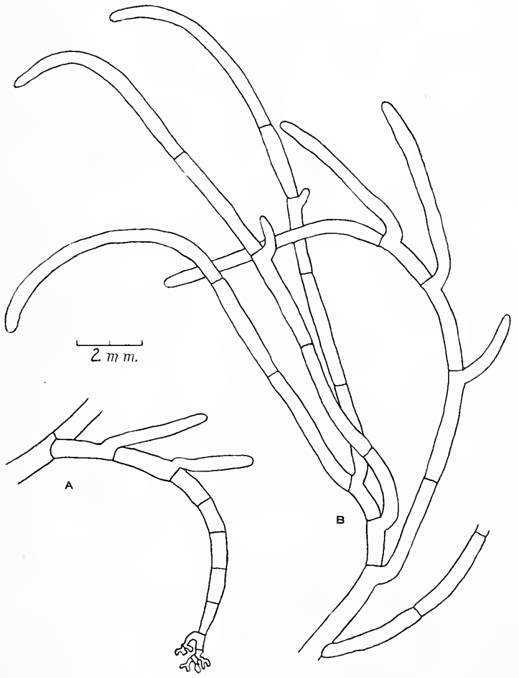

FIG. 3. *Cladophoropsis luxurians* sp. nov. *A,* A terminal branch with holdfast at its tip. *B,* Habit drawing to show secund branching and curving characteristic of the terminal branches.

OTHER COLLECTIONS: *Gilbert 9209,* Hokipa Park, Maui, March 24, 1959; *9335,* near Laie Point, Oahu, April 2, 1959; *9544,* Wailua, Kauai, April 25, 1959; *9841,* Onekehakeha Beach, Hilo, Hawaii, May 22, 1959.

6. *Derbesia fastigiata* Taylor (prox.), 1928, p. 94, pl. 11, figs. 1–3.

Fig. 4, *A–C*

COLLECTIONS: *Gilbert 9012b,* from cement pilings of dock at Kuhio Beach, Waikiki, Oahu, March 11, 1959; *9020,* from cement pilings of dock at Kuhio Beach, Waikiki, Honolulu, Oahu, March 14, 1959.

This plant was at first thought to be undescribed but on comparison with material of *Derbesia fastigiata* Taylor[1] it seemed so similar that it is being listed as near that species. The thallus is 1–2 cm. across and consists of a plexus of interwoven basal and erect filaments. The interwoven basal filaments, the distant branching of the erect filaments, and the fasciculate character of the dichotomous branching when it does occur in the upper part of the erect filaments all suggest *D. fastigiata.* Filaments of the Hawaiian material are 47–79 μ in diameter below the branching portion and the ultimate segments are 14.5–20 μ in diameter a short distance below their rounded tips. In the latter measurement they differ somewhat from Taylor's description, which indicates the ultimate divisions to be 7.5–11 μ in diameter.

In selected specimens the unbranched portions of the erect filaments are up to 4.2 mm. long and the tuft may be up to 4.0 mm. long, but the usual height of the erect portions of the plant is considerably less. The Hawaiian material shows the slight thickening at right angles to the dichotomies referred to by Taylor. Successive dichotomies appear to be at right angles to one another. No complete cross-walls were seen in the erect filaments, although rarely a partially formed callus-like plug was observed in one of the branches immediately above a dichotomy. In the interwoven basal filaments an

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[1] In his new book Taylor (1960; 129) includes *Derbesia? fastigiata* from Florida as a species of uncertain record.

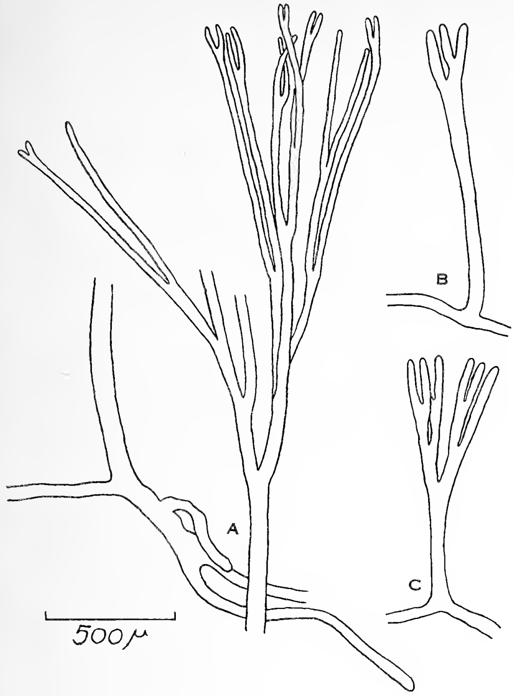

FIG. 4. *Derbesia fastigiata* Taylor (prox.). *A,* An older portion of the filamentous thallus showing an erect filament and a bit of the basal filament. *B, C,* Developing erect branches.

occasional wall is formed, usually in connection with a laterally formed rhizoid-like branch.

Similar to the Florida material, the Hawaiian plants are sterile so it is with some uncertainty that the plant is assigned to *Derbesia.*

7. *Derbesia minima* Weber-van Bosse, 1913, p. 95, fig. 23.

COLLECTIONS: *Gilbert 9109,* Lahaina Junction, Maui, March 22, 1959; *9206,* Hokipa Park, Maui, March 24, 1959; *9323,* from cement pilings, Kuhio Beach, Waikiki, Honolulu, Oahu, March 30, 1959; *9412,* from cement pilings, Kuhio Beach, Waikiki, Honolulu, Oahu, April 9, 1959.

The plants are up to 2.0–2.3 cm. long, with filament branches infrequent, often unilateral; filaments up to 38 μ in largest diameter, decreasing to 20–25 μ diameter near their rounded tips; all collections are sterile.

8. *Halimeda gracilis* Harvey ex J. Ag., 1887, p. 82.

COLLECTIONS: *Gilbert 9776,* washed in at Kailua Beach Park, Oahu, May 13, 1959; *Strasburg* (no number) washed in at Kailua, Oahu, May 19, 1950; *Doty 19133 Y,* coral and sand at 25 fathoms, Makapuu Pt., off Bird Island, Oahu, July 25, 1959.

Although Svedelius (1924: 33) included the Hawaiian Islands in the range of *Halimeda gracilis,* only *H. discoidea* Decaisne and *H. opuntia* (L.) Lamx. were recognized by Egerod (1952) from Hawaii. Hillis (1960: 356), in her recently published monograph on *Halimeda* affirmed the presence in the Islands of *H. gracilis* and cited as a single collection *Setchell and Setchell 10345,* July 12, 1924 (*U. C. 622514*). I have examined this collection, which was also made at Kailua, Oahu, and agree that it is *H. gracilis.* The three additional records above amply confirm the presence of *H. gracilis* in Hawaiian waters. Since all four collections are of material which was either dredged or found unattached in the wash it seems safe to assume that in Hawaii, as elsewhere, this species is found only in deep water.

9. ***Microdictyon japonicum*** var. ***laxum*** var. nov.

Figs. 5, *C, D;* 6

Cellulae frondium basales ut in var. typico; cellulae mediae distalesque quasi eaedem diametro ac var. typicum, 2–6 plo, autem, longiores quam latae; ramificatio eodem in plano, cellulis filiabus in ordinationem alternam aut oppositam aut flagellatam abscissis; segmenta anastomosantia frequentia ad rara; planta, anastomosibus raris, fruticosa ob partes retis et/aut ramorum superpositas, planta anastomosibus frequentibus laxe retiformis, maculis (150) 200–713 μ lat.

Planta typica Gilbert num. 9252 nomine, in rimis proiecturae basalticae in aqua non profunda, fluctu, autem, magno, crescens, in loco McGregor's Pt., Is. Maui dicto, m. Mar. 21, an. 1959.

Basal cells of fronds as in var. *typicum*; intermediate and distal cells approximately same diameter as in var. *typicum* but from 2–6 diam-

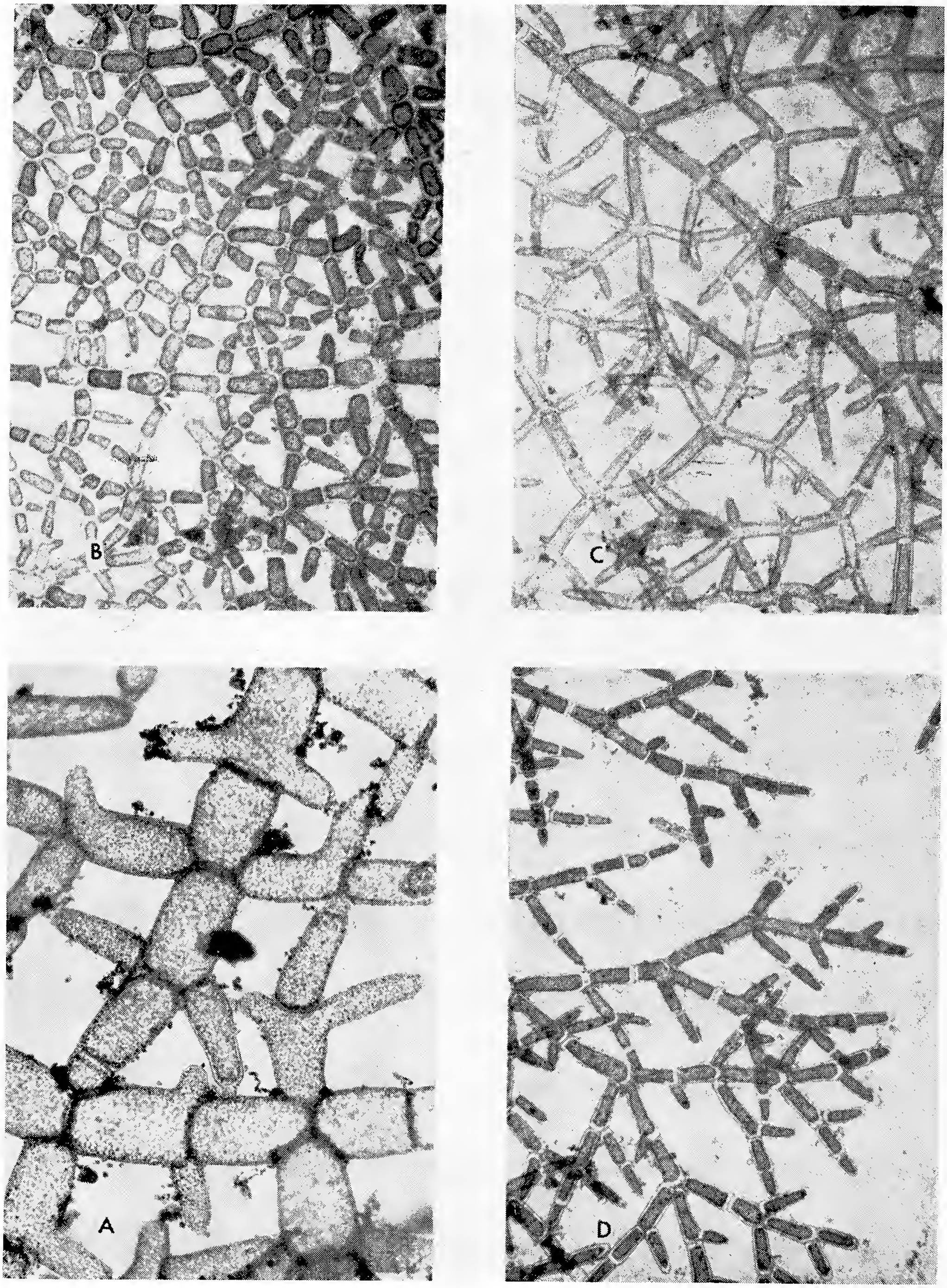

FIG. 5. *Microdictyon* spp. *A, M. montagnei* Harvey ex J. E. Gray. *B, M. japonicum* Setchell. *C, D, M. japonicum* var. *laxum* var. nov., typical appearance of plant in quiet tide pools.

eters long; branching in one plane, the daughter cells cut off in alternate, opposite, or flabellate arrangement; anastamosing segments frequent to rare; portions of net and/or branches overlapping when anastamoses are rare, resulting in a bushy habit; a loose network formed when anastamoses are frequent, with meshes from (150) 200–713 μ wide.

TYPE: *Gilbert 9252*, growing in cracks of basalt ledge in shallow water but where surf was high, McGregor's Pt., Maui, March 24, 1959.

In his monumental work on *Microdictyon*, Setchell (1929: 533) observed that in the Siboga Expedition specimens of *Microdictyon japonicum* from the Borneo Bank there was a tendency toward more delicate plants, with more slender filaments and longer ultimate segments. He also called attention to intermediates from Sailus Besar, Juan Fernandez, and Tongatabu. Setchell felt that the variations were not sufficiently different from the type specimen, however, to be segregated from it.

On the other hand I found a strong tendency among the Hawaiian plants to be divided into two groups, that which represents the type description (Fig. 5, *B*) and that which is here described as *M. japonicum* var. *laxum*. My material represents collections from a wide range of conditions, including quiet tide pools to cracks and surge channels exposed to the full force of waves. In the tide pools a loose network develops (Fig. 5, *C, D*) but the longer cells of the variety remain distinct, thus resulting in much wider meshes and frequent crossing over of segments of the net and of branch tips. Material taken where the water is rough does not develop an extensive network but is characterized, rather, by a bushy habit as the result of much overlapping of branches and the development of relatively few anastamoses (Fig. 6).

Inasmuch as the pattern of relatively longer cells, wider meshes, and overlapping of branches of segments of net (where formed), persists in the Hawaiian material and is found together with the typical form of development, it seems desirable to recognize as new *Microdictyon japonicum* var. *laxum*.

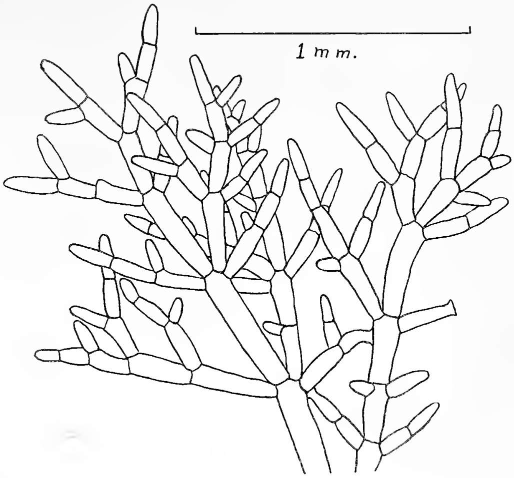

FIG. 6. *Microdictyon japonicum* var. *laxum* var. nov. Portion of a frond showing the bushy character developed when the plant is exposed to rough water.

OTHER COLLECTIONS: *Gilbert 9510*, Kaena Pt., Oahu, April 18, 1959; *9561*, Moloaa Bay, Kauai, April 25, 1959.

10. *Microdictyon montagnei* Harvey ex J. E. Gray, 1866, p. 69.

Fig. 5, *A*

COLLECTIONS: *Gilbert 9019*, from cement pilings, Diamond Head side of War Memorial Natatorium, Waikiki, Honolulu, Oahu, March 14, 1959; *9290*, ½ mile E. of McGregor's Point, Maui, March 25, 1959; *9388*, Ala Moana Park, Honolulu, Oahu, April 8, 1959.

The material agrees well with published descriptions. Some of the blades are up to 5.0 cm. in width and show only slight tendency at their margins for filaments making up the blade to branch in several planes; otherwise the plants are plane-bladed as in other species of *Microdictyon*.

I am retaining this species in the genus *Microdictyon* although some (as Egerod, 1952: 332) would transfer it to *Boodlea*.

11. ***Pseudochlorodesmis parva*** sp. nov.

Fig. 7

Planta filamentosa, ubique siphonacea, e parte basali prostrata in coralio inclusa, ramos erectos discretos efficiente constans, pars basalis abunde et irregulariter ramosa, diametro magnopere varians, 15–35 μ, alternis angusta et lata, sic piluliformis aspectu, rami erecti ad 5 mm. long., plerumque breviores, diametro aequi, plerumque simplices, interdum, autem, semel (rarissime bis) ramosi, 29–35 (40) μ diam.; rami filamentorum erectorum laterales, saepe, autem, subdichotomosi apparentes. Reproductio ignota.

Planta typica, Gilbert num. 9767 nomine, in saxis corallinis ⅔–2 metra profundis crescens, in rupibus corallinis submarinis oppositis loco Marine Biological Laboratory, Waikiki, Honolulu, Is. Oahu, m. May 9, an. 1959.

Plant filamentous and siphonous throughout, consisting of a prostrate basal portion embedded in coral, which gives rise to erect free branches; the basal portion abundantly and irregularly branched, extremely variable in diameter ranging from 15–35 μ, alternately narrow and wide, thus producing a bead-like appearance; erect branches to 5 mm. in length, usually less, uniform in diameter, mostly simple but occasionally once-branched (very rarely twice), measuring 29–35 (40) μ diameter; branches of erect filaments lateral but often appearing subdichotomous. Reproduction unknown.

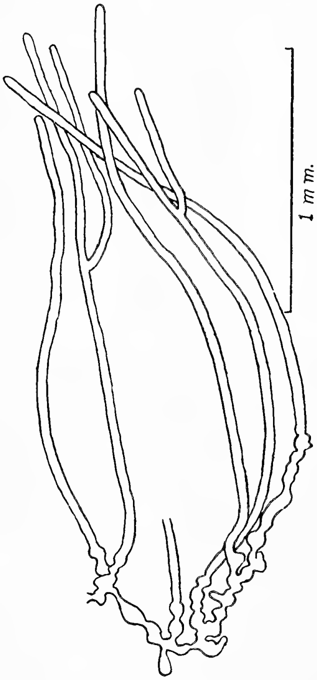

FIG. 7. *Pseudochlorodesmis parva* sp. nov. Habit drawing to show prostrate and erect branches.

TYPE: *Gilbert 9767*, growing on coral rocks, 2–6 feet deep, reef opposite Marine Biological Laboratory, Waikiki, Honolulu, Oahu, May 9, 1959.

This plant appears as a soft felt-like growth on the surface of corals. In order to study the basal portion of the plant it is necessary to cut out pieces of the coral in which the plant is growing and to decalcify the specimen.

Except for its diminutive size and the infrequency of branching in the erect filaments, this species is suggestive of *Pseudochlorodesmis furcellata* (Zanard.) Børgesen (1925: 78). While similar to *P. tenuis* Ercegovic (1957: 33–35) in diameter of the erect filaments, *P. parva* differs from that species in the scarceness of branches in its erect filaments, the bead-like character of its basal filaments, the lack of repent branches, and in the absence of the cluster of short lateral branches sometimes occuring at the tips of the longer filaments.

OTHER COLLECTIONS: *Gilbert 9661,* Anahola Beach, Kauai, April 29, 1959; *10141*, Waikiki, Honolulu, Oahu, June 10, 1959.

12. *Tetraselmis tetrathele* (West) Butcher, 1959, p. 64.

COLLECTION: *Gilbert 9765*, Koko Head Parking Lot, Oahu, May 7, 1959.

This interesting alga was found in abundance in a high-lying spray pool that was obviously fouled with bird excreta. I am assigning it to this species but with considerable uncertainty. The cells were slightly broader (up to 10–11 μ) than some published descriptions (as *Platymonas subcordiformis* (Wille) Hazen, 1921: 251).

13. ***Udotea? abbreviata*** sp. nov.

Fig. 8, *A–C*

Plantae ubique siphonaceae partem basalem irregulariter ramosam frondes erectas laxe ordinatas efficientem habentes; frondes e stipite monosiphonaceo, supra ter ad quinquies dichotome ramoso, constantes, dichotomiis successivis magna ex parte eodem in plano, confertis aut distantibus; filamenta frondium non calcifacta,

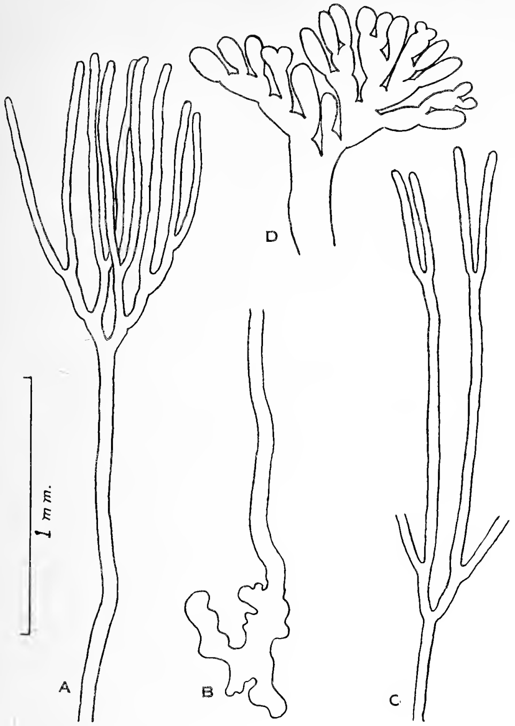

FIG. 8. *Udotea? abbreviata* sp. nov. *A, B,* Upper and lower portions of the same plant. *C,* Upper portion of a plant to illustrate that dichotomies may be close or distant. *D, Udotea javensis,* a young plant.

non cohaerentia, sine constrictionibus super dichotomias; plantae ad 5 mm. alt., stipite ad 72 μ diam., ordines successivos ramulorum minorum habentes, ramulis terminalibus 25–38 μ lat.

Planta typica, Gilbert num. 9511 nomine, in saxis calcariis 1 ad 1½ m. infra superficiem crescens, in rupibus submarinis corallinis oppositis loco Marine Biological Laboratory, Waikiki, Honolulu, Is. Oahu dicto, m. Apr. 21, an. 1959.

Plants completely siphonous with an irregularly branching basal portion giving rise to erect loosely organized fronds; fronds consisting of a monosiphonous stalk branching above dichotomously three to five times, the successive dichotomies largely in one plane and close or distant; filaments of frond uncalcified, not cohering, and without constrictions above the dichotomies; plants to 5 mm. in height, diameter stalk to 72 μ, with successive orders of branches smaller in size with the terminal branchlets from 25–38 μ in width.

TYPE: *Gilbert 9511,* on calcareous rocks, 3–4 feet below surface on reef opposite Marine Biological Laboratory, Waikiki, Honolulu, Oahu, April 21, 1959.

These small plants, which are very easily overlooked in the field, were thought for some time to be either young or depaupurate plants of *Udotea javensis* (Montagne) A. & E. S. Gepp (1911). After study of many plants of *U. javensis,* both young (Fig. 8, *D*) and old, I came to the conclusion that the plants described above did not represent that species.

They differ from *U. javensis* in that the entire stature of the plant is smaller, including the diameter of the monosiphonous stalk, in the lack of calcification, in the absence of constrictions above the dichotomies, and in the fewer dichotomies of the filaments making up the blade. In their dimorphic habit and free noncalcareous filaments the plants are suggestive of *Flabellaria minima* (Ernst) A. & E. S. Gepp (1911), which is generally assigned to *Udotea,* but the Hawaiian plants differ from this species in their smaller stature, their much more slender filaments, and in the fact that the stalk is never multisiphonous. Due to the uncalcified character of the filaments making up the blade there is real uncertainty as to the correct genus to which this species should be assigned.

14. *Ulva reticulata* Forsskål, 1775, p. 187.

COLLECTIONS: *Gilbert 9013,* entangled on other algae near War Memorial Natatorium, Waikiki Beach, Honolulu, Oahu, March 11, 1959; *9125,* Kahana, West Maui, March 22, 1959; *9547,* on reef flat just N. of Wailua River mouth, Wailua, Kauai, April 25, 1959; *9947,* Kahaluu Park, S. of Kailua, Hawaii, May 26, 1959; *10108,* Napelehu, Molokai, June 7, 1959.

It is difficult to understand why this well-known *Ulva* has not been reported previously from Hawaii. I found it one of the commonest elements in the green algal flora of the five islands which I visited.

REFERENCES

AGARDH, J. G. 1847. Nya alger från Mexico. Svenska Vetensk. Akad., Ofversigt af.... Förhandl. 1847(1): 5–17.

——— 1887. Till algernes systematik. VIII. Siphoneae. Lunds Univ. Årsskr., 23: 1–174, pls. 1–5.

BØRGESEN, F. 1911. Some Chlorophyceae from the Danish West Indies, I. Bot. Tidsskr. 31: 127–152.

——— 1925. Marine algae from the Canary Islands . . . I. Chlorophyceae. K. Danske Vidensk., Biol. Meddel. 5(3): 1–123.

——— 1949. Some marine algae from Mauritius. Additions to the parts previously published. Det Kgl. Danske Vidensk. Selskap 21(5): 3–48, 2 pls.

BUTCHER, R. W. 1959. An introductory account of the smaller algae of British coastal waters, Part I. Introduction and Chlorophyceae. Fishery Investigations Series IV, Ministry of Agriculture, Fisheries and Food, London. 74 pp.

DAWSON, E. YALE. 1956. Some marine algae of the southern Marshall Islands. Pacific Science 10(1): 25–66.

EGEROD, LOIS. 1952. An analysis of the siphonous Chlorophycophyta....Univ. Cal. Publ. Bot. 25(5): 325–454, 14 pls.

ERCEGOVIC, A. 1957. La flore sous-marine de l'ilot de Jabuka. Acta Adriatica 8(8): 1–130.

EUBANK, LOIS L. 1946. Hawaiian representatives of the genus *Caulerpa*. Univ. Cal. Publ. Bot. 18(18): 409–432, pl. 22.

FORSSKÅL, P. 1775. Flora Aegyptiace-arabica. Hauniae. 220 pp., 1 map.

GEPP, A., and E. S. GEPP. 1911. Codiaceae of the Siboga Expedition. Siboga Expeditie Monog. 62. 150 pp., 22 pls.

GRAY, J. E. 1866. On *Anadyomene* and *Microdictyon*, with the description of three new allied genera discovered by Menzies in the Gulf of Mexico. Jour. Bot. 4: 41–51, 65–72, pl. 44.

HAZEN, T. E. 1921. *Platymonas subcordiformis* (Wille) Hazen. In: I. F. Lewis and W. R. Taylor, Notes from the Woods Hole Laboratory. Rhodora 23: 249–256, pl. 133.

HILLIS, L. 1960. A revision of the genus *Halimeda*. Pub. Institute of Marine Science 6(1959): 321–403.

LAMOUROUX, J. V. 1809. Memoire sur trois nouveaux genres de la famille des algues marines. Jour. de Bot., 2: 129–135, 1 pl.

OKAMURA, K. 1897. On the algae from Ogasawarajima (Bonin Islands). Bot. Mag. (Tokyo) 11: 1–16.

SETCHELL, W. A. 1929. The genus *Microdictyon*. Univ. Cal. Publ. Bot. 14: 453–588.

SETCHELL, W. A., and N. L. GARDNER. 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The marine algae. Proc. Cal. Acad. Sci., 4th ser., 12: 695–949.

SVEDELIUS, NILS. 1924. On the discontinuous geographical distribution of some tropical and subtropical marine algae. Arkiv fő́r Botanik 19(3): 1–70.

TAYLOR, W. R. 1928. Marine algae of Florida with special reference to the Dry Tortugas. Carn. Inst. Wash. 25 (Publ. no. 379): 1–219, 37 pls.

——— 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. Univ. of Mich. Press. 870 pp.

WEBER-VAN BOSSE, A. 1913. Liste des algues du Siboga I. Myxophyceae, Chlorophyceae, Phaeophyceae....Siboga Expeditie Monograph 59a. 186 pp., 5 pls.

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Rainfall and Runoff in the Leeward Koolau Mountains, Oahu, Hawaii[1]

JOHN F. MINK[2]

DURING THE COURSE of the investigation of the ground-water resources of southern Oahu, made by the U. S. Geological Survey in cooperation with the State of Hawaii, a water-budget study was used to estimate the quantity of ground water available for development. The effective use of this approach required a detailed knowledge of rainfall and runoff in the area being studied, especially in that part of it lying in the wet Koolau mountains, where most of the ground water is recharged. Past estimates for the rainfall-runoff relationship in this environment were rather speculative, and were based either on extrapolations from areas of lower rainfall or on experience obtained elsewhere. In the present study it became obvious that this relationship would have to be refined.

At the start of the investigation adequate long-term records of rainfall were available for the Schofield plateau and the coastal plain, but records for the rugged central Koolau Range were spotty and not definitive. To alleviate this deficiency, 17 storage rain gages were installed in that part of Kipapa Stream basin that is representative of the high rainfall region of the leeward central part of the Koolau Range (Fig. 1). This part of the basin is covered by an unbroken closed forest.

The gages were made of 5-ft lengths of 3-inch aluminum pipe welded shut at one end. Fourteen of the gages were distributed along the ridge on the south side of the valley (Kipapa Ridge) between the isohyet for an average annual rainfall of approximately 70 inches and the summit of the Koolau Range, and 3 were placed on the floor of the valley over the same distance covered by the first 4 gages on the ridge (see Fig. 1). A tipping bucket recording rain gage with an 8-inch catch was paired with the first of the 3-inch aluminum gages in the valley. The differences in rainfall recorded by the 8-inch gage and measured in the 3-inch gage were insignificant in relation to the amount of rain that fell in the intervals between readings (Mink, 1960).

A recording stream gage was constructed where the stream emerges from the forest, coinciding in location with the first of the rain gages (Fig. 1). Thus two of the variables in the water-budget equation were subjected to close measurement. This paper analyzes the records of rainfall and runoff in the basin for 3 complete calendar years (1957–59). Computations of rainfall and runoff quantities are given in millions of gallons to accord with the terminology usually employed in hydrologic investigations in the Hawaiian Islands.

LOCATION AND DESCRIPTION OF KIPAPA BASIN

The basin of Kipapa Stream is in the central part of leeward Oahu, and, over its full extent, it reaches from the crest of the Koolau Range to the junction of Kipapa Stream with Waikakalaua Stream, which is about 2 miles from Pearl Harbor. Only the long and narrow upper third of the basin was included in the study. This part of the basin is almost 5 miles long, ranges in width from about 2,000 to 7,000 ft, and has a drainage area of 4.3 sq miles. The gaging station on the stream is 700 ft above sea level and the rain gage on the ridge overlooking the stream gage is 1,150 ft above sea level. The widest and highest part of the basin is at its east end, near the crest of the range. The average altitude of this part of the crest bounding the valley is 2,650 ft above sea level, and the highest altitude is 2,785 ft.

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[1] Publication authorized by the Director, U. S. Geological Survey. Manuscript received May 8, 1961.

[2] Present address, Board of Water Supply, City and County of Honolulu, Hawaii.

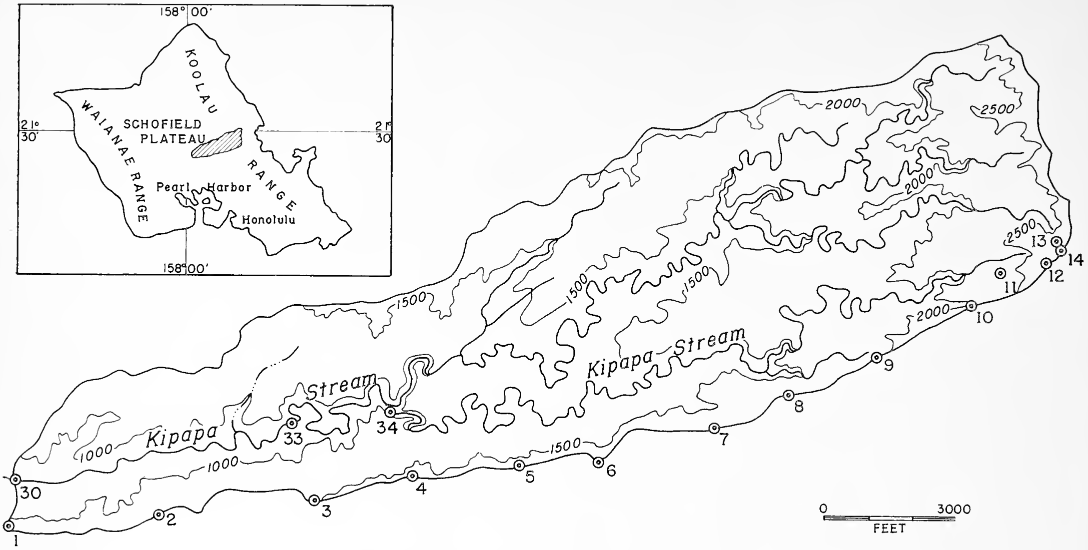

FIG. 1. Map of Kipapa Stream basin showing location of rain gages.

Drainage

The basin of Kipapa Stream, like all the stream basins in the central Koolau Range, is the result of consequent drainage that originally followed a radial pattern on the surface of the Koolau volcanic dome. The present direction of drainage is approximately normal to the northwest trend of the range. The principal drainage pattern in the basin consists of a single channel that extends about one third of the way from the gaging station toward the crest of the range, after which it divides into a main branch and a secondary branch, which extend to a break in slope half a mile from the summit. Near the summit the branches flare out into several smaller watercourses. Throughout the basin small tributaries cascade down the steep sides of the valley into the principal branches. Only the main branch is perennial. The secondary branch has flow during most of the year, but the small tributaries are active only during periods of rainfall. Below the gaging station the flow of the stream is ephemeral.

The main valley is V-shaped in cross-section, and has walls with slopes averaging 25° to 30°. The small tributaries have incised sharp embayments in the steep walls. Over the first 22,000 ft along its longitudinal axis the gradient of the bottom of the valley is about 3°, but about 2,500 ft from the crest the over-all gradient of the basin abruptly increases to approximately 20° and each stream becomes a series of small cascades. Along that part of the stream having the gentle gradient the bottom of the main valley is 100–200 ft wide; in the upper steep part of the basin the valley bottoms are only as wide as the stream channels. The width of the main channel throughout the valley is ordinarily less than 20 ft.

The closed montane forest that covers the drainage basin consists of dense vegetation growing over all but a few of the most precipitous slopes. The typical larger plants include *ohia lehua, koa,* tree fern, false staghorn fern (*uluhe*), guava, and ginger. Near the southwest end of the area groves of eucalyptus trees are common. A mat of vegetation below the larger plants provides an almost complete cover over the soil. The thick vegetation discourages travel within the area except along an established ridge trail and in the stream bed.

Geology

All of Kipapa basin is underlain by basalt and olivine basalt of the Koolau volcanic series. These basalts occur as thin flows of pahoehoe and aa that dip about 5° toward the southwest. Neither dikes nor pyroclastic materials are found in the basin. Measurements taken at vertical sections along the stream show a higher proportion of aa than pahoehoe, but the difference may be based upon a sample too small to be significant. The proportion of aa-clinker could be expected to increase, however, with distance from the rift zone of the Koolau dome from which the lavas effused, which is approximately coincident with the crest of the range.

The rocks of the Koolau volcanic series weather quickly and give rise to soils belonging to the Latasol suborder. Within the Latasol classification are the groups of soils that form through the laterization process. In Hawaii the stages of laterization are determined chiefly by the amount and distribution of rainfall. According to the Soil Survey of Hawaii (Cline et al., 1955), the soils of the mountain section of Kipapa basin are classed generally as Lithosols because of their lack of a genetic profile. However, it is probable that the soils of the wetter portion of the basin are akin to the Hydrol Humic Latasols whereas those nearer the stream gage resemble Humic Latasols. Hydrol Humic Latasols are typical of forest-covered areas with very high rainfall. They are continually wet, and their moisture content accounts for a large proportion of their total weight. The Humic Latasols are less highly weathered and are subject to occasional drying. Both of these soils have high porosity and permeability and are able to hold large amounts of water.

The floor of the valley above the stream channel consists of an irregular terrace, which is underlain by soil intercalated with small lenses of gravel, the whole of which averages from 5 to 8 ft in thickness. The valley walls, except where cliffs occur, are covered by 2 to 3 ft of soil. Small patches of highly weathered talus and large boulders are common in the basin. The stream bed usually consists of deposits of poorly sorted gravel 3 to 5 ft thick, but over short stretches the stream may flow directly on the weathered parent basalt. The mixed gravel contains particles ranging in size from sand to boulders, all of which are moderately to well rounded. Virtually no silt or mud occurs in the stream bed. The smaller pieces of gravel commonly are completely weathered and the larger fragments have a fresh core. Fragments derived from pahoehoe are generally smaller, more rounded and more thoroughly weathered than those from aa.

Heavy, dense vegetation covers the terrace in the valley bottom. The terrace lies about 5 ft above the stream during normal flow, but it is often inundated by high runoff from frequent heavy rains in the narrow valley. During normal flow the stream is free of sediment, and even during flooding it is only slightly turbid. The turbidity probably consists mostly of organic debris and colloidal material from weathered basalt. The stream is in a down-cutting phase, but most of the cutting is due to chemical erosion and little physical erosion is taking place. The thick carpet of vegetation that covers the highly porous soil mantle effectively retards the removal of soil. Also the basalt is highly permeable and can absorb water at a high rate. Occasionally small landslides occur where slippage takes place between the weathered bedrock and the residuum above it, but the sliding material generally is trapped on the slopes, and quickly becomes revegetated. Any of the material from landslides that reaches the stream becomes part of the channel gravel and remains within the drainage basin. However, in the lower part of the basin outside the area of study, where rainfall is less and the land is cultivated, physical erosion is active, and it is this region which provides the sediment that discharges into Pearl Harbor.

RAINFALL

Most of the rain that falls in the Koolau Range is the direct result of either of the two principal atmospheric circulation patterns. The cyclonic pattern associated with low-pressure systems brings storms from which general rains often fall, and the anti-cyclonic pattern associated with high-pressure systems results in orographic rainfall. The precipitation from cyclonic storms is uniformly distributed over wide areas, whereas orographic rainfall is usually restricted to the mountain region. Cyclonic storms are most common during the winter months (November through March), although they occur infrequently during the remainder of the year. Orographic conditions occur throughout the year but are most continuous during the summer period.

The areal distribution pattern of rainfall in the Koolau Range is determined by the orographic component. Orographic rainfall is the result of cooling of trade-wind air as it flows from the northeast over the mountain barrier, which lies approximately normal to the direction of flow of the air mass. The maximum rainfall is about half a mile leeward of the crest of the range. Farther to the southwest it decreases

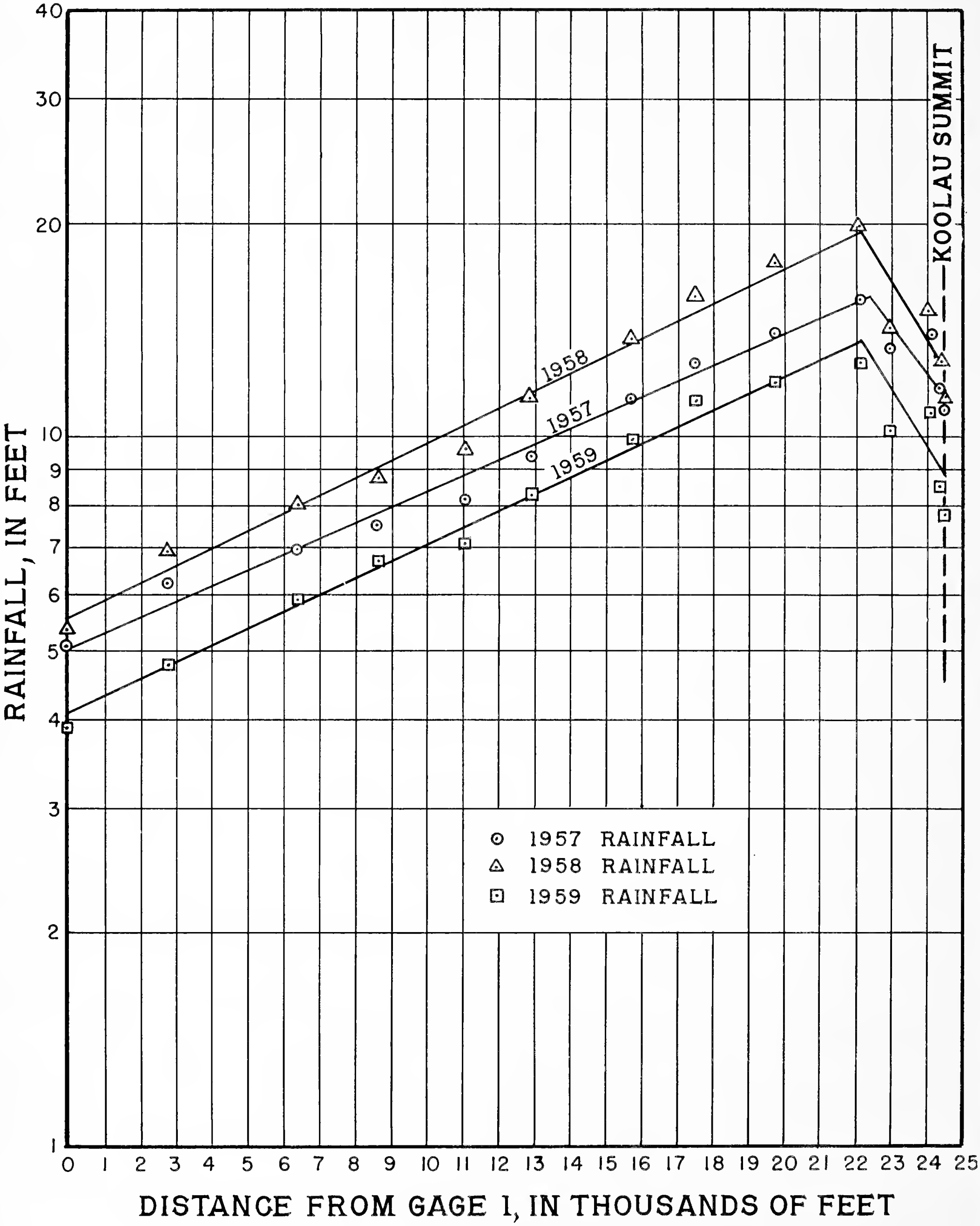

FIG. 2. Rainfall as a function of distance from gage 1 for 1957–59.

TABLE 1

RAINFALL SUMMARY

GAGE	DISTANCE FROM GAGE 1 (ft)	ANNUAL RAINFALL (ft) 1957	1958	1959	1957–59 av.
Ridge					
1	0	5.07	5.37	3.90	4.79
2	2.750	6.20	6.93	4.76	5.97
3	6 400	6.89	8.02	5.87	6.93
4	8,650	7.42	8.79	6.63	7.62
5	11,050	8.17	9.59	7.05	8.27
6	12.900	9.33	11.37	8.28	9.66
7	15,700	11.36	13.72	9.82	11.63
8	17,500	12.69	15.63	11.15	13.16
9	19,730	13.92	17.54	11.88	14.45
10	22,130	15.52	19.87	12.65	16.01
11	23,000	13.38	14.34	10.05	12.59
12	24,100	13.91	15.01	10.78	13.23
13	24.400	11.70	12.71	8.54	10.98
14	24,500	10.58	11.38	7.66	9.88
Valley					
30	0	5.69	6.23	4.14	5.36
33	6,500	7.92	8.80	6.24	7.66
34	8,800	9.13	10.17	7.55	8.95

according to a geometric regression. The point of maximum rainfall apparently coincides very closely with the location of rain gage 10 (Fig. 1). Because cyclonic rains have general uniform areal distribution, they increase the total amount of rainfall over an extended period during which orographic rains may also occur but do not alter the distribution pattern (Mink, 1960).

Early in the investigation it became obvious that the decrease in rainfall in the leeward direction from the point of maximum fall follows the simple decay expression:

$$y = ke^{-ax}$$

where y is the rainfall at any distance, x, from the point of maximum fall; k is the rainfall at the maximum; a is a constant of decrement; and e is equal to 2.7128. By referring the origin to gage 1 for ease of handling in volumetric computations, the rainfall may be considered to increase toward the point of maximum fall, and the equation then becomes:

$$y = ke^{ax}$$

where y is the rainfall at any distance, x, from gage 1, k is the rainfall at gage 1, a is a constant of increment; and e is equal to 2.7128. The effect of cyclonic rain on this equation would be to increase the value of k. Between the point of maximum fall and the crest of the Koolau Range the rainfall appears to decrease geometrically, but the relationship is considerably less perfect than that of the increase from gage 1 (Mink, 1960).

Figure 2 gives plots on semilogarithmic paper of rainfall on Kipapa ridge as a function of distance from gage 1 to gage 14, which is on the Koolau summit, during the years 1957–59. The linear relationships are drawn to accord with regression equations derived by the least squares method. These equations and the equation for the 3-year average are given in Table 2 with pertinent statistical parameters. In all cases the parameters suggest that the equations are highly reliable. A significance test of each of the correlation coefficients shows that it is unlikely that the correlation is a matter of chance. The Sy (standard error of estimate) values fall very close to the line of regression for each of the 3 years and for the 3-year average. In terms of deviation in rainfall at any given point on the line of regression the Sy values are 1.8% for 1957, 7.5% for 1958, 3.9% for 1959, and 4.5% for the 3-year average.

Rainfall on the valley floor is somewhat higher than on the ridge above it on which gages 1–14 are located (see Table 1). The 3 gages on the valley floor cover the same distance relative to the crest as the first 4 gages on the ridge (Fig. 1). Gage 30 lies opposite gage 1, gage 33 is opposite gage 3, and gage 34 is opposite gage 4. Gages on the valley floor cover only the lower third of the distance covered by gages on the ridge, but the plot of their rainfall as a function of distance toward the crest parallels the relationship obtained on the ridge. Assuming that this parallelism holds all the way to the point of maximum rainfall, which approximately coincides with the break in slope, then only the value of k in the rainfall equations as determined for the ridge would be affected.

The 3-year period covered here was, overall, considerably drier than would be expected on the basis of long-term averages obtained elsewhere in the Koolau Range. The year 1957 was moderately dry, having about 20% less rainfall than normal in the wet mountains; 1958 was nearly normal but only because of heavy summer rains; and 1959 was extraordinarily dry, having about 35% less rainfall than normal in the wet mountains. However, the absolute quantities of rainfall have no significant effect on the relative variations in rainfall as expressed in the equations.

Use of the transformed regression equations (see Table 2) enables simple and accurate calculations of the volume of rainfall in the basin. The volume of rainfall is obtained by taking the product of the area under the rainfall-distance curve for the portion of the basin subject to the curve and the width of the basin as follows:

$$V=z\int_{0}^{x_n} ke^{ax}dx$$

where V is the volume of rainfall, z is the width of the basin, and x_n is the distance between gage 1 and the point of maximum rainfall, which is taken to be at gage 10. However, because the outline of the basin is irregular, no single average width is applicable. Therefore, to assure accurate computations, the basin between gage 1 and gage 10 was divided into 22 strips, each of which covered 1,000 ft along the axis of the valley. The distance across the basin measured at the midpoint of each strip then became the width of the basin for that particular strip. The volume of rainfall could then be calculated as follows:

$$V=z_1\int_{0}^{x_1} ke^{ax}\,dx+z_2\int_{x_1}^{x_2} ke^{ax}\,dx+\dots z_{22}\int_{x_{21}}^{x_{22}} ke^{ax}\,dx$$

where V is the volume of rainfall and z is the width of the basin for each strip. The volume computed by this method for 1957 fell within 3.5% of the volume determined by careful planimetry of an isohyetal map whose spacings of isohyets conformed with the equation. The value of k in all the computations was taken as the mean between the rainfall at gage 1 and gage 30 in the valley below.

For the region between the maximum rainfall and the crest of the range the average rainfall was used in volume computations because

TABLE 2

RAINFALL REGRESSION EQUATIONS FOR KIPAPA RIDGE, ANNUAL BASIS

PERIOD	REGRESSION EQUATION*	COEFFICIENT OF CORRELATION (r)	STANDARD ERROR OF ESTIMATE (Sy) (log units)	TRANSFORMED REGRESSION EQUATIONS*
1957	$\log_{10}y=.0221x+.7000$	.9987	.0078	$y=5.01\ e^{.0509x}$
1958	$\log_{10}y=.0255x+.7346$	.9847	.0313	$y=5.43\ e^{.0586x}$
1959	$\log_{10}y=.0237x+.6073$	.9950	.0165	$y=4.05\ e^{.0546x}$
1957–59 (average)	$\log_{10}y=.0235x+.6886$	.9933	.0190	$y=4.88\ e^{.0541x}$

* y=rainfall (ft); x=distance (ft) from gage 1 toward summit.

of the imperfect regression relationship. The volume thus computed for 1957 nearly equaled the volume determined by planimetry.

Rainfall volumes for selected periods other than annual were obtained similarly when the rainfall included an orographic component. The equations for these periods were graphically derived, however, rather than by the method of least squares. These equations are believed to be sufficiently accurate to give significant results. For periods during which only cyclonic rains fell, volumes were computed by taking the average rainfall for the basin, because cyclonic rainfall is uniformly distributed. Two such periods were selected for analysis. For each of these periods the total average catch amounted to somewhat more than 14 inches, and for each period the difference in catch among the gages was less than 10%.

STREAM FLOW

Kipapa Stream has a perennial flow at the gaging station near Wahiawa, although the minimum flow is only a few thousand gallons per day. The part of the basin above the station lies far above the basal water table, which is about 25 ft above sea level in the Pearl Harbor region. It also lies southwest of the high-level ground water in the dike complex, so that virtually all stream flow derives either from immediate rainfall or from rainfall stored temporarily in the porous soil and vegetative mantle. A very small part of the stream flow may be water discharging from small, perched aquifers on local impermeable layers in the basalt. Aside from information obtained from field observations on the movement of water in the basin, evidence of the relationship between stream water, rainfall, and soil water is apparent also from the chemistry of each of these waters.

Figure 3 is a plot of specific conductance as a function of chloride for Kipapa Stream water, rainfall, soil water, stream water flowing from dike compartments in the Koolau Range, and water from tunnels penetrating into Koolau dike compartments. The plots show that at similar chloride concentrations the dike stream and tunnel waters have the highest conductances, suggesting that they have a higher burden of dissolved solids acquired during a longer period of contact with the restraining environment. The plots also illustrate a close relationship between Kipapa Stream water, rainfall, and soil water, as distinct from the relationship between the dike stream and tunnel water. Such relationships may be useful in determining whether other mountain streams whose sources of water are unknown have a significant dike-water component. The fact that virtually all the flow of Kipapa Stream derives immediately from rainfall and soil water within the basin precludes uncertainties in analysis that would arise if water moving to the stream from outside the basin were a component in the streamflow.

Kipapa Stream is "flashy" and responds quickly to rainfall. Figure 4, which is a flow-duration curve for the stream at the gaging station, illustrates the highly variable flow characteristics of the stream. The curve is based on flow records for the 3 calendar years, 1957–59. Although this period was drier than normal, the curve clearly indicates the wide range of flows expectable for the stream. The central measures of tendency and the maximum and minimum daily flow for each of the calendar years and the 3-year average are given in Table 3.

The relatively rapid return of the stream to base flow following rainfall is suggested by the flow-decay curves in Figure 5. These curves represent the cumulative per cent of the measured daily runoff plotted as a function of days after isolated storms that were restricted to about a 1-day period. Prior to each isolated storm the flow of the stream was at base level, and after each storm no rain fell in the basin during the interval of decay. The curves indicate that more than 99% of runoff traceable to each storm occurs within 10 days after the storm. No significant difference in decay time was apparent between orographic rains and cyclonic storms.

Miscellaneous flow measurements made with a current meter in Kipapa Stream from a point about a mile downstream from the gaging station to the fork in the stream at rain gage 34 during low-flow periods provided the interesting, and unexpected, conclusion that the stream acts as either a gaining or a losing stream, depending upon antecedent rainfall conditions in the basin. For periods preceded by moderate to high rainfall it continually gains from the fork to about ½ mile below the gaging station, prob-

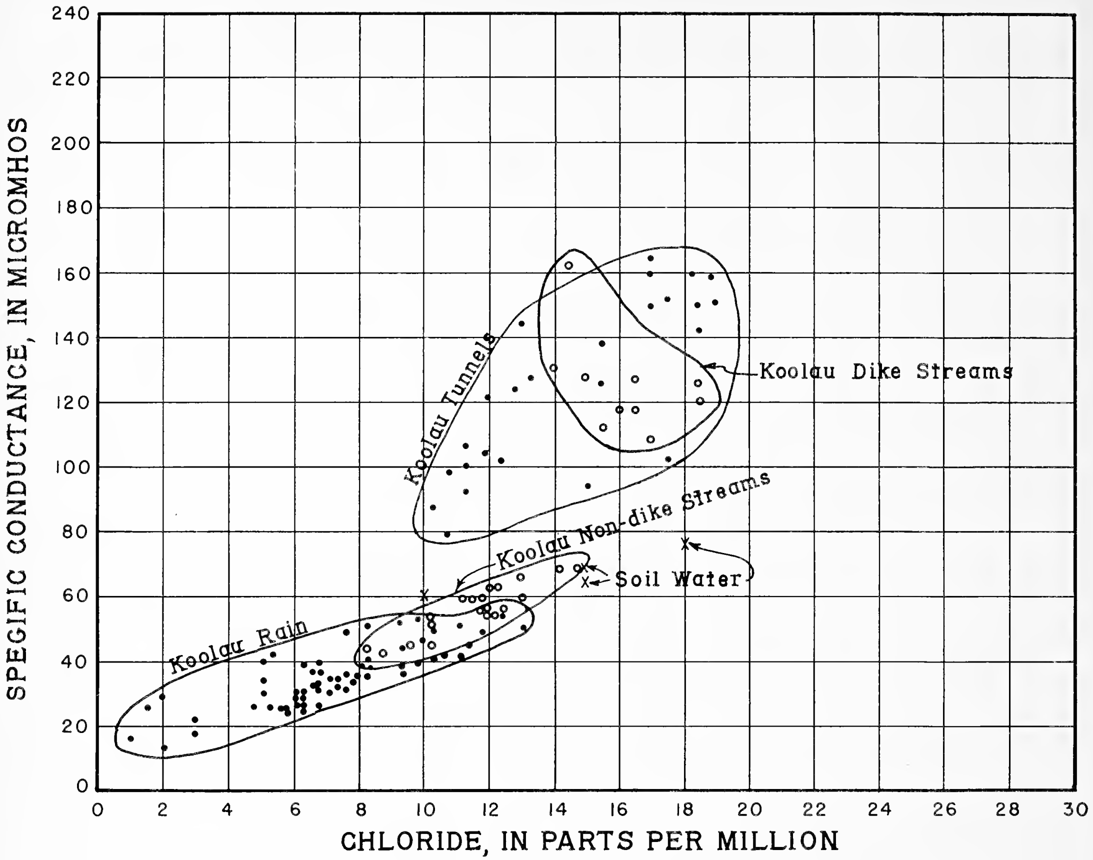

FIG. 3. Specific conductance-chloride relationship for various types of mountain water.

ably because the increase in terrace area downstream provides a concomitant increase in water stored in the soil. However, after periods of low rainfall, the flow decreases progressively in the downstream direction, because storage in the alluvial terrace is at a minimum and loss through the stream bed exceeds replenishment from the terrace deposits.

RAINFALL-RUNOFF RELATIONSHIPS

An appreciable amount of data relating rainfall and runoff has been reviewed in the literature but most of it refers to areas with temperate climates. Langbein et al. (1949) summarized annual runoff in the United States and related rainfall and runoff for selected drainage basins throughout the country. Similar data of a general nature are included in a study by Langbein and Schumm (1958) relating sediment yield to mean annual precipitation. In these works the maximum rainfalls considered are approximately 60 inches per year, which in the Temperate Zone represents a humid climate. However, the relationships suggested evidently are not applicable to the wet Koolau mountains. For instance, the extrapolation of the annual rainfall-runoff relationship given in Langbein and Schumm (1958: 1077, fig. 1), adjusted to a mean annual temperature of 70 F, which approximates conditions in the central Koolau mountains, would give a considerably higher ratio of runoff to rainfall than actually occurs in these mountains.

In Table 4 are listed rainfall and runoff quantities, and runoff as a percentage of rainfall in upper Kipapa basin for the 3 years of record, the 3-year average, and selected shorter periods.

TABLE 3

DAILY FLOW IN KIPAPA STREAM IN MILLION GALLONS PER DAY

PERIOD	MEAN	MEDIAN	PRINCIPAL MODE	MINIMUM	MAXIMUM
1957	5.6	1.1	1.5	.01	145
1958	8.2	1.4	1.5	.08	388
1959	3.2	.45	.15	approx. 0	102
1957–59	5.7	.88	1.5	approx. 0	388

The rainfall volumes were computed as outlined previously in this paper, and the runoff values were obtained from the daily stream-gage records. In cases where runoff had not returned to base flow before the end of the selected period, the proportion flowing beyond the limits of the period that was traceable to rain falling during the period was determined by using the cumulative decay curves in Figure 5. This was needed most for the isolated cyclonic storm of March 5–6, 1958. In general, however, the shorter periods were chosen so that the stream was at low flow at the beginning and at the end of the period. The rain gages were read on the first and last day of each period. Both the wettest and driest intervals between rain-gage readings for the 3 years of record are included in Table 4. The remarks column suggests the rainfall conditions in the basin relative to the normal.

The runoff expressed as a percentage of rainfall shows that on an annual basis the ratio of runoff to rainfall is much smaller than would be expected from extrapolation of the generalization determined in humid temperate climates. The ratios for the calendar years and for the 3-year average indicate that the mean annual runoff is 20 to 30% of the mean annual rainfall in the basin, although in the very dry year of 1959 only 13.6% of the rainfall was accounted for as runoff. The reduction in streamflow during dry years is proportionately greater than the reduction in rainfall.

In a very wet 26-day period of predominantly cyclonic rainfall in January, 1957, during which

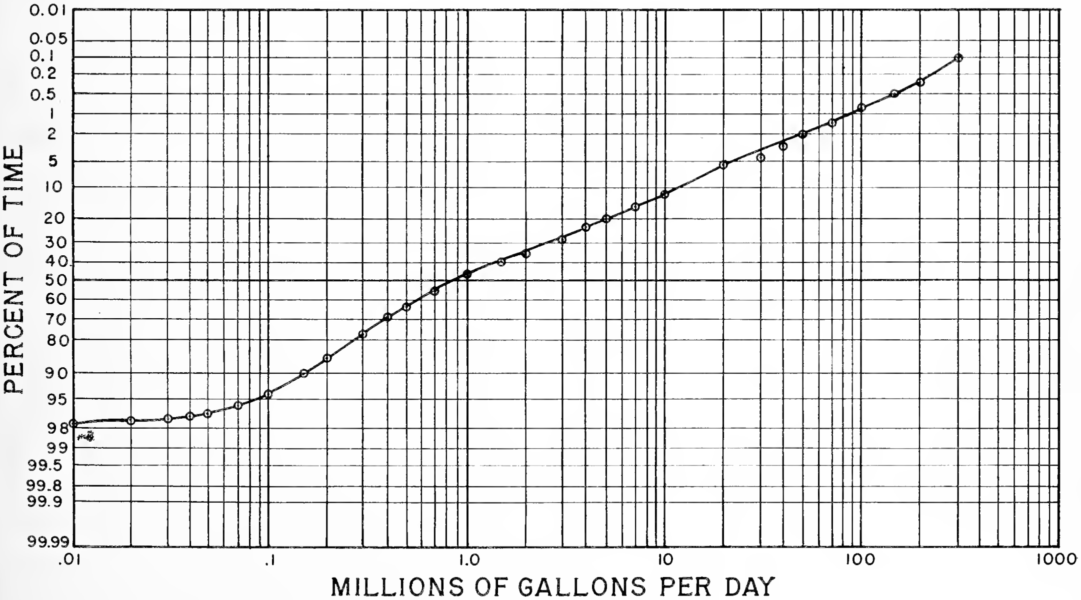

FIG. 4. Flow-duration curve of Kipapa Stream.

an average of 19.5 inches of precipitation was measured in the basin, 38.2% of the rainfall left the basin as runoff. This interval was characterized by moderate daily rains during the first 12 days, heavy daily rains during the following 12 days, and no rain during the remaining 2 days. It is likely that this period represented a nearly minimum opportunity for evapotranspiration because it occurred during a winter month when temperatures were low, the days were short, and clouds covered the basin much of the time. The runoff-rainfall ratio could be expected to approach a maximum under such conditions.

The intense cyclonic storm of March 5–6, 1958, during which an average of 14.2 inches of rain fell in the basin in a 36-hour period, resulted in a total runoff of 33.4% of the total rainfall. The runoff during the 2-day storm accounted for 89% of the total runoff from the storm, and the day following accounted for an additional 7%. The month preceding the storm was unusually dry, having produced only 2.8 inches of rain at the stream-gaging station, and the 20 days following the storm were even drier. A portion of the storm rainfall unquestionably was taken up in satisfying soil-moisture requirements because of the relatively dry antecedent conditions, but nevertheless the runoff-rainfall ratio shows that even under intense storm conditions only a moderate quantity of the rainfall leaves the basin as runoff.

During dry periods the runoff, expressed as a fraction of rainfall, decreases sharply so that in the driest extended period (February 26–April 3, 1957) in the 3-year record only 4.5% of the rainfall flowed from the basin as runoff. According to the U. S. Weather Bureau Climatological Reports, this period included the driest month of March in 10 years. On most days of this dry period the basin had only a spotty cloud cover or none at all, and gentle variable winds predominated. High evapotranspiration rates prevail under such conditions and most of the small quantity of precipitation that fell probably was consumed by vegetation or evaporated. No intense rain showers were reported during the period.

The data in Table 4 suggest that the fraction of cyclonic rainfall running off exceeds that of orographic rainfall. This is reasonable to expect because cyclonic storms normally yield high rainfall amounts that are evenly distributed throughout the basin. On the other hand, orographic rainfall is greatest in the upper portion of the basin but decreases toward the southwest in the direction of the stream-gaging station. During cyclonic storms, the stream thus picks

TABLE 4

RAINFALL-RUNOFF RELATIONS IN THE PART OF KIPAPA BASIN UPSTREAM FROM THE STREAM-GAGING STATION NEAR WAHIAWA

PERIOD	CIRCULATION PATTERN	MILLION GALLONS		RUNOFF AS % OF RAINFALL	REMARKS
		Rainfall	Runoff		
Annual					
1957	mixed	9,909	2,024	20.4	moderately dry
1958	mixed	11,798	3,002	25.4	nearly normal
1959	mixed	8,568	1,166	13.6	very dry
1957–59 (total)	mixed	30,275	6,192	20.5	dry
Short Period					
Jan 2–28, 1957	cyclonic	1,146	437	38.2	average rainfall in basin for 26-day period=19.50 inches
Mar 5–6, 1958	cyclonic	1,056	353	33.4	average rainfall in basin for 36-hour period=14.16 inches
Oct 21, 1958–Jan 6, 1959	mixed	2,642	830	31.4	wet
Mar 11–May 13, 1959	orographic	1,644	277	16.9	dry
July 29–Oct 29, 1959	mixed	2,200	311	14.0	dry
May 28–Sept 3, 1957	orographic	2,687	319	11.9	very dry
May 13–July 29, 1959	orographic	1,438	110	7.7	very dry
Feb 26–Apr 3, 1957	mixed	243	10.9	4.5	extremely dry

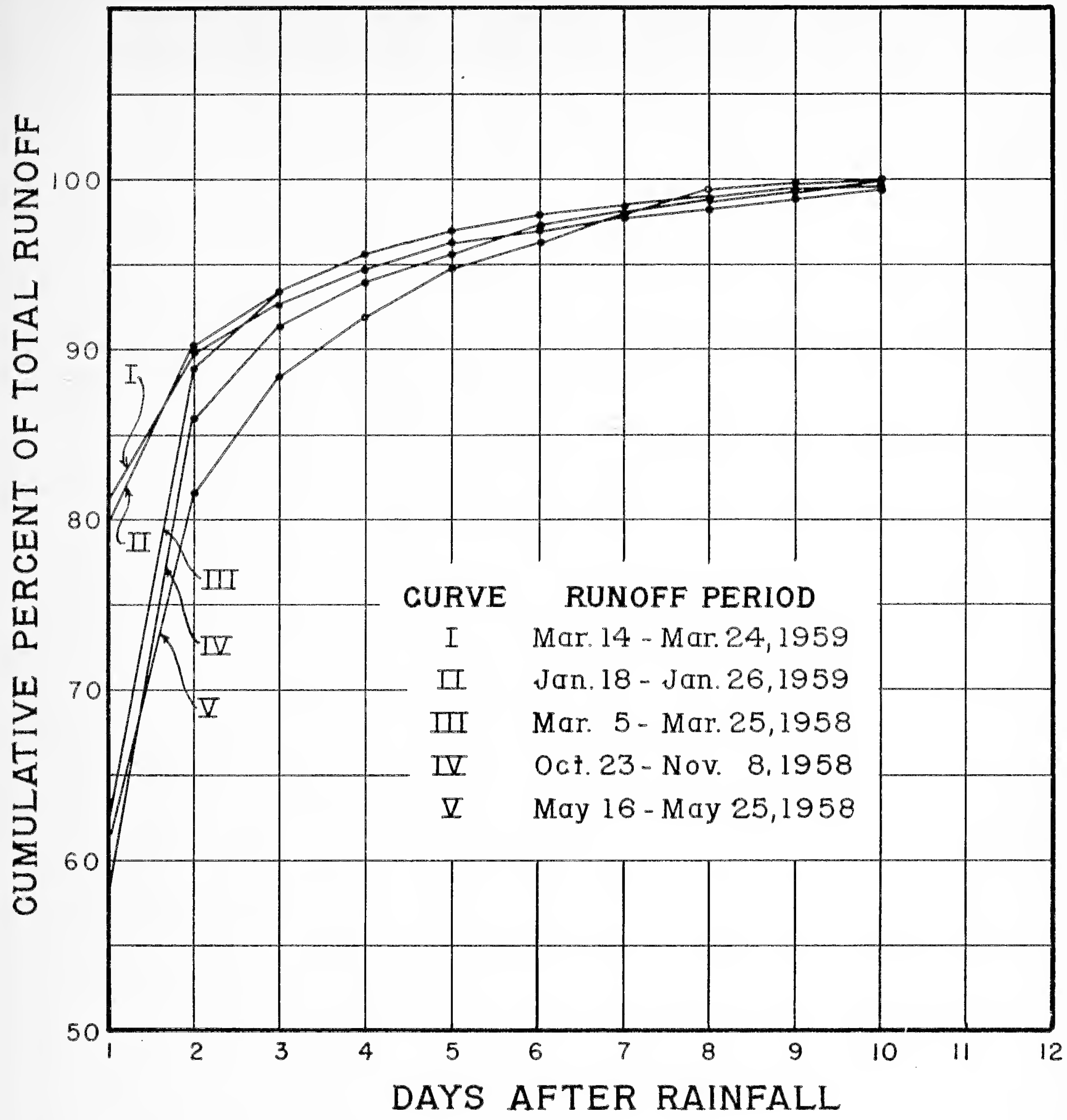

FIG. 5. Flow-decay curves for Kipapa Stream. Each curve shows the progressive reduction in stream flow following a single isolated storm.

up comparable amounts of water throughout the basin, whereas during orographic showers the water available to the stream decreases markedly leeward. The loss of flow into the stream banks and through the stream bed is therefore greater for orographic rains.

It should be reiterated that runoff-rainfall relationships explained above apply to a basin in the leeward central Koolau Range that has a mean annual rainfall of about 70 inches at its leeward terminus and 240 inches at the point of maximum fall. A change in the isohyetal dimensions of the basin would result in different runoff-rainfall characteristics. A basin having less than 70 inches of rainfall at its leeward end probably would have a smaller runoff-rainfall ratio, and a basin having more than 70 inches at the leeward end would have a higher ratio.

No long-term records are available for a basin having less rainfall at the leeward end but otherwise having similar environmental conditions as Kipapa. A direct comparison can be made, however, between Kipapa Stream and Kaukonahua Stream which drains a similar central Koolau basin but has considerably greater isohyetal dimensions. Rainfall and runoff records were obtained for many years on the part of Kaukonahua basin lying above the mean annual 220-inch isohyet. Kaukonahua is north of Kipapa in the wettest section of the leeward Koolau Range, and the part of the basin referred to lies within the 220- and 300-inch isohyets. Annual rainfall volumes were computed for this part of the Kaukonahua basin by using the rainfall curve derived from the Kipapa study. Figure 6 is a plot of the cumulative annual rainfall against cumulative annual runoff for the 17-year period between 1935 and 1951. The plot shows that in this area of very high rainfall annual runoff accounts for about 50% of the annual rainfall.

CONCLUSIONS AND ADDITIONAL REMARKS

Three years of records have shown that rainfall in the wet mountain part of Kipapa basin, which is representative of the leeward central Koolau Range, increases exponentially with distance toward the summit of the range, reaching a maximum about half a mile from the summit ridge. The empirical equations derived for this relationship are statistically reliable and permit easy calculation of the volume of precipitation that falls in the basin. The area investigated is in the wet zone where the rainfall ranges from about 70 inches at the leeward end to about 240 inches at the point of maximum fall.

Although the annual rainfall is heavy, only about ¼ leaves the basin as runoff. The remainder either infiltrates to the basal ground-water body or is consumed by evapotranspiration. The amount of infiltration was not possible to determine directly, and the measure of evapotranspiration is fraught with uncertainties. However, the geology of the basin system suggests that a large proportion of the rainfall moves down through the rocks as recharge to the basal ground-water body. The soil mantle is highly absorptive and the basalts underlying it are highly permeable.

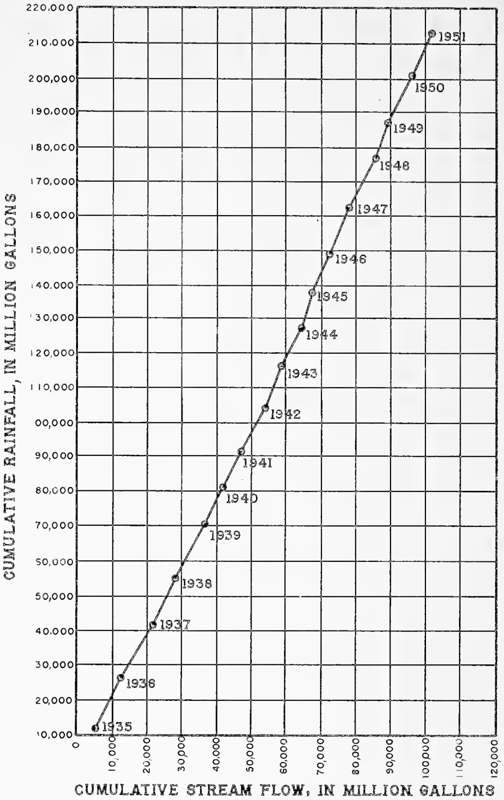

FIG. 6. Double mass curve of cumulative rainfall against cumulative stream flow for Kaukonahua Stream near Wahiawa.

The rate of evapotranspiration also could be expected to be considerable because the mean annual temperature is about 70 F and a closed montane forest covers the basin. A preliminary interpretation of evaporation data from similar wet Koolau environments suggests that in this humid area evaporation can be correlated with rainfall, decreasing as the rainfall increases. This is reasonable, because the increase in rainfall implies more cloudiness, which in turn would result in a smaller amount of solar radiation reaching the ground. The apparent relationship between rainfall and evaporation can be expressed in terms of evaporation as a function of distance toward the crest. In this relationship the equation approximates the rainfall-distance equation, except that the exponential term is in reciprocal form.

Assuming for simplicity that evapotranspiration is the equivalent of evaporation, calculations based on the evaporation-distance curve for 1957 gave the loss due to consumptive use as 30% of the rainfall. For wetter years the ratio would be less, and conversely it would be greater for drier years. A higher limit of evapotranspiration results if it is assumed that the evapotranspiration throughout the basin is the same as the potential evapotranspiration estimated for irrigated sugar cane in the leeward lowlands, or about 60 inches per year. In 1957 this would have amounted to 42% of the rainfall, which probably represents an upper limit. It is more likely that the true evapotranspiration falls somewhere between the limits determined by the two approximations. If in 1957 the evapotranspiration fell between 30 and 42% of the rainfall, and if the runoff was 20% of the rainfall (Table 4), by subtraction the infiltration was between 38 and 50% of the rainfall. The assumptions made in the preceding approximation, however, would support a value nearer to 50 than to 38% as being most reliable.

Thus, from even such a rudimentary water-budget analysis we can conclude that the wet leeward central Koolau mountains provide a highly effective environment for ground-water recharge.

SUMMARY

Rainfall and runoff data have been collected for the 3-year period, 1957–59, in the upper part of the basin of Kipapa Stream in the central Koolau Range. This part of the basin is covered entirely by a closed montane forest. The soils are highly absorptive and the underlying rocks, which consist of basalt and olivine basalt of the Koolau volcanic series, are highly permeable.

The pattern of distribution of orographic rainfall was found to correlate with distance from the crest of the range, decreasing leeward according to a geometric regression. Cyclonic storm rainfall was found to be uniformly distributed. Empirical equations for the rainfall-distance relationship were derived for the 3 calendar years and selected shorter periods, and volumes of rainfall were computed from the equations.

A gage on Kipapa Stream at approximately the mean annual 70-inch isohyet provided daily flow records. A comparison of rainfall volumes with runoff volumes for the 3 years shows that the yearly runoff accounts for about 25% of the yearly rainfall. During wet periods, the runoff may amount to nearly 40% of the rainfall, and in dry periods it can be as low as about 5%. Calculations based upon two different assumptions for evapotranspiration suggest that as high as 50% of the annual rainfall may move down as recharge to ground-water bodies.

REFERENCES

CLINE, M. G., et al. 1955. Soil Survey of the Territory of Hawaii. U.S. Dept. Agr. Soil Survey Series 1939, no. 25. 644 pp.

LANGBEIN, W. B., et al. 1949. Annual Runoff in the United States. U.S. Geol. Survey, Circ. 52. 14 pp.

——— and S. A. SCHUMM. 1958. Yield of sediment in relation to mean annual precipitation. Am. Geophys. Union Trans. 39: 1076–1084.

MINK, J. F. 1960. Distribution pattern of rainfall in the leeward Koolau Mountains, Oahu, Hawaii. J. Geophysical Res. 65: 2869–2876.

Hawaii as a Natural Laboratory for Research on Climate and Plant Response[1]

E. J. BRITTEN[2]

THE INTERPLAY of genetic and environmental forces has resulted in the process of evolution. The distribution of indigenous plants is a product of the genetic make-up of the successful invaders of a particular area and the total physical and biological environment of that area. Native plants have achieved a point in which their genetic constitution is in a certain degree of harmony with their environment. Plants in extreme latitudes, for example, have a genetic constitution which few, if any, tropical plants possess and so are able to withstand the low temperatures. The successful cultivation of economic plants is in even greater measure dependent upon the harmonious interaction of the plant's genes and its environment. One of the most important components of the plant's environment is climate.

Adaptability studies of plants have been of major concern to research workers from the standpoint of both genetics and physiology. Clausen, Keck, and Hiesey (1940) and Clausen and Hiesey (1958) have emphasized the role of interaction of environment with particular genotypes. Went (1957) has demonstrated the practicability of greenhouses with close environmental control.

Research workers concerned with crop production have been studying adaptability in an attempt to find the best phenotype for a particular environment. Plant breeders try to create highly adapted phenotypes. Recently much emphasis has been placed on agricultural meteorology in an attempt to refine studies on this phase of the plant's environment. Sprague (1959) and others have shown the importance of microclimate in understanding the plant's development.

Experimental work on the relationship of the genotype to its environment points up the magnitude of the problem. Probably more such studies have not been made because of the difficulty of obtaining adequate comparative data. The interest in methods of obtaining controlled environment for research on plant growth and reproduction attests to the need for this type of information.

Two general methods may be used to obtain data on this problem. First, plants may be grown in the field, and, second, they may be grown under controlled environment conditions. Field studies usually provide greater size and number of plants in a test and require small capital outlay. In a controlled environment greater precision of climatic regulations may be obtained plus a greater number of treatments. A combination of both methods gives the most useful information, since field studies may then be confirmed by laboratory methods but few locations provide sufficiently different conditions in the field for studies of this kind. Also, installations on the scale of the Phytotron at the California Institute of Technology are beyond the resources of most institutions.

This study demonstrates that the Hawaiian Islands by virtue of their diverse climatic zones present a natural laboratory for studying effects of environment on plant growth and reproduction. The data reported, for the most part, are concerned with the physical environment, temperature, and rainfall. Concurrent studies were made of growth and reproduction of *Trifolium repens*. These findings will be reported in other papers for which this paper will serve as a reference for the data on physical phenomena.

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[2] Associate Agronomist, Hawaii Agricultural Experiment Station.

There are many stations in Hawaii reporting to the U. S. Weather Bureau (USWB) most of which report only rainfall. Temperature stations are, for the most part, in the low elevations. Relatively little data are available at the intermediate and higher elevations. All Hawaiian temperature data reported herein are from original data except those at the 10,000-ft elevation on Maui. Air temperature data at sea level, 2,000, and 7,030 ft have been extended by data from the USWB in order to increase the length of time of observations. All soil temperature data are original. Air temperatures at 3,500 and 5,000 ft on Maui are reported for the first time.

The importance of islands in the study of biological phenomena has been emphasized by Darwin (1839) and his contemporary, Wallace (1881). In Hawaii Ripperton and Hosaka (1942) have reported the effects of climate on vegetation zones. A bibliography on Hawaiian rainfall was published by Taliaferro in 1959. A summary of the climate of Hawaii was published by the U. S. Department of Agriculture in 1941.

MATERIALS AND METHODS

Air temperatures were obtained at the experimental plots from USWB maximum and minimum thermometers read daily or, at remote stations, from thermograph tracings. The thermographs were checked periodically against a thermometer and at most stations a maximum and minimum thermometer was read weekly for further check. A series of temperature readings was made by exposing a thermometer at 500-ft intervals of elevation while driving to the experimental plots. Corrections for diurnal variations which occurred during the time of travel were made by examination of thermograph tracings at three stations along the route, and by adjusting the temperature to 10:00 AM. Elevations were obtained by an airplane altimeter. Altimeter readings were checked against locations of known elevation.

Soil temperatures were read from soil thermographs (either Friez or Dickson "minicorder") with the sensing bulb 3 inches below the surface of an adapted grass cover. Instruments were housed in standard USWB shelters.

RESULTS AND DISCUSSION

Temperature

The seven major islands in the Hawaiian group represent the eroded peaks of volcanoes which extend from great ocean depths. Two of them, Maui and Hawaii, have peaks over 10,000 ft above sea level. Differences in time since cessation of volcanic activity and in amounts of rainfall on different islands have caused great topographical differences. The islands range from land areas with relatively smooth contours, in one case still actively growing from vulcanism, to highly dissected mountain masses with deep canyons and shore cliffs several thousand feet high.

Geographically, the islands are just within the northern belt of the tropics, ranging from approximately 19° to 22° 15′ N. They are separated from the nearest continent, North America, by 2,400 miles—thus are probably as little under the direct effect of other land masses as any other land area of the world.

The location within the Tropical Zone plus the insular condition give the islands temperatures which at sea level are warm throughout the year. Excessively high temperatures are not encountered because of the maritime conditions. The highest recorded temperature at Honolulu, which is just above sea level, is 90 F. Increase in elevation tends to be accompanied by a decrease in temperature of approximately 3 F for each 1,000 ft. From the mean annual temperature of 75 F at Honolulu to that of a station at 11,000 ft on Mauna Loa on Hawaii, the temperature range corresponds to that from the southern tip of Florida to a point midway in Maine (U. S. Dept. Agr., 1941).

Mean annual temperatures do not present a complete picture of temperature relationships as far as plant growth is concerned, as they fail to show diurnal and seasonal fluctuations. Mean monthly temperatures at different altitudes are given in Figure 1. Mean temperatures rather than mean maxima and minima are shown so that all may be placed on one graph for comparison. It is possible to select the approximate temperature desired by selecting the altitude.

Mean monthly maxima and minima are given for a number of locations in Figures 2–8. Figure 2 compares the mean maximum and minimum

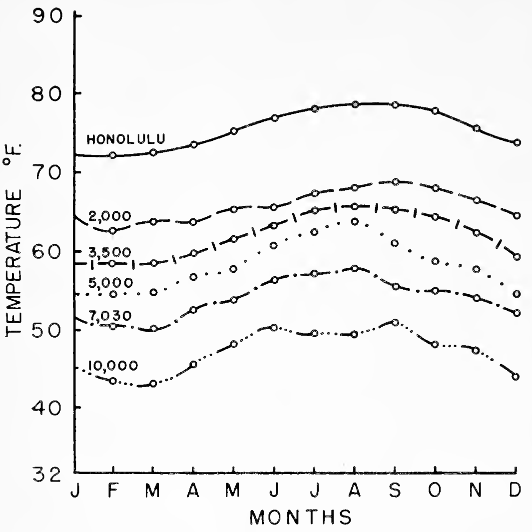


FIG. 1. Mean monthly air temperature of six locations varying in elevation from Honolulu at sea level to summit of Haleakala at 10,000 ft. Increasing elevations bring progressively lower temperatures. Selection of temperature desired may be made by choice of elevation. Note relatively uniform temperatures at each station throughout year.

temperatures of a station at 2,000 ft and one at 7,030 ft. There is some overlapping of temperature bands. If a comparison is made between Honolulu near sea level and the station at 7,030 ft (Fig. 3) there is no overlapping when means are compared, but there would be overlapping of extremes. Range between maximum and minimum increases with altitude.

The temperature of the air is usually measured about 5 ft above the ground surface. However, temperatures taken close to the plant are of great importance. Ideally, a series of readings at soil level and at a few inches above and below soil level would provide complete information on this point. However, instrumentation to this degree was not possible. Accordingly a soil thermograph was installed to record temperatures 3 inches below the soil surface. A comparison of air temperatures at different elevations with corresponding soil temperatures is shown in Figures 4–8.

Temperatures of air and soil follow similar patterns in most cases. The maxima at the 2,000-ft station (Fig. 4) intersect each other twice, the soil maxima being higher than the air maxima during the summer but lower in the winter. The air minima are consistently less than those of the soil. Air temperatures at 3,500 ft (Fig. 5) are cooler than at 2,000 ft, but the range is similar. No soil thermometer was available for this location. The range of temperatures at the 5,000-ft station (Fig. 6) is about the same as at 2,000 and 3,500 ft, but again the temperatures are lower. Air minima are consistently lower than those of the soil. The lower air temperatures may be explained by the cooling of the air to a greater extent than that of the soil because of faster radiation. The condition might be intensified by drainage of air from higher elevations, thus lowering the air temperature but having relatively little effect on the soil.

The pattern of air and soil temperatures at 7,030 ft (Fig. 7) is marked by the greater range between maxima and minima of both air and soil and the higher temperature of the soil than of the air. The soil maximum is actually greater than that of soil at 5,000 ft probably because the 5,000 ft elevation station is within the cloud zone and so may not receive as much direct sun as at the higher station, at the upper edge of the cloud zone.

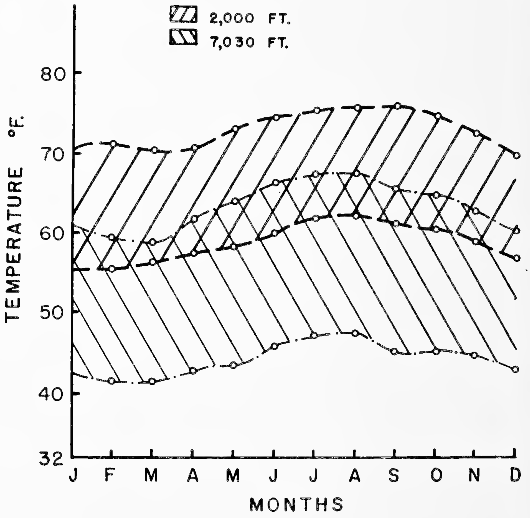


FIG. 2. Mean monthly maxima and minima air temperatures at 2,000 ft and 7,030 ft, Maui. Temperatures at higher elevation are lower and show greater range than at lower elevation. Maxima of 7,030 station exceeds minima of 2,000-ft station; i.e., temperature ranges overlap. Years of records: 2,000 ft, 13–14 years; 7,030 ft, 15–18 years.

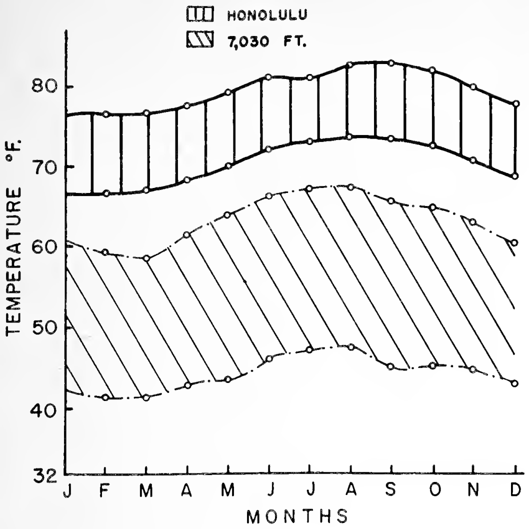


FIG. 3. Mean monthly maxima and minima air temperatures near sea level (Honolulu) and at 7,030-ft station shown in Figure 2. Note complete separation of temperature ranges. Years of record: Honolulu, 1951–53.

The anomalous situation of higher soil temperatures at 7,030 than at 5,000 ft might be used to argue against the validity of using a mountain slope to obtain progressively lower temperatures with increasing altitudes. However, this particular situation is exceptional and shows that temperature measurements are necessary, regardless of station. An investigator of the effect of temperature on plants would certainly measure not only the elevation of experimental plots but also the temperatures.

Temperature records at the summit of Haleakala have recently been available on a continuous basis. The air temperatures in Figure 8 (courtesy of USWB), show lower temperatures than any at the other stations. Rainfall in this area is sparse and no experimental plots have been established.

Where both air and soil temperatures are shown (Figs. 4–7) the period covered is approximately the same for both and is for about 2 years. Other graphs (Figs. 1, in part; 2, 3, 12, 13) showing air temperatures of these locations have been taken from long-term USWB records. This accounts for slight discrepancies between air temperatures for the same location in different graphs.

Island temperatures fluctuate less than those in continental areas. The mean diurnal change in Honolulu is 9.3 F (USWB, 1960*a*). The mean maximum of Sep, the warmest month, is 82.9 F and for both Jan and Feb, the coldest months, is 76.4 F. The difference between maximum of the coldest and the warmest months is then only 6.5 F, which is less than the diurnal change. The significance of this relatively stable temperature relationship throughout the year is that plants can be grown at any season and that somewhat similar temperatures are found at all times, particularly at the lower elevation stations.

The stabilizing effect of the ocean on temperatures produces highly predictable temperature conditions for a given location and time of year. The temperature of any location tends to be a function of elevation, but this is modified slightly by the cloud cover and the presence of an inversion layer. Clouds may cover certain areas more than others. At a given elevation, the temperatures may be about one degree higher in one location than in another because of the effect of local insolation. The inversion layer varies in altitude depending on the day and the time.

The change in temperature with elevation was investigated by periodically recording temperatures while driving up Haleakala Mountain.

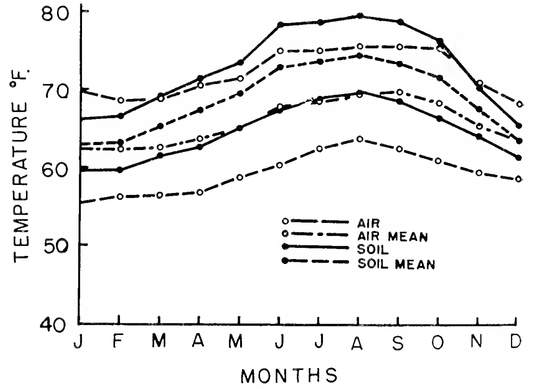


FIG. 4. Air and soil temperatures at 2,000-ft station on Haleakala, Maui. Maximum, minimum, and mean temperatures are shown for both air and soil. Soil temperatures lines have solid circles, air temperatures are designated by clear circles. Generally soil temperatures are higher than air temperatures, but both follow similar patterns. Period of record, 2½ years.

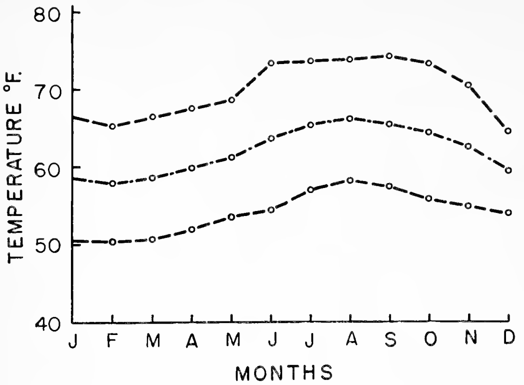


FIG. 5. Air temperatures, maximum, minimum, and mean at 3,500-ft station. Temperatures are lower than at 2,000 ft. No soil thermograph was available. Period of record, 2½ years.

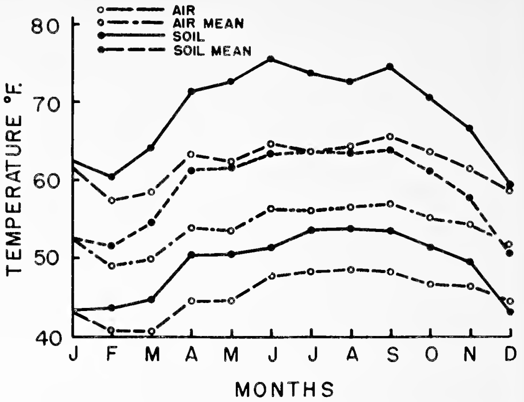


FIG. 7. Air and soil temperatures at 7,030-ft on Haleakala. Soil temperatures exceed air temperatures and range between maxima and minima is greater than at lower elevations. Period of record, 2½ years.

Because of relatively small horizontal distances in Hawaii, it is possible to plot temperatures against altitude within a reasonable time. Air temperatures are shown for two different dates in Figures 9 and 10. To compensate for diurnal changes in temperature which occurred during the drive, thermograph tracings for stations on the route were examined. Appropriate corrections were then made to the original readings to adjust all temperatures to 10:00 AM. In the two instances given, temperature inversion occurred between 4,000 and 4,500 ft in one case and between 6,000 and 6,500 ft in the other. The most frequently encountered inversion was between 5,000 and 5,500 ft. In two instances inversions occurred between 1,500 and 2,000 ft. The records confirmed previous reports that for each 1,000 ft increase in altitude, a drop of approximately 3 F occurred. This figure represents the total drop including the inversion layer. The location of the inversion layer may often be identified by clouds (Fig. 11).

Comparisons of temperatures in Hawaii with those of certain continental locations are instructive. The headquarters of the Haleakala National Park at 7,030 ft and 20° 46′ latitude

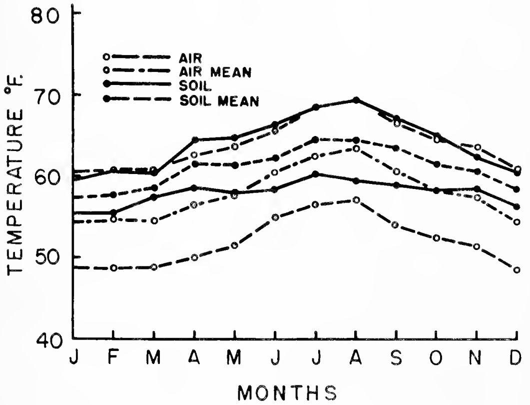


FIG. 6. Air and soil temperatures at 5,000-ft on Haleakala. Temperatures of both air and soil are very similar except that air minima are consistently less than minima of soil. Period of record, 2 years.

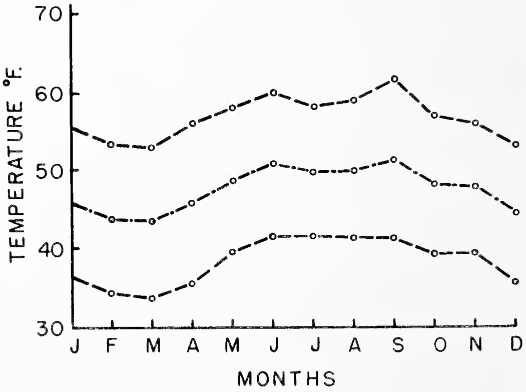


FIG. 8. Air temperatures near summit of Haleakala at approximately 10,000 ft. Temperatures are lower than at lower elevations. Period of record, 3 years. Data courtesy USWB.

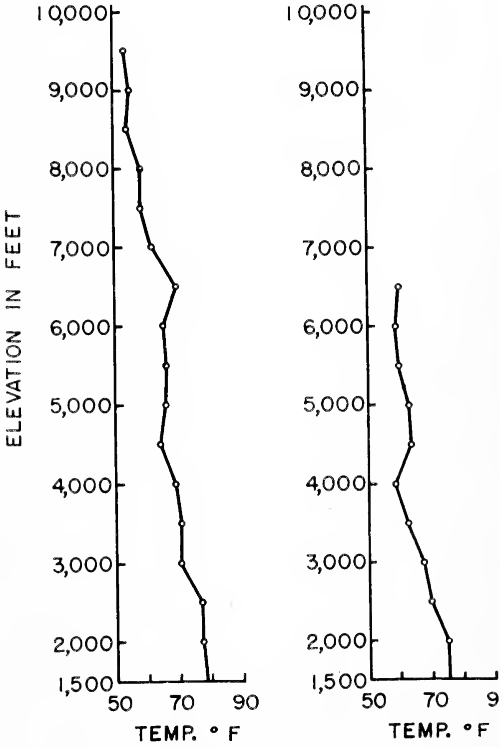
has the same annual mean temperature (54 F) as Beltsville, Maryland, at 120 ft and 39° 40′ latitude (USWB, 1957, 1960*b*). Graphs showing mean monthly maxima and minima for the two locations are in Figure 12. The Beltsville station has colder winters and warmer summers than its Hawaiian thermal counterpart. The cooler summer of the Hawaii station indicates that it is more favorable to plants adapted to cool conditions than is Beltsville, nearly twice the distance from the equator. Experiments with white clover (*Trifolium repens*) have shown that at 7,000 ft in Hawaii growth is virtually stopped for about 2 months in the winter but except for some damage to the edge of the leaves, the clover remains green and flowers continuously. Summer growth is excellent. Frost is frequent in the winter but snow never falls. From 9,000 ft to the summit at 10,025 ft snow may sometimes cover the ground but does not persist. On Hawaii, with two peaks over 13,000 ft snow frequently occurs and may last for days. Because of relative inaccessibility, low rainfall, and lack of soil, the higher elevations have not been used for plant research.

The 7,030 ft Hawaiian location and a continental location at about the same elevation are compared in Figure 13. Marshall, Wyoming, has an elevation of 7,010 ft and latitude of 39° 03′. The mean annual temperatures differ markedly, being 54 and 38 F (USWB, 1955, 1960*b*) for the Hawaiian and Wyoming locations, respectively. Despite the higher mean annual temperature of the Hawaiian station, the summer maximum in Wyoming is actually higher than the maximum in Hawaii at the same elevation. This indicates that even though Hawaii is in the Torrid Zone, at the higher elevations low temperatures may be more limiting for growth than are places within the Temperate Zone.

These differences between the two locations are reflected in the plant life of the two areas. The temperate zone station is characterized by extremely cold winters and relatively warm summers. Perennial plants in such an area must possess genes for cold resistance. Perennials in Hawaii do not need the genes to withstand a rigorous winter. But there is not the same heat energy in the Hawaiian high-altitude summer which proves so favorable for annuals in the mountains of the Temperate Zone, where, besides adapted perennials there is a profusion of annuals. The Hawaiian mountain flora, on the other hand, is predominantly perennial.

RAINFALL

The rainfall pattern in Hawaii is extremely complex. Rainfall in different localities ranges from less than 10 to 456 inches on a mean annual basis. Rainfall is determined by exposure to the prevailing wind, elevation, and local topography. During the major part of the year, the northeast trades are the main factor governing precipitation in most parts of the islands. Areas exposed to the trades, if backed by high mountains (10,000 ft or more), receive heavy rainfall. Conversely the lee sides of such mountains (and any other smaller island to the leeward) may be very arid.



FIGS. 9, 10. Air temperatures at 500-ft intervals, Haleakala, Maui. Temperatures adjusted to 10:00 AM. Fig. 9 (left) data obtained on Sep. 24, 1959. A temperature inversion was encountered between 6,000–7,000 ft. Fig. 10 (right) data were obtained on Jan. 29, 1959. A temperature inversion was found above 4,000 ft. An average 3 F drop in temperature occurs for each 1,000 ft increase in elevation.

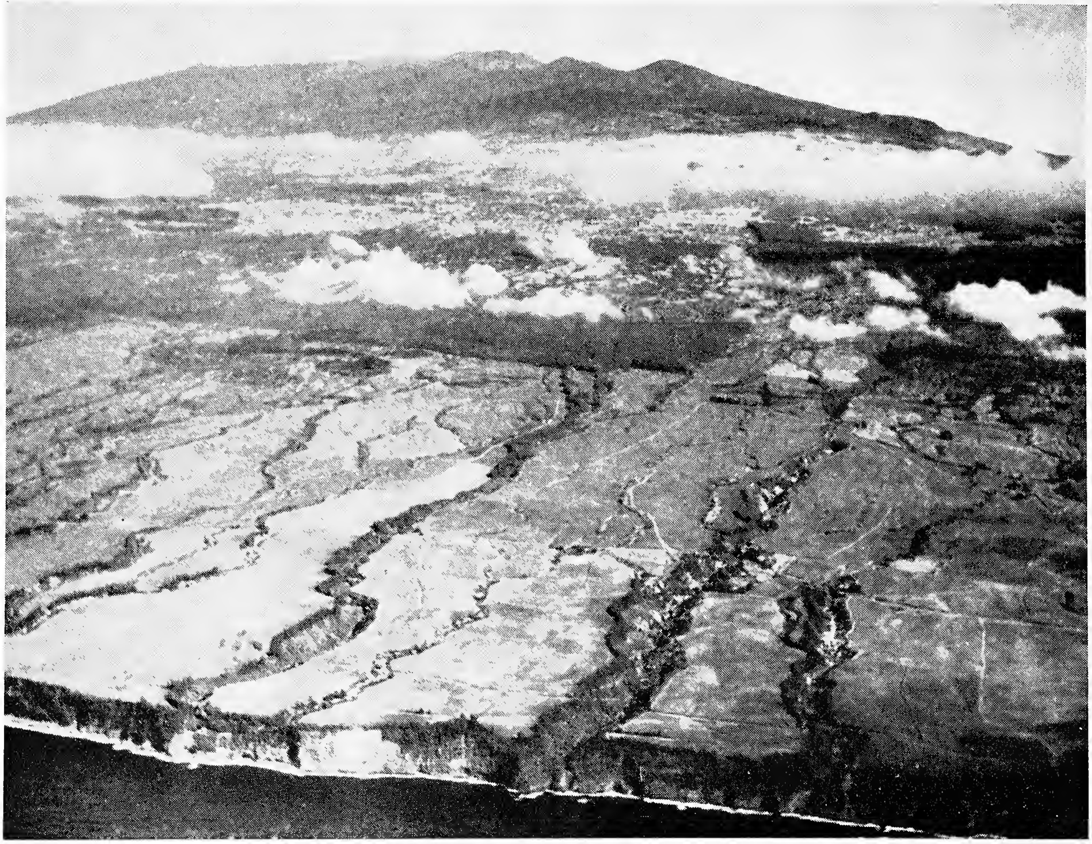


FIG. 11. Few locations afford an opportunity to observe a mountain stretching from sea level to 13,796 ft elevation, as in this photograph of Mauna Kea on Hawaii. The inversion layer is marked by the line of clouds.

Where the mountains are not as high (i.e., less than 5,000 ft), the rainfall on the windward side is not as heavy at the base as on the high mountains. Rain increases toward the crest, and is swept over the summit and down the lee side. Lee slopes therefore receive heavy precipitation which falls off rapidly with distance from the peak. Honolulu is on the lee side of a low mountain range. Rainfall on the windward side at sea level is 40 inches; at the crest it is over 200 inches. Rainfall at the head of the lee valleys is over 100 inches. At the head of the valley in which the University of Hawaii is located it is 150 inches; at the lee shore, about 5 miles from the mountain ridge, it is about 25 inches. The vegetation on the adjoining ridge parallel to the valley changes from the arid type of prickly pear cactus and associated plants to rain forest within a distance of 2 miles. Lawns become visibly greener block by block as one goes up the valley.

The rainfall pattern on Haleakala, Maui (Pineapple Res. Inst., 1955), a 10,025 ft mountain, is simpler. Topographical and rainfall contours (isohyets) are given in Figure 14. The seacoast area, being in the direct path of the trade winds, records precipitation of about 125 inches. Rainfall at this location increases rapidly with elevation until maximum amounts of 400 inches are received at about 3,000 ft. From this point, rainfall falls off rapidly so that at the summit it is less than 30 inches. Here rainfall increases then decreases with altitude. However, the isohyets describe ever enlarging ellipses as they approach that part of the mountain which is somewhat sheltered from the prevailing winds but not yet in its lee. The rainfall tends to be constant from sea level to near the summit.

Therefore, in this region, indicated by the arrows (Fig. 14), rainfall tends to be constant while temperature tends to decrease with altitude. This situation is of interest since one variable is changed at a time.

The foregoing discussion refers to annual means. It is apparent that at any one time there may be a departure from the mean which may or may not be significant. There are also seasonal differences. In parts of the islands sheltered from the trades, winters tend to be wetter than summers.

Important in studying plants in relationship to their environment is accessibility. On Maui paved roads extend to the summit (10,025 ft). On Hawaii automobiles may be driven to 9,000 ft and 4-wheel-drive vehicles to the summit of Mauna Loa (13,680 ft).

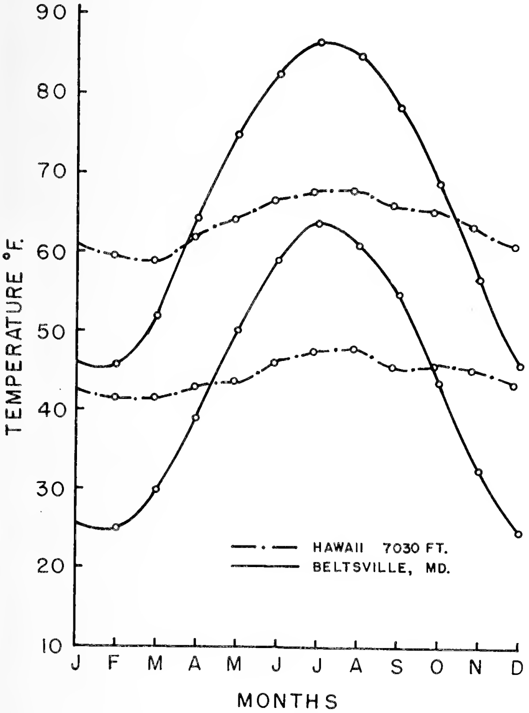


FIG. 12. Air temperatures at 7,030 ft, Haleakala, Hawaii, and Beltsville, Maryland. Both stations have same mean annual temperature. Winter temperatures at Beltsville are much lower than at Hawaii location and summer temperatures correspondingly warmer. Beltsville station is about twice the distance of Hawaii location from equator. Period of record: Beltsville, 5 years; Haleakala, 15–18 years.

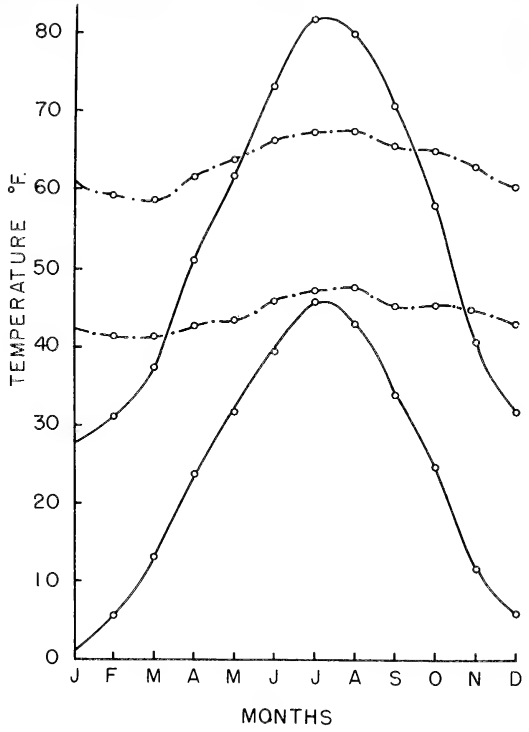


FIG. 13. Air temperatures at 7,030 ft, Haleakala, Hawaii (broken line) compared with a location of similar elevation (7,010 ft) in Marshall, Wyoming (solid line). Winter temperatures in Temperate Zone station are extremely low compared with Hawaii. Even though both stations are at same elevation and Hawaiian station is within Tropical Zone, summer maxima are greater for Temperate Zone station than for Hawaiian location. Period of Marshall record, 20 years.

Experiments utilizing the unique conditions of the Hawaiian Islands have been described by Britten (1960, 1961) who has investigated the role of genotype and temperature in flowering of *Trifolium repens.* The combination of a natural field laboratory and controlled environment facilities offers an opportunity to study fundamental and applied problems of plant growth and reproduction.

SUMMARY

The Hawaiian Islands are in the northern fringe of the tropics. Elevations range from sea level to over 13,000 ft. Mean annual temperatures associated with differences in elevation compare with those ranging from southern

Florida to Maine. By selection of elevation, desired temperature conditions may be secured. The unique conditions obtained by a high oceanic island can be utilized for research on plant response to climate.

Details of air and soil temperatures are given for different locations at different elevations. Comparisons are made between two Temperate Zone stations with a location in the islands. Rainfall patterns are discussed and attention is drawn to a situation where rainfall remains constant but temperature changes with elevation from sea level to high elevation. Utilization of such conditions in conjunction with controlled environment cabinets makes possible integration of field and laboratory experiments.

REFERENCES

BRITTEN, E. J. 1960. Genetic and environmental control of flowering of *Trifolium repens* in the tropics. Science 13: 100–101.

——— 1961. The influence of genotype and temperature on flowering in *Trifolium repens.* Agron. Jour. 53: 11–14.

CLAUSEN, JENS, DAVID D. KECK, and WILLIAM M. HIESEY. 1940. Experimental Studies on the Nature of Species, I. Effects of Varied Environments on Western North American Plants. Carnegie Inst. of Washington Publ. 520. 452 pp.

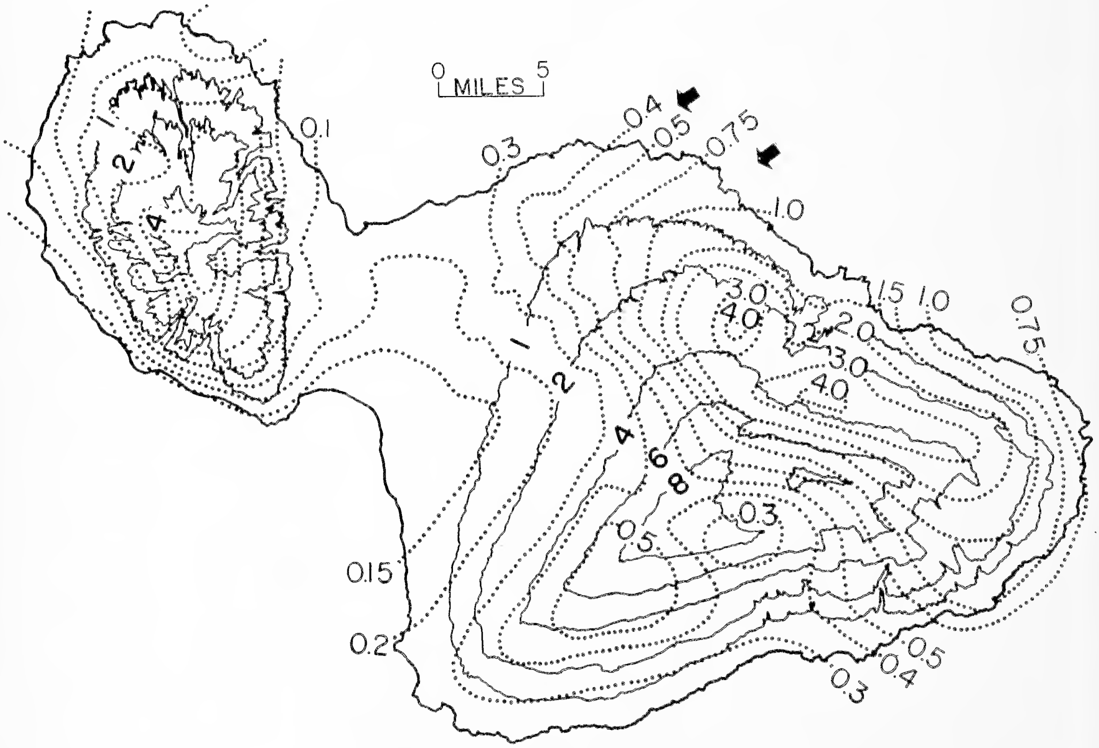


FIG. 14. Map of Maui. The 10,025-ft mountain, Haleakala, forms southeastern part of island. Topographical contours are shown as solid lines and mean annual rainfall contours (isohyets) as dotted lines. Figures for elevations are shown in thousands of feet and for rainfall in hundreds of inches. Rainfall figures for Haleakala only are given. Rainfall ranges from 10–400 inches in about 20 miles. In region denoted by arrows, rainfall is constant from sea level to approximately 6,000 ft. In this region, temperature varies with elevation while rainfall is constant. Rainfall data from Pineapple Research Institute, 1954.

——— and WILLIAM M. HIESEY. 1958. Experimental Studies on the Nature of Species, IV. Genetic Structure of Ecological Races. Carnegie Inst. of Washington Publ. 615. 312 pp.

DARWIN, CHARLES. 1839. The Voyage of the Beagle. New York.

PINEAPPLE RESEARCH INSTITUTE, and EXPERIMENT STATION, HAWAIIAN SUGAR PLANTERS' ASSOCIATION, in cooperation with the U. S. Weather Bureau. 1955. Average Monthly Rainfall Maps. 13 pp.

RIPPERTON, J. C., and E. Y. HOSAKA. 1942. Vegetation Zones of Hawaii. Hawaii Agr. Expt. Sta. Bull. 89. 60 pp.

SPRAGUE, HOWARD B. 1959. Grasslands. Am. Ass. Advancement of Science Publ. 53. 406 pp.

TALIAFERRO, WILLIAM J. 1959. Rainfall of the Hawaiian Islands. [Mimeo.] Honolulu. 394 pp.

U. S. DEPARTMENT OF AGRICULTURE. 1941. 1941 Yearbook of Agriculture. Climate and Man. Washington D. C. 1,248 pp.

U. S. WEATHER BUREAU. 1955. Climatic Summary of the United States. Supplement for 1931 through 1952. Wyoming. Washington D. C. No. 42. 44 pp.

——— 1957. Climatic Summary of the United States. Supplement for 1931 through 1952. Maryland and Delaware. Washington D. C. No. 15. 33 pp.

——— 1960*a*. Local Climatological Data with Comparative Data 1959, Honolulu, Hawaii. Asheville, N. C. 4 pp.

——— 1960*b*. Climatological data, Hawaii. Annual Summary (1959) 55: 154–162.

WALLACE, ALFRED RUSSEL. 1881. Island Life. London.

WENT, FRITS W. 1957. The Experimental Control of Plant Growth. Chronica Botanica 17. 343 pp.

Additional Eighteenth-Century Sketches of the Polynesian Native Dog, Including the Maori

KATHARINE LUOMALA[1]

WHILE AT THE BRITISH MUSEUM in May and June, 1960, I discovered five additional eighteenth-century sketches which include views of what presumably are native Polynesian dogs. Two are of the Maori native dog, of which no other sketches are known. Three sketches show dogs of the Society Islands but do not portray them as clearly as in the views presented earlier (Luomala, 1960*a*) in this journal. However, they may be of general historical and anthropological interest. Also included is a sketch showing a native pig of the Society Islands.

The five sketches come from "A collection of drawings by A. Buchan, S. Parkinson and J. F. Miller, made in the countries visited by Captain Cook in his first voyage (1768–71), also of prints published in John Hawkesworth's Voyages of Biron, Wallis and Cook, 1773, as well as in Cook's second and third voyages (1762–5, 1776–80)." This is the same collection from which the British Museum had sent me photographs (Luomala, 1960*a*: figs. 5–8) of two scenes from the Society Islands, "Double Canoes, Tipaerua" and "Canoes of Ulietea." The collection, which may have come into the possession of the British Museum from the estate of Sir Joseph Banks, who accompanied Captain Cook on the first voyage to the Pacific, also includes, besides unpublished sketches and engravings, duplicates of prints which Hawkesworth used in preparing Captain Cook's journal of the first voyage for publication. Because these duplicates were larger or clearer than the published engravings I had an opportunity to verify details which had not been very distinct in Hawkesworth's published prints.

What can be learned of the Maori dog from these eighteenth-century sketches? Figures 1 and 2 show a light-colored dog with dark spots. One large, dark spot is on the dog's back and right side above its right hind flank. Another is on its left side somewhere between the neck and the left shoulder. Another dark patch is around its ears above the eyes. The ears are erect, pointed, and large in proportion to the skull. The muzzle is long. The dog, in relation to the man behind, seems quite small. The tail is not shown. The

FIG. 1. Detail of dog shown in Figure 2.

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[1] Department of Anthropology, University of Hawaii, Honolulu. Fellow of the John Simon Guggenheim Memorial Foundation, 1956, 1960. Manuscript received May 1, 1961.

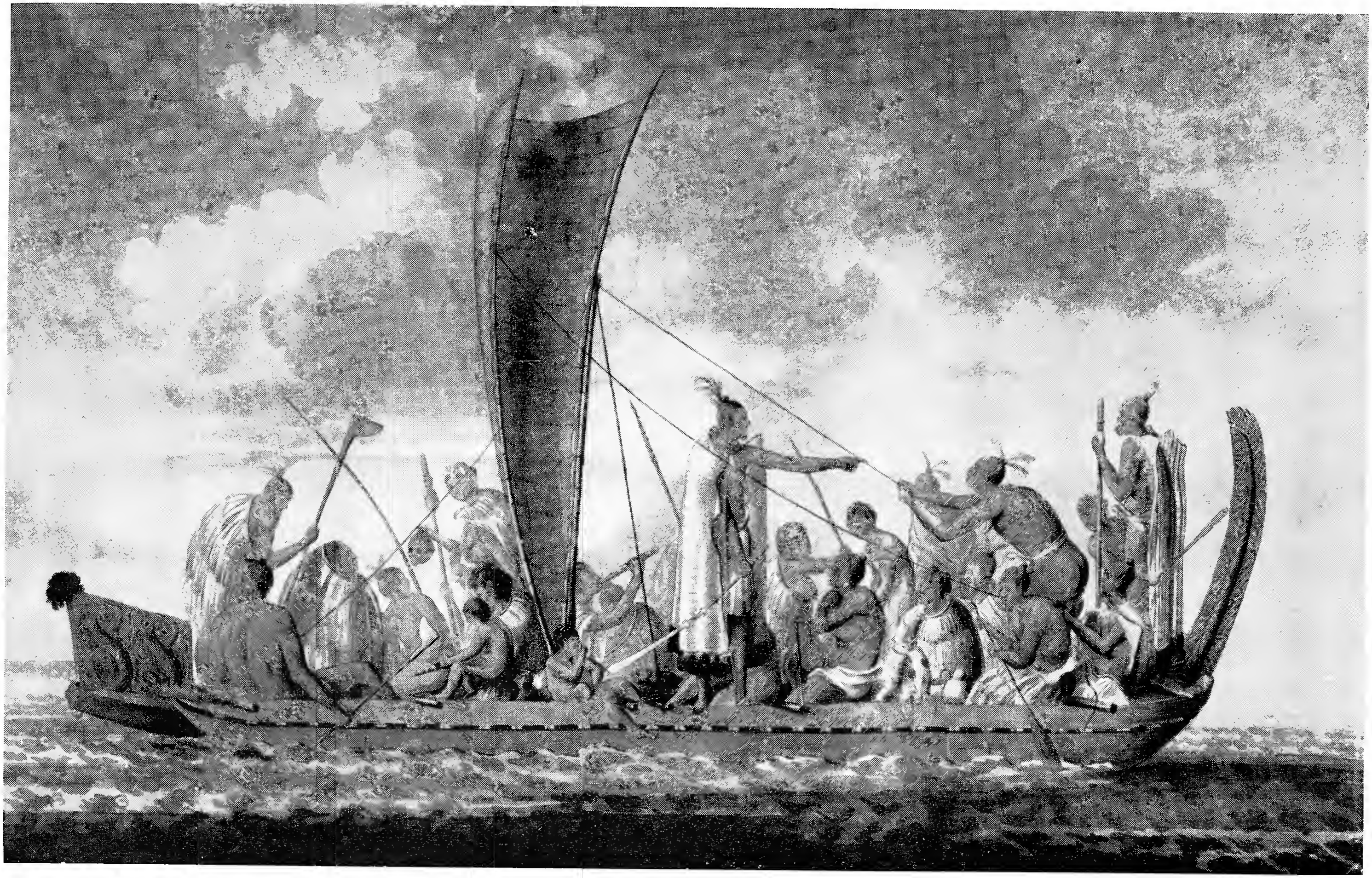

FIG. 2. "New Zealand War Canoe." A white dog with dark spots is sitting at the center right.

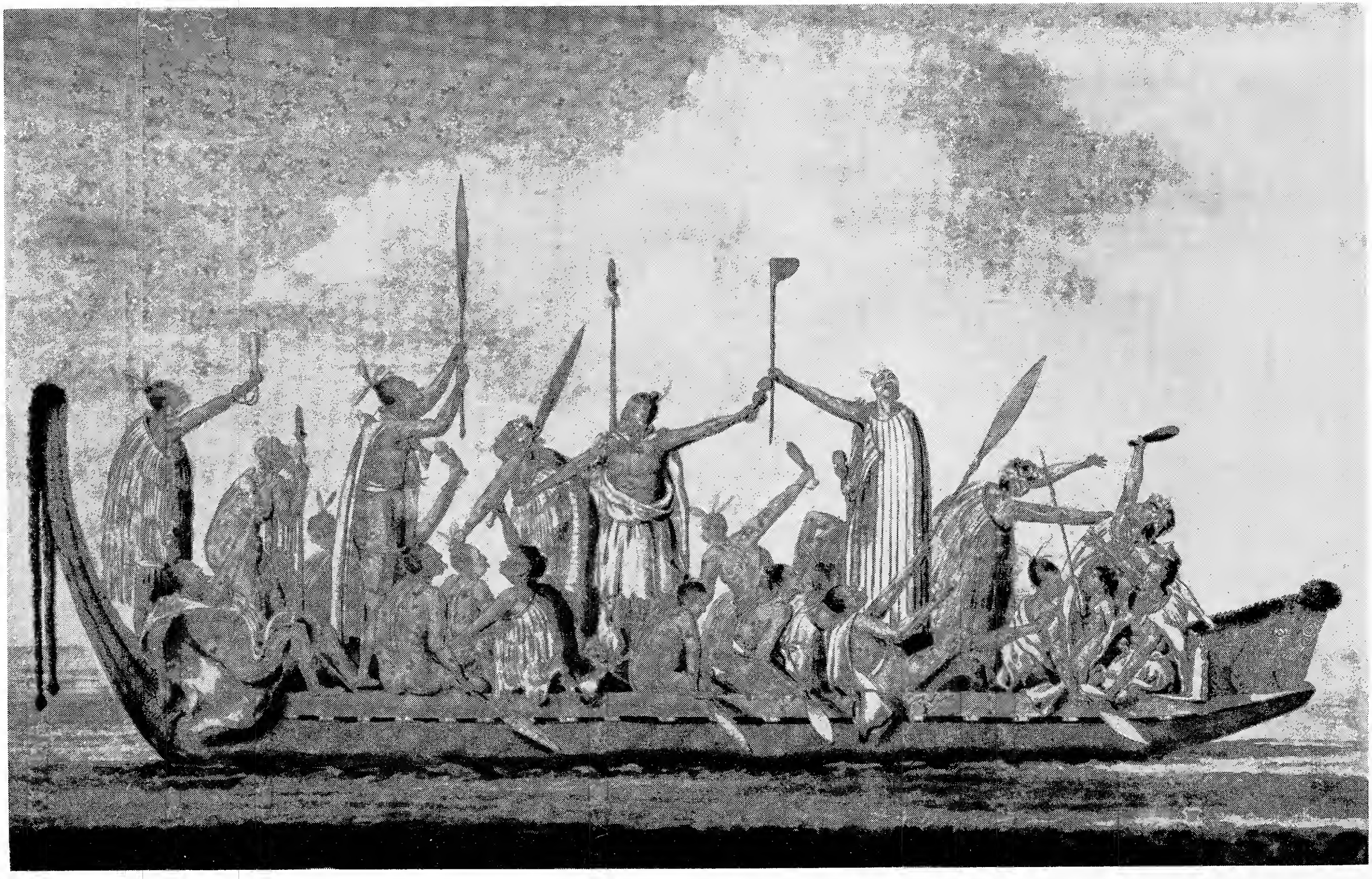

FIG. 3. "New Zealand War Canoe bidding defiance to the Ship." A white dog is sitting in mid-center looking up at the man who has both arms outstretched and holds a mere in his left hand.

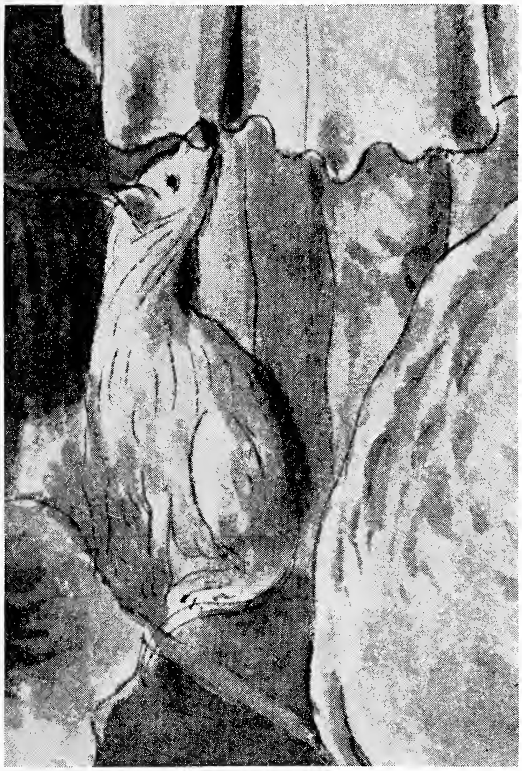

FIG. 4. Detail of dog shown in Figure 3.

nature of the hair, whether long or short, rough or smooth, is difficult to determine. The shading and lines on the dog's left side suggest thick hair, disarranged by the dog's attitude, but, contrarily, the right side has a sleek look.

The dog in Figures 3 and 4 appears to be entirely of one light color. It has a long muzzle, erect ears, and rather short spindly legs supporting a very plump body. The length and the texture of the hair are not indicated unless the parallel lines made to show the twisting of the body as the dog looks up at the man are also intended to suggest the partings that might occur in a wooly coat by such a movement. The sketcher has scarcely drawn the tail except by narrow curves which he has not filled in. When compared with the man behind him the dog is quite small in size. The dog is sitting on a thwart at about mid-calf of the man who is standing on the bottom of the canoe. The upturned muzzle of the dog touches the hem of the man's garment which falls just above his knees.

The eighteenth-century descriptions of the Maori native dog provide more information than the sketches. The latter do not include an all-black dog or show the dogs in attitudes by which the body length, the hair length, or the appearance of the tail might be judged.

The first descriptions of the Maori native dog come from Captain Cook and his crew. Cook described the dogs he saw in October, 1769, at Poverty Bay, North Island, as "very small and ugly" (Hawkesworth, 1773, II: 313) and of unspecified different colors (Hawkesworth, 1773, III: 444). In the journal of the third voyage (Cook, 1784, I: 153), the Maori dog is described as "a sort of fox-dog," which echoes Crozet's account.

Crozet (Roth, 1891: 76) described the dogs he saw in 1772 in New Zealand as "a sort of domesticated fox, quite black or white, very low on the legs, straight ears, thick tail, long body, full jaws but more pointed than that of the

FIG. 5. Detail of dog in Figure 6. The long ears of another creature, a pig, are visible in the hull.

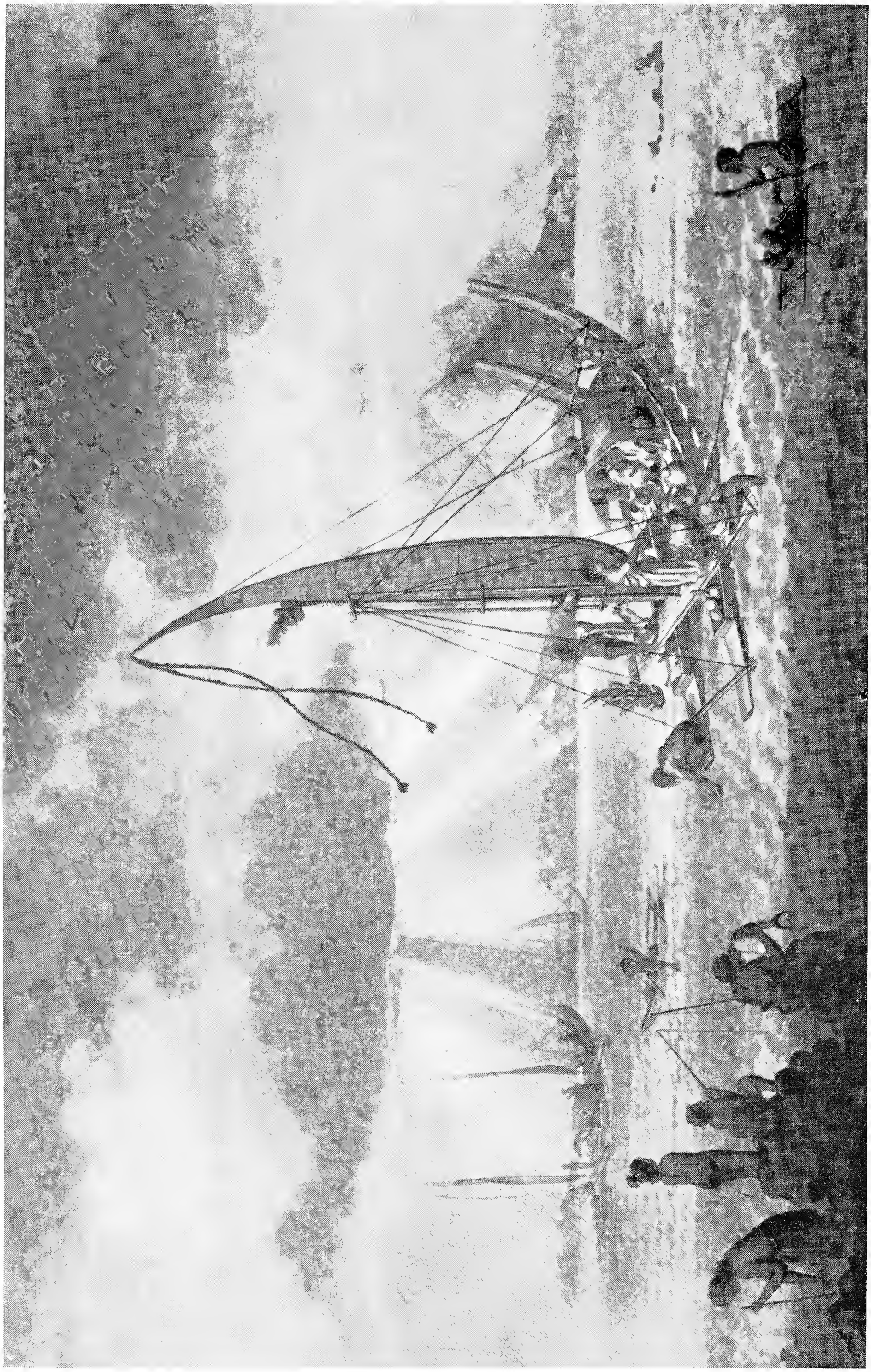

FIG. 6. "Vessels of the Island of Otaha," Society Islands. A spotted dog is partly visible beyond the mast.

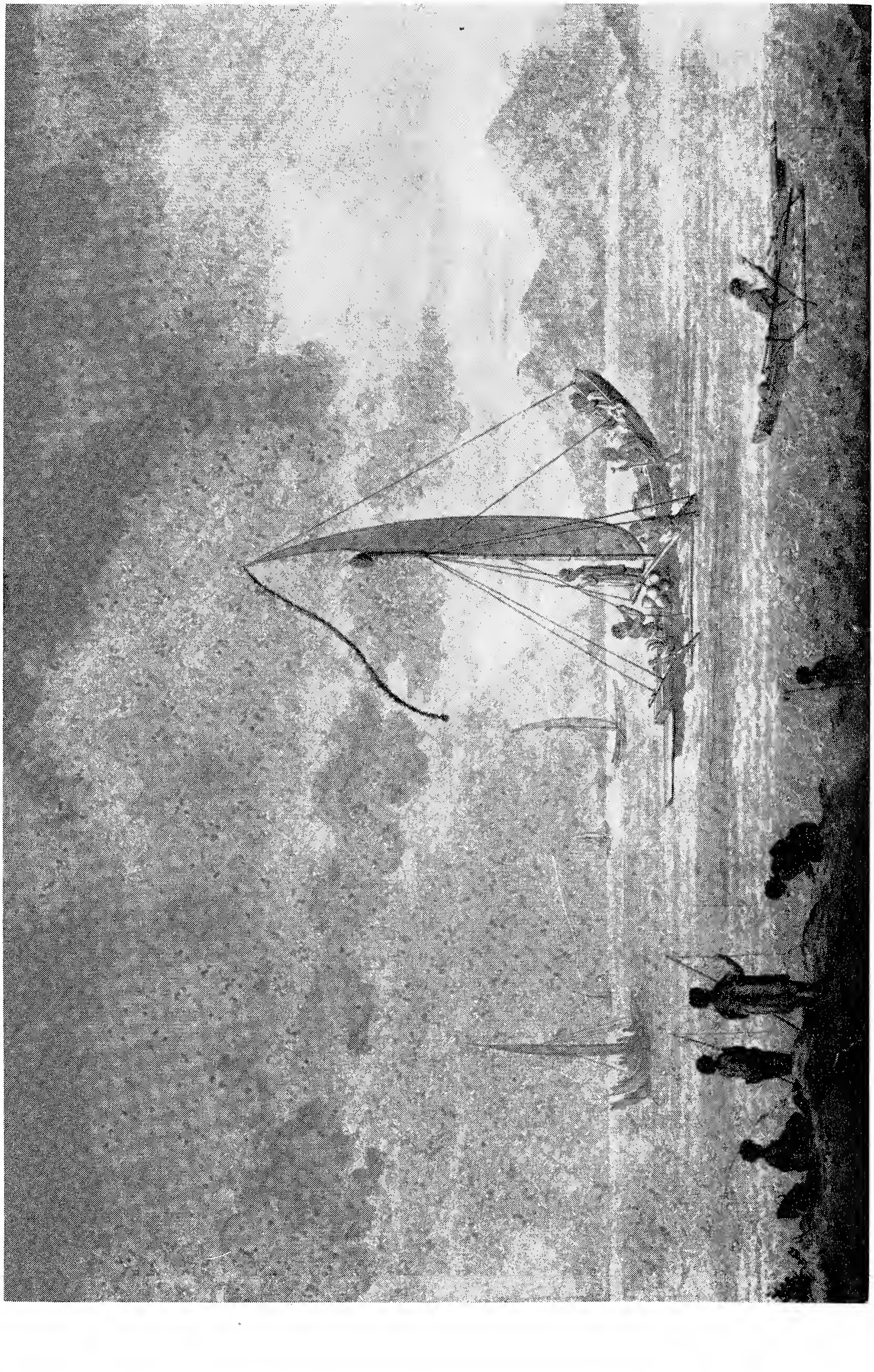

FIG. 7. "View of the Island of Otaha," Society Islands. A dog sits in the stern.

FIG. 8. Detail of dog in Figure 7.

fox...." The dogs he took aboard were "treacherous" and bit the strangers who had acquired them.

George Forster (1777, I: 377), naturalist on Cook's second voyage, likened the Maori dogs he saw in 1773 to the "common shepherd's cur, or count Buffon's *chien de berger*" (Luomala, 1960*a*: fig. 17). Forster described the Maori dog's hair as rough and long. The dogs varied in color, for there were "some spotted, some quite black, and others perfectly white." The ears were pricked.

Bellingshausen (1945: 215) in 1820 said that the dogs were of "rather a small breed...not large." They had thick tails, erect ears, a broad muzzle, and short legs.

My earlier article (Luomala, 1960*a*: fig. 16) includes a photograph of a stuffed dog (B. 3527, Dominion Museum, Wellington, New Zealand), sometimes regarded as of the native type although obtained in modern times. Moa Hunter archaeological sites in South Island have yielded dog bones and artifacts made of dog bone but I know of no analyses of the bones (Luomala, 1960*b*: 192). However, they serve to establish the pre-European presence of dogs in New Zealand.

The three harbor scenes (Figs. 6, 7, 10) from the Society Islands show canoes with dogs and other native livestock on board. Unlike the Maoris who had only dogs, the Society Islanders had dogs, pigs, and chickens. These drawings do not seem to have been published before, so they may be of anthropological interest. The close-ups of the dog show that it is far less sharply and fully delineated than in the sketches published earlier.

In Figure 5 at the left is part of a long-eared animal head. That it is a pig is evident from comparing it with Figures 11 and 12. The pig is mentioned here because earlier (Luomala, 1960*a*: fig. 1, 195) a similar creature, of which only the head is visible in a canoe, is described as a horned cow being transported from the

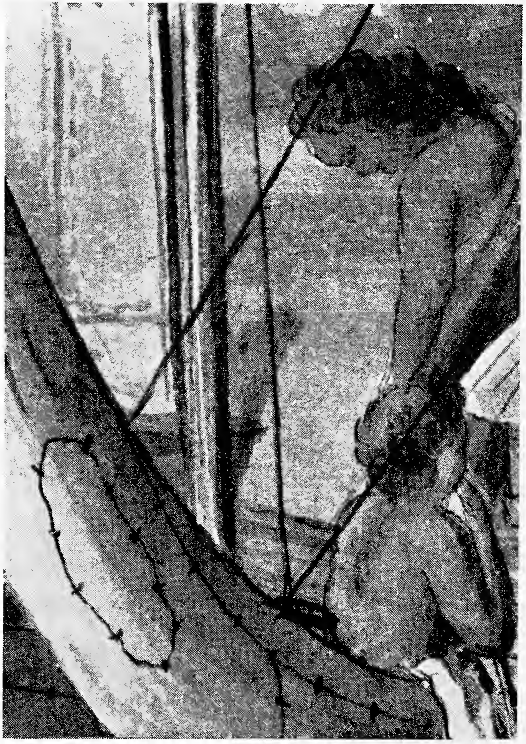

FIG. 9. Detail of dog in Figure 10. The irregular oval section on the hull is a patch.

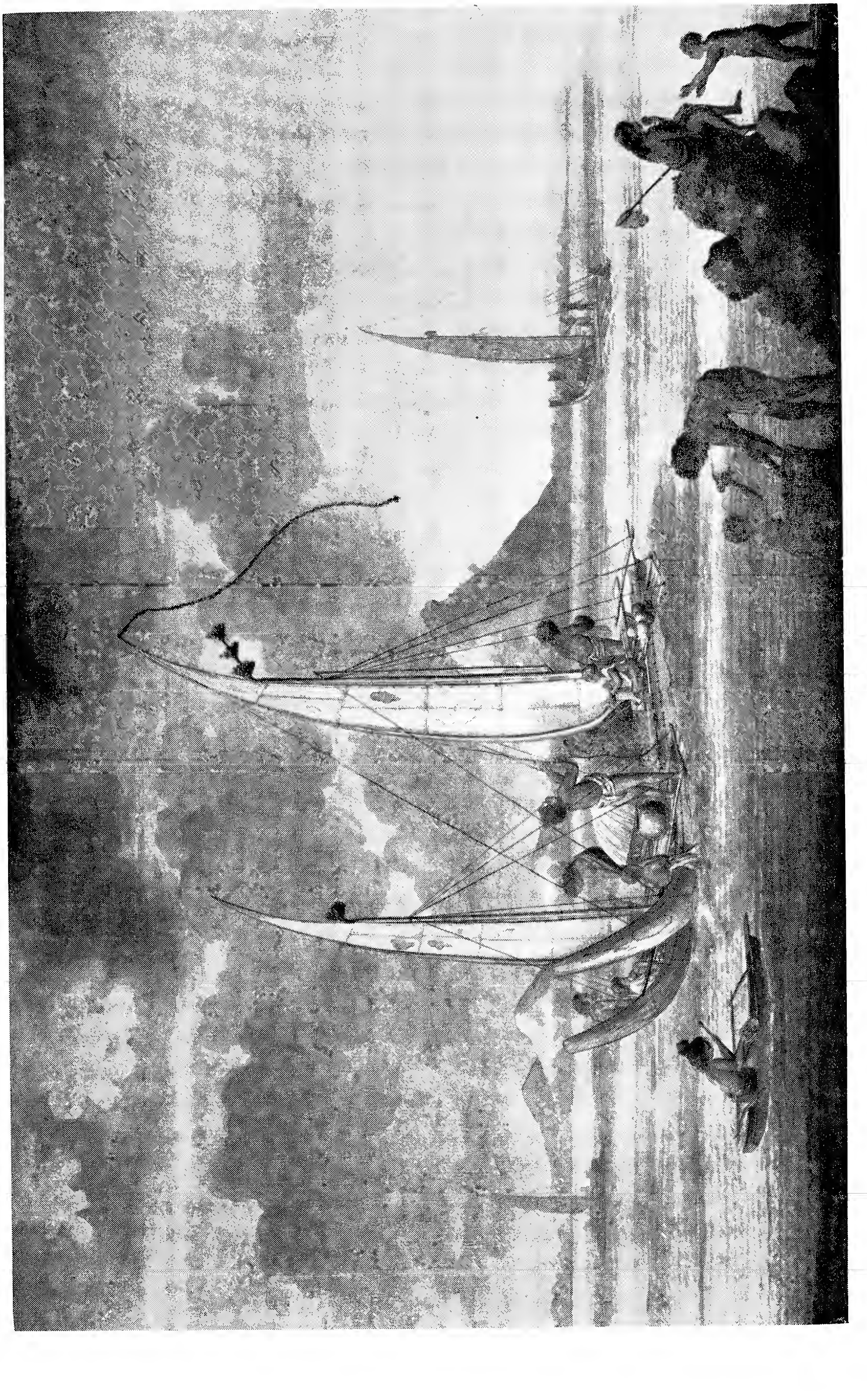

FIG. 10. An unlabeled scene in the Society Islands. A dog's pointed muzzle is visible near the aft mast.

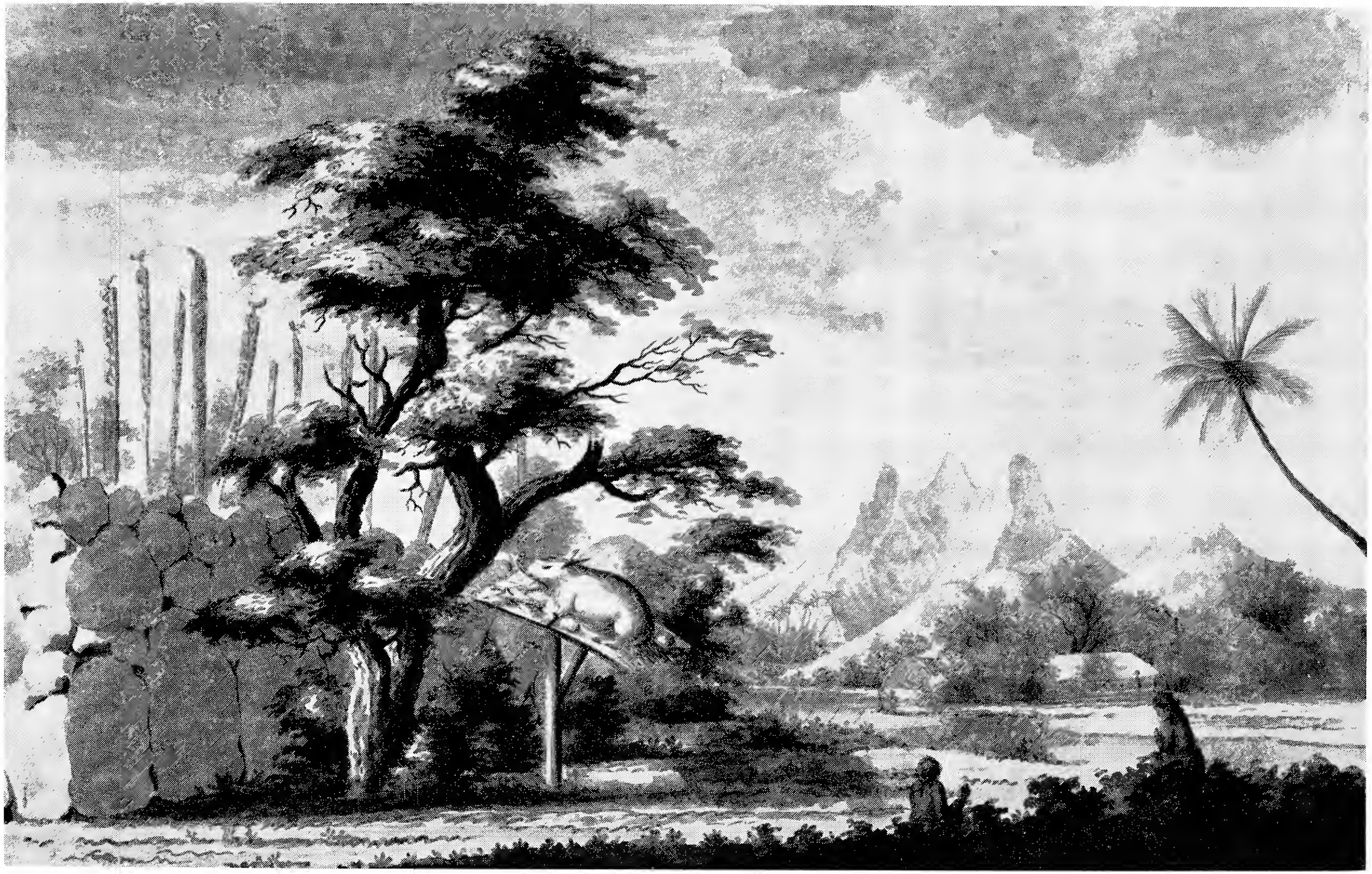

FIG. 11. "A Morai with an offering to the Dead," Society Islands. A pig and some fish lie on the single-poled sacrificial platform.

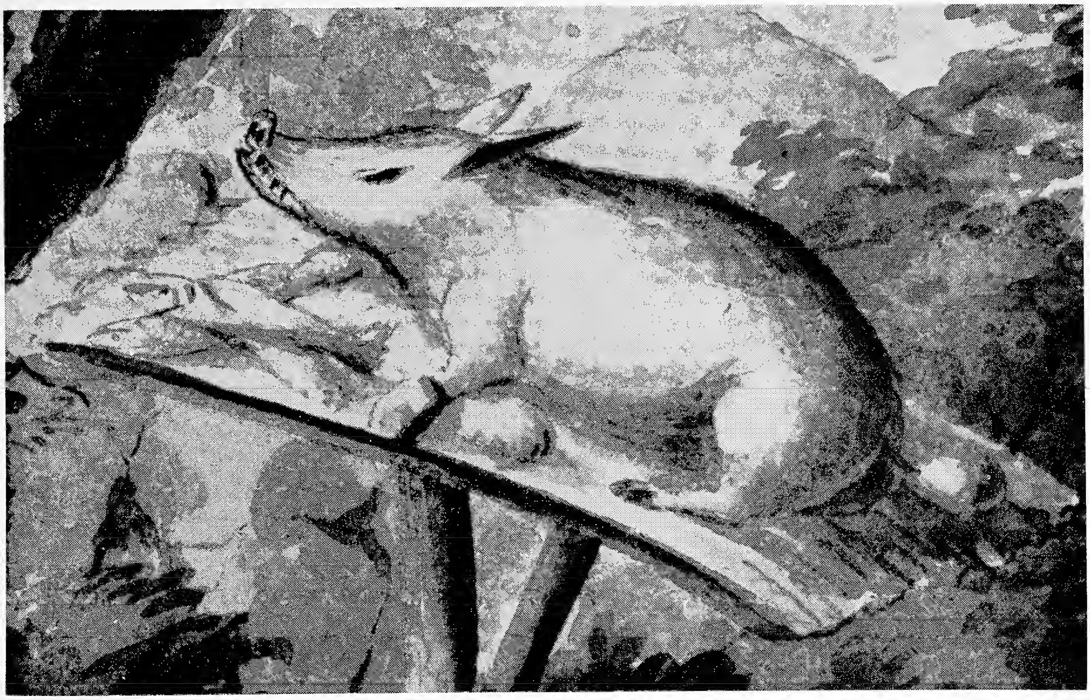

FIG. 12. Detail of pig in Figure 11.

European ship. At the British Museum where I saw a clearer engraving of the same scene and compared it with Figures 5, 6, 11, and 12, it seemed to me that the creature was really one of the long-eared native pigs.

Another incidental point, also puzzling, that examination of the collection clarified for me had to do with identifying the animals indistinctly depicted, except for their tails, in J. Webber's scene, "A Human Sacrifice, in a Morai, in Otaheite" (Cook, 1784, Atlas: pl. 25). On the offering platform are animals whose clearly drawn tails hang over the edge. Two pig tails hang between two long, thick, wooly-looking tails which it had occurred to me might be those of dogs, for dogs were frequent sacrifices. A better copy of Webber's scene in the collection left no doubt that the thick tails were like those of the dogs depicted in figures 4 and 5 (Luomala, 1960*a*). In the same scene a pig is being singed on a fire.

This paper has presented photographs of eighteenth-century sketches of the native Maori dog, of which no illustrations have been previously noted. Also included here are additional sketches of the native dog of the Society Islands and of the native hog of that archipelago. The study of illustrations made by artists who accompanied the early expeditions has led me to the discovery of the previously ignored drawings depicting the native dog. The sketches made in the Society Islands also include views of native fowls and pigs. It would seem that further knowledge of these two animals might be gained by examining sketches made by early voyagers to the Pacific islands.

REFERENCES

BELLINGSHAUSEN, F. G., VON. [1945] The Voyages of Captain Bellingshausen to the Antarctic Seas, 1819–1821. Trans. from Russian. Frank Debenham, ed. Hakluyt Soc., London. Vol. I, ser. II, vol. XCI.

COOK, J. 1784. A Voyage to the Pacific Ocean ... 1776–1780. London. 3 vols. and atlas. (Vol. III by James King; atlas of plates by J. Webber.)

CROZET, (?). [1891] Crozet's Voyage to Tasmania, New Zealand, the Ladrone Islands, and the Philippines in the Years 1771–1772. English trans., H. Ling Roth. London.

FORSTER, G. 1777. A Voyage Round the World. London. 2 vols.

HAWKESWORTH, J. 1773. An Account of the Voyages Undertaken ... for making Discoveries in the Southern Hemisphere. London. 3 vols.

LUOMALA, K. 1960*a*. A history of the binominal classification of the Polynesian native dog. Pacif. Sci. 14(3): 193–223.

——— 1960*b*. The native dog in the Polynesian system of values. In: Culture in History, S. Diamond, ed., Columbia University Press.

On the Hawaiian Scallops of the Genus *Pecten* Muller (Pelecypoda)

C. A. FLEMING[1]

STRONGLY INEQUIVALVE SCALLOPS of the genus *Pecten* (s.str.) are represented in the western and central Pacific by relatively few living forms, most of which have widely separated distribution areas in Japanese and Australasian seas. Their fossil record and morphological affinities have suggested a rather unusual history of late Cenozoic dispersal and speciation, at least for the majority of Western Pacific species, which are discussed in a recent publication (Fleming, 1957). The most isolated of all Pacific scallops, recorded from the Hawaiian Islands as two new species, *Pecten waikikius* and *P. diomedeus,* by Dall, Bartsch, and Rehder (1938), were known only from left valves, and as a consequence their relationships have been difficult to interpret.

During the past few years, through the interest of Hawaiian conchologists, in particular of Mrs. M. E. King, extensive collections of offshore Mollusca have been dredged off the island of Oahu, including a number of specimens of both valves of a scallop. After examining the type specimens in the United States National Museum in October, 1960, the writer was able to study some of the new material during a short visit to Honolulu in November, 1960.

I am grateful to Dr. Yoshio Kondo, Bernice P. Bishop Museum, and to Dr. P. Burgess, Honolulu, for the opportunity to examine the specimens that are the subject of this paper. To Dr. F. Stearns MacNeil, United States Geological Survey, I am indebted for the reference to *Pecten byoritsuensis* Nomura and its record from Okinawa.

FAMILY PECTINIDAE

GENUS *Pecten* Muller, 1776

1776. *Zool. Danicae Prodromus:* 248.

Type species (by subsequent designation, Children, 1823): *Ostrea maxima* Linn.

The form described below is a typical member of the genus *Pecten* s. str., so closely similar to *Pecten jacobaeus* Linn. that it is here ranked as a subspecies of that species, which is a near relative of the type species of the genus.

The other form named from Hawaii (*Pecten diomedeus* Dall, Bartsch, and Rehder) is known from a unique valve and its relationships are thus uncertain.

Pecten jacobaeus (Linnaeus)

1758. *Ostrea jacobaea* Linn. Syst. nat. (ed. X): 696.

The races grouped in the polytypic species *Pecten jacobaeus* (see Fleming, 1957: 39) are characterised by their generally square-cut ribs, strong secondary radial threads on the surface of the main ribs, and well-developed concentric lamellae, which extend across both interspaces and ribs. The subspecies recognised to date are:

P. jacobaeus jacobaeus (Linn.). Mediterranean (Pliocene–Recent)
P. jacobaeus keppelianus Sow. Atlantic Islands (Recent)
P. jacobaeus byronensis Fleming. New South Wales (Recent)
P. jacobaeus toi Fleming. New Zealand (Pleistocene)
P. jacobaeus byoritsuensis Nomura. Formosa and Okinawa (Plio–Pleistocene)
P. jacobaeus meridionalis Tate. Tasmania–S.E. Australia (Pleistocene–Recent)
P. jacobaeus waikikius Dall, Bartsch, and Rehder. Hawaii (Recent)

Two other groups of far-flung populations related to *P. jacobaeus* have been grouped under different polytypic species, *Pecten modestus* Reeve (5 subspecies) and *Pecten maximus* (Linn.) (3 subspecies), because each seems to have had a separate history and to have retained a morphological unity since it separated from the *jacobaeus* stock, probably in the earliest Pliocene. As already hinted, however (Fleming,

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[1] New Zealand Geological Survey, Lower Hutt, New Zealand. Manuscript received April 10, 1961.

1957: 25), these species could be united into a single polytypic species if one were willing to attribute certain morphological resemblances to homeomorphy. The subspecies described below falls easily into the formenkreis of *jacobaeus,* which is known elsewhere in the North Pacific, yet it has some features in common with races of *maximus* (Atlantic–South Africa). Economy of hypothesis demands that these features be attributed to homeomorphy.

Pecten jacobaeus waikikius Dall, Bartsch, and Rehder

Fig. 1, *1–4*

1938. *Pecten waikikius.* B. P. Bishop Mus. Bull. 153: 95, pl. 24, figs. 5–6.

DIAGNOSIS: A small subspecies of *P. jacobaeus* distinguished from all other subspecies by the following combination of characters: extreme inflation of right valve, high swollen beaks, subangular-to-rounded primary ribs, secondary radial threads on both ribs and interspaces, crossed by concentric lamellae; left valve concave, with an asymmetrically raised adductor muscle scar.

Right Valve: Small, up to 52.5 mm long; length/height ratio 89.3, 89.5; beaks high and swollen; inflation 43.8 to 44.2% of length; ribs 17 or 18.

Sculpture: Ribs well defined but becoming more rounded towards the ventral margin than in most subspecies; interspaces about half their width. Rib summits on disc bearing rounded, secondary radial threads, somewhat irregular in strength and spacing, increasing by bifurcation from about 4 at 15 mm from beak to 6 or 8 at ventral margin. Flank ribs narrower, generally with about 2 secondary threads. Interspaces between ribs often with a single median secondary thread. Concentric lamellae, regularly spaced, first developed 12 mm from beak, crossing ribs, secondary ribs and interspaces alike. Ears with up to 5 radial threads, crossed by incremental lamellae. Colour, white.

Left Valve: (See Dall et al. 1938: 95). Strongly concave (more than 15% of length). Rib interspaces sometimes with up to 3 secondary grooves (corresponding with right valve threads) and ribs generally weakly grooved (corresponding with right valve interspace thread). Ears mostly with 2–5 weak radiating threads. Adductor muscle scar set on a thickened callus bounded in front by a linear ridge bisecting the beak angle. External colour, pale pink with subdued reddish flashes; interior, white.

Variation: The sample seen (5 right and 11 left valves) is remarkably uniform in shape and sculpture. A few right valves lack intercostal threads and a few left valves lack costal grooves. Auricular ribs are absent in two specimens.

LOCALITIES: Dall, Bartsch, and Rehder recorded left valves from off Waikiki, Oahu (type), off northeast Hawaii, and off Mala Bay, Maui. The new material is from off Keehi Lagoon, including the explosive anchorage area, Oahu, off Pekai Bay, and 1½ miles off Sand Island, Oahu. The depths range from 4–8 to 90–105 fathoms, but all specimens are single valves except a juvenile in the collection of Dr. P. Burgess, which was collected alive in 25 fathoms off Honolulu Harbor.

AFFINITIES: *P. j. waikikius* differs from *jacobaeus* s.str. and from the subspecies *keppelianius, byronensis, byoritsuensis,* and *meridionalis* in its high beak and inflation, strongly concave left valve, and distinctive left adductor scar. In sculpture it most closely resembles the ornamented phase of the extinct New Zealand Pleistocene form *P. j. toi,* but the latter is larger (up to 131 mm long), less inflated (29.5% compared with 44%), has a normal muscle scar, and is diphasic. In its rounded ribs, *P. j. waikikius* approach s subspecies of *P. maximus,* but this resemblance is probably homeomorphy.

In studying the relationships between different living and extinct populations of Pacific *Pecten,* the writer was led to the conclusion that members of the *jacobaeus* group were capable of hybridising with members of the *benedictus* group, when they came into geographical proximity, despite the evidence that the two groups had long been differentiated in the Mediterranean and had maintained themselves as distinct for most of Upper Tertiary time. For this reason, the subgenus *Oppenheimopecten* von Teppner, 1922, proposed for *Pecten subbenedictus* Fontannes, cannot be maintained. A member of the *benedictus* group, *P. benedictus excavatus* Anton (of authors, =*sinensis* Sowerby) lives in the China Sea, Formosa, and Japan, is

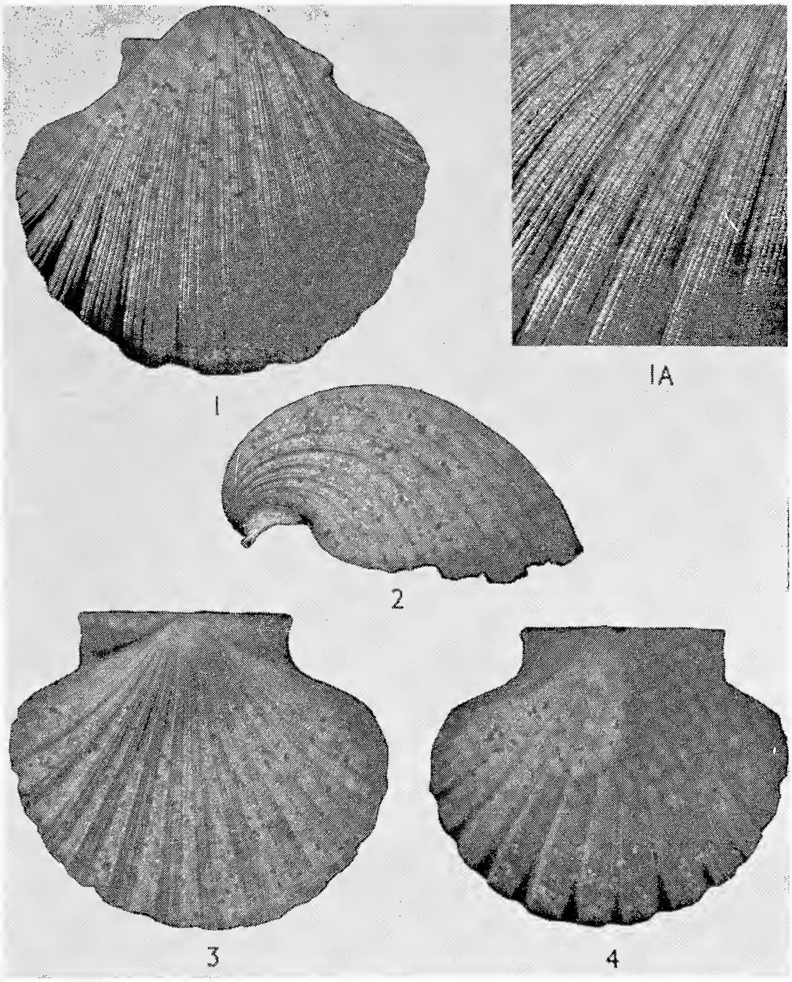

FIG. 1. *Pecten jacobaeus waikikius* Dall, Bartsch, and Rehder. Taken off Keehi Lagoon, Oahu, Hawaii, explosives anchorage area, 42–58 fathoms (King Dredging Exped. Stn. 236, Aug. 1959). *1, 2,* Right valve, lateral and posterior views, × 1. *1A,* Detail of sculpture, right valve, × 1.5. *3, 4,* Left valve, exterior and interior views, × 1. Photograph, S. N. Beatus.

present at the Philippine Islands as dead valves (U. S. Nat. Mus., Bur. Fisheries Sta. 5162, 230 fathoms off Sanga Sanga Island), and perhaps formerly ranged far enough east to influence the Hawaiian population. It is even possible, as noted below, that a form of *benedictus* still lives at Hawaii. The characters of *waikikius* that could be attributed to interbreeding with a *benedictus* population are its extreme inflation, concave left valve, and rounded ribs. The peculiar adductor muscle scar of *waikikius* resembles that of a specimen of *sinensis* from Japan, but this character probably has a functional relationship to the extreme inflation of the right valve and is not necessarily an indication of close affinity.

Pecten (? *benedictus*) *diomedeus* Dall, Bartsch and Rehder

1938. *Pecten diomedeus,* B. P. Bishop Mus. Bull. 153: 96, pl. 24, figs. 7–8.
1957. *Pecten* (? *benedictus*) *diomedeus* Dall, Bartsch and Rehder; Fleming, N. Z. Geol. Surv. Pal. Bull. 26: 9.

This species is still known only from the type, a left valve differing from those of *waikikius* in being much less concave, and in its lack of auricular radial threads, in its ill-defined muscle scar, and in its lower ribs.

Examination of the holotype confirmed the impression that led to classification under *benedictus* (Fleming, 1957), and the uniformity of the *waikikius* sample now available strengthens the case for its specific distinction. This will not be certain, however, until right valves are obtained, since left valve concavity (and thus probably the nature of the adductor scar) are known to vary markedly in some *Pecten* populations (cf Fleming, 1957: 47) and auricular ribs are obsolete in some specimens of *waikikius*.

BIOGEOGRAPHY OF PACIFIC *Pecten*

In the light of later discoveries, the hypothesis that several species groups of *Pecten*, originating in other regions, colonised the Pacific in late Cenozoic times (Fleming, 1957: 23–25), is here recapitulated.

Of the several groups that entered the western Pacific, only one, now represented by the Japanese *Pecten albicans* Schroeter, shows relationships with America, where its extinct relations occur in the Miocene and Pliocene. Recently, however, Kanno (1960: 220) reported a poorly preserved shell close to *P. albicans* from the upper Oligocene of Japan. If this relationship were confirmed, the dispersal of the *albicans-aletes* group may have been from west to east, and not the reverse, as Grant and Gale (1931) postulated, but the matter must be left open at present.

Early members of the *jacobaeus* group had entered the Indian Ocean by the Miocene, and were represented there by a group of forms centred on *P. vasseli* Fuchs. Pliocene dispersals of members of the same group led to the widespread polytypic species *P. maximus* (northern Europe, with a representative in South Africa) and *P. modestus* (Mediterranean, Indian Ocean, and New Zealand). *P. jacobaeus* first appeared in the Mediterranean at the very beginning of the Pliocene, and by an unknown route (since it is not recorded as a fossil at intermediate localites) reached New Zealand (*toi*, Pleistocene), New South Wales (*byronensis*, Recent), Tasmania and southeast Australia (*meridionalis*, Pleistocene-Recent), Formosa and the Ryukyu Islands (*byoritsuensis*, Plio-Pleistocene), and Hawaii (*waikikius*, Recent). The earliest dates given in literature for these scallops in the Pacific is Pliocene, but downward revision of the Plio-Pleistocene boundary may eventually make them all Pleistocene. Some of the derivative races closely resemble the Mediterranean *jacobaeus*, but others have diverged in various ways. On the west side of the Tasman Sea, *P. j. meridionalis* has diverged in rib profile. In New Zealand a well-documented succession of Pleistocene populations suggests that the Recent species *P. novaezelandiae* was derived by loss of secondary sculpture from *P. jacobaeus toi*, and that the Kermadec Islands were colonised at an intermediate date in this Pleistocene history to produce *P. novaezelandiae raoulensis* Powell (1958).[2] It seems possible that the Formosa race *byoritsuensis* similarly gave rise to the smooth form *naganumanus* by loss of secondary sculpture, but this suggestion is not known to be supported by a stratigraphic sequence and the two occur together in Formosa (Nomura, 1933).[3] Other populations have retained the distinctive sculpture of *jacobaeus*, for instance *byronensis* in northern New South Wales and *waikikius* in Hawaii.

By a similar process of late Cenozoic range expansion by uncertain routes from the Mediterranean to the Pacific and subsequent disruption into isolated populations, the *benedictus* group of *Pecten* has reached the Red Sea (*erythraensis* Sow., Pliocene-Recent), New Zealand (several Pleistocene forms), Australia (*fumatus* and *albus*), the Philippine and China seas (*excavatus* of recent authors = *sinensis*), and perhaps Honolulu (*diomedeus*). Races of *benedictus* are more conservative than the *jacobaeus* group and are still quite close-knit in morphology.

The zoogeographic history of *Pecten* in the Indo-Pacific has some analogies with that of

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[2] Wrongly shown as a member of the *benedictus* group in Fleming, 1957: fig. 3, but correctly classified in fig. 1. Originally described as *Pecten raoulensis* Powell.

[3] Nomura's record of *P. naganumanus* Yokoyama from Miocene of the Philippines is not supported by the reference to Dickerson (1922) that he cites.

Indo-Pacific Strombidae summarised by Abbot (1960: 842). Whereas *Strombus* first appeared in the early Miocene of the Tethys Sea, the groups of *Pecten* here considered arose in the Mediterranean basin and only later spread east into the Indo-Pacific. While tropical *Strombus* spread widely during the Pliocene, *Pecten,* preferring cooler seas, continued its spread in the early Pleistocene, when intermittent cool temperatures must have been more favourable than those of warmer Pliocene seas. As in *Strombus,* there was a shrinkage of ranges some time during the Pleistocene, so that the present distribution areas of *Pecten* subspecies are as strikingly discontinuous as are those of some subspecies of *Strombus*. Further discoveries of fossil or living populations in the Indian and Pacific oceans and the intervening archipelagos are likely to bridge the notable gaps in the known distribution of *Pecten* along the presumptive dispersal routes from the Red Sea to New Zealand, Japan, and Hawaii.

SUMMARY

The right valve of a rare Hawaiian scallop, named on the basis of left valves, is described and figured for the first time, and classed as a subspecies of *Pecten jacobaeus* (Linn.). Its place in the biogeographic history of the genus *Pecten* is discussed.

REFERENCES

ABBOTT, R. T. 1960. The genus *Strombus* in the Indo-Pacific. Indo-Pacific Mollusca 1 (2): 33–146.

DALL, W. H., P. BARTSCH, and H. A. REHDER. 1938. A manual of the Recent and Fossil marine pelecypod mollusks of the Hawaiian Islands. B. P. Bishop Mus. Bull. 153.

DICKERSON, R. E. 1922. Review of Philippine paleontology. Philippine J. Sci. 20 (2): 195–229.

FLEMING, C. A. 1957. The genus *Pecten* in New Zealand. N. Z. Geol. Surv. Pal. Bull. 26.

GRANT, U. S., and H. R. GALE. 1931. Pliocene and Pleistocene Mollusca of California. Mem. San Diego Soc. Nat. Hist. I.

KANNO, S. 1960. The Tertiary System of the Chichibu Basin, Saitama Prefecture, Central Japan, Part II. Palaeontology. Jap. Soc. Prom. Sci., Tokyo.

NOMURA, S. 1933. Catalogue of the Tertiary and Quaternary Mollusca from the Island of Taiwan (Formosa) in the Institute of Geology and Palaeontology, Tohoku Imperial University, Sendai, Japan, Part I. Pelecypoda. Sci. Rep. Tohoku Imp. Univ. Sec. Ser. (Geol.) 16 (1).

POWELL, A. W. B. 1958. Mollusca of the Kermadec Islands, Part 1. Rec. Auck. Inst. Mus. 5 (1–2): 65–85.

Taxonomic Revision of *Sagitta robusta* and *Sagitta ferox* Doncaster, and Notes on Their Distribution in the Pacific

ANGELES ALVARIÑO[1]

THE MATERIAL for this study was provided by the monthly cruises of the California Cooperative Fisheries Investigation (CalCOFI) during 1954 and 1958, and by the following expeditions of Scripps Institution of Oceanography in the Pacific Ocean: Northern Holiday (1951), Shellback (1952), Capricorn (1952–53), Transpac (1953), East Tropic (1955), North Pacific (1955), POFI (1955), Troll (1955), Chinook (1956), Equapac Horizon (1956), Equapac Stranger (1956), Downwind (1957), Tethys (1960), and a few samples from the Naga (1959–61).

Thirty species of Chaetognatha were found in the plankton samples from the Pacific expeditions; 24 of these were observed also in the 2,000 samples examined from the area covered by the CalCOFI cruises off California in 1954 and 1958. The identities of two of the species found, *Sagitta robusta* Doncaster and *S. ferox* Doncaster, are confused in the literature. The principal aim of this article is to discuss and establish the valid taxonomic characteristics of these two species prior to publishing a study of the distribution and abundance of the chaetognaths in the area of the CalCOFI cruises.

TAXONOMIC NOTES

A clear statement on the systematics of these species was perhaps difficult, in the past, since only a small number of specimens was available. The various Scripps expeditions cover an extensive distributional area in the Pacific. The numerous plankton samples collected are generally well preserved, providing good material for an accurate taxonomic study. A large number of *S. robusta* and *S. ferox* specimens, therefore, have been carefully examined.

S. robusta Doncaster and *S. ferox* Doncaster could be included in a taxonomic group with their closest relatives *S. hispida* Conant, *S. helenae* Ritter-Zahony of the Atlantic, and *S. bipunctata* Quoy and Gaimard, a cosmopolitan species. They have strong, firm bodies, because of the well-developed muscles, small lateral fields, large heads, and conspicuous collarettes.

S. robusta and *S. ferox,* although very closely related, can be easily distinguished by several characteristics which appear consistently in each. These two species are found in equatorial and tropical Pacific waters, spreading to the subtropical region. They both have a firm, opaque body, strong muscles, large head, and a well-developed collarette. One of the species is smaller than the other. The smaller has the characteristics of *S. robusta* Doncaster and the larger those of *S. ferox* Doncaster. However, the size notations recorded in this study do not agree with the size Doncaster (1903) reports in the original description. This fact shows that perhaps for some reason the size notations in the original descriptions are erroneous. Similar discrepancies are found in successive revisions.

The taxonomic confusion in the literature is explained by the fact that Doncaster (1903) originally applied one series of characteristics to the smaller species and the other series to the larger. His first description of *S. robusta* and *S. ferox* is incomplete; nevertheless a few well-defined characteristics given by Doncaster provide good reason for separating the two species.

The main distinctive characteristics for both *S. robusta* (a) and *S. ferox* (b) in the original description (Doncaster 1903) are as follows:

(a) "posterior fins reach the seminal vesicles,"
(b) "do not quite reach the seminal vesicles";
(a) "ovaries extremely long and extend in fully mature specimens to the anterior transverse septum,"

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[1] Scripps Institution of Oceanography, University of California, San Diego, California. Manuscript received June 1, 1961.

(b) "long as in *S. robusta,* but do not quite reach the front end of the trunk cavity";
(a) "seminal vesicles touch both posterior and tail fins, project somewhat,"
(b) "project slightly";
(a) "hooks 7–8, usually 8,"
(b) "hooks 5–6."

Doncaster also gives *S. robusta* a very important characteristic; namely "the anterior fin's front end is opposite the posterior end of the abdominal ganglion." This distinctive characteristic is the clue for a clear-cut separation of the two species.

Size is the one difference between Doncaster's diagnosis and those studied here. He gives a mature size of 16 mm for *S. robusta* and of 12 mm for *S. ferox,* whereas the specimens from the Pacific and China Sea collections with the characteristics of *S. ferox* mature when at least 16 mm in length, and specimens with the characteristics of *S. robusta* when at sizes 8–12 mm.

This size discrepancy could be a misprint in the original description, and has apparently been the cause of the controversy regarding the identity of these species and the resultant mistaken identifications which have been published. Apparently many authors separate these species by size alone, disregarding the other anatomical features. For this reason, specimens with the characteristics of *S. ferox* have been considered as *S. robusta* and vice versa. The belief that the sizes were inadvertently transposed from one species to the other in the original description is supported by the fact that the specimens from the Pacific Expeditions consistently have the characteristics of *S. robusta* with sizes 8–12 mm and *S. ferox* with a size of 16 mm.

Descriptions of *S. robusta* and *S. ferox* found in material from the Pacific and China Sea collections follow.

Sagitta robusta Doncaster

Total length when mature, 8–12 mm.

Average % tail length in relation to the total length, 27.5.

Head large, but smaller than in *S. ferox* (Fig. 1).

The clove-shaped body is strong, firm, broad, of nearly uniform width from the neck to the tail septum. It is opaque because of the strong longitudinal muscles (Fig. 2*d*). Lateral fields small.

Collarette well developed, extends from the head to the posterior end of the ventral ganglion, spreading to the tail as a thin layer that becomes thicker in front of the anterior end of the seminal vesicles.

The corona ciliata was not studied because it could not be seen clearly in preserved material; therefore it was of small value for identification purposes.

Gut diverticula present and rather conspicuous.

The anterior fins are shorter than the posterior fins. They extend up to the level of the posterior end of the ventral ganglion. They are wider than in *S. ferox* and no rayless zone is present.

The posterior fins are rounded. They lie more on the tail than on the trunk. About ⅔ of the length of the fin lies on the tail segment. The posterior fins are wider at a point slightly behind or in front of the tail septum. A small rayless zone appears at the internal portion of the fins, in front of the tail septum, by the external openings of the female organs.

The distance between both the anterior fins and the posterior fins is longer than in *S. ferox.*

The seminal vesicles (Fig. 3) are conspicuous even in the young species. They touch both tail fin and posterior end of the posterior fins. They

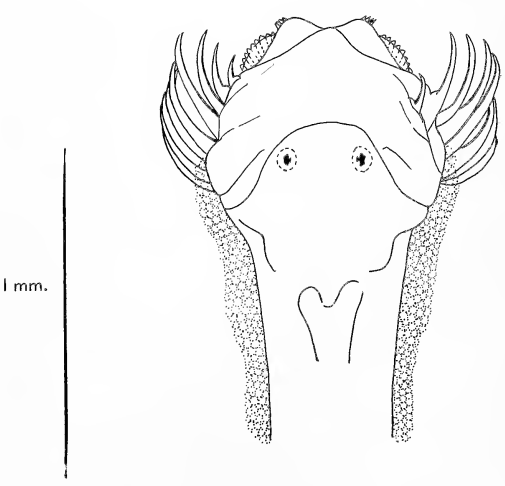

FIG. 1. Head of *S. robusta* Doncaster.

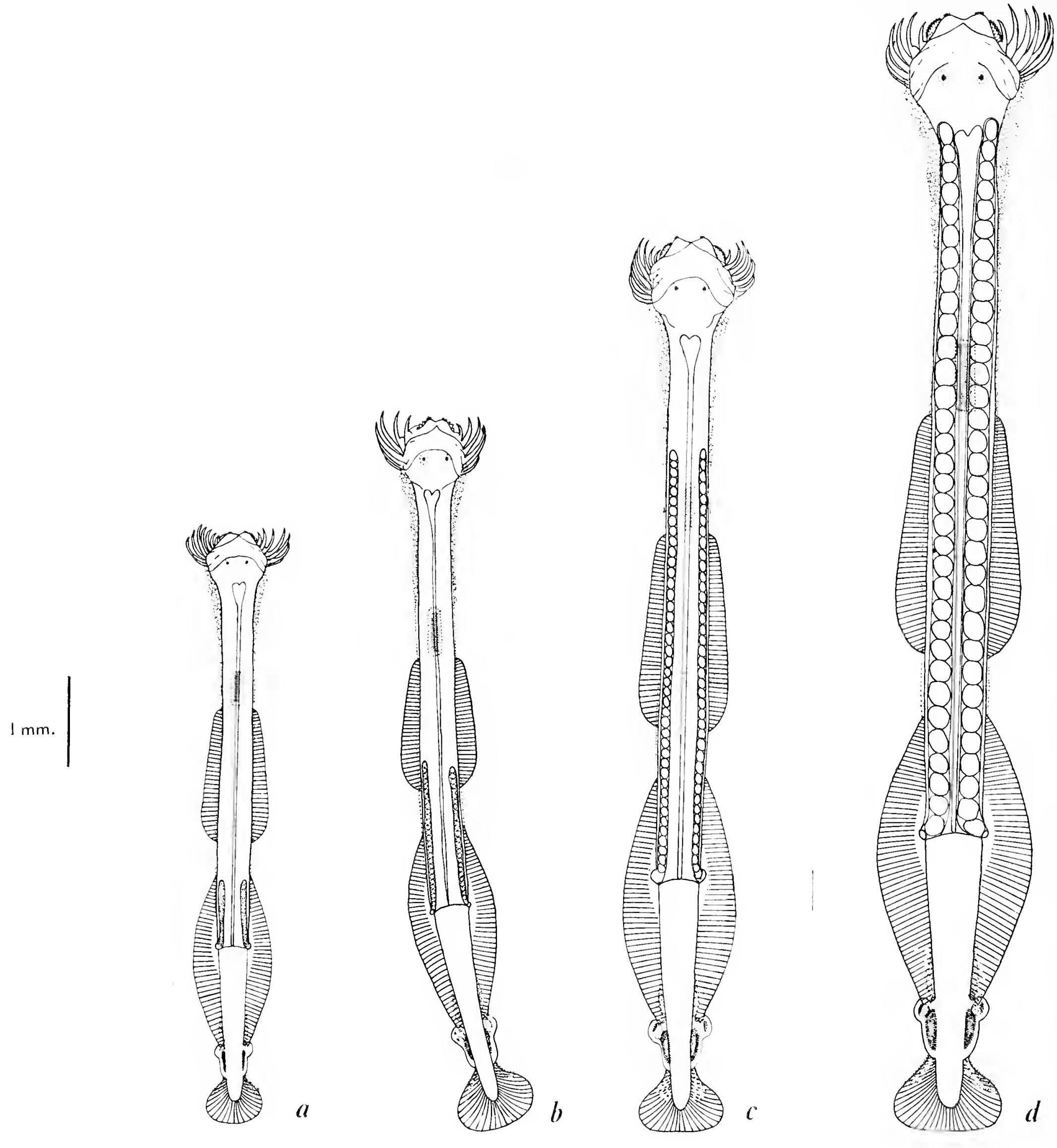

FIG. 2. *S. robusta: a,* 6 mm long, maturity stage I; *b,* 7.6 mm long, maturity stage II; *c,* 9.6 mm long, maturity stage III; *d,* 12 mm long, maturity stage IV.

have a well-developed head and a voluminous posterior sperm sac, and rupture occurs ventrally at the anterior lateral side. The seminal vesicles in *S. robusta* resemble in shape those of *S. bipunctata.* In both *S. robusta* and *S. bipunctata* there is swelling of the collarette tissue on the tail in front of the anterior end of the seminal vesicles, but in *S. bipunctata* the posterior fins do not touch the the seminal vesicles as in *S. robusta,* and the distance between the anterior end of the seminal vesicles and the posterior end of the posterior fins is occupied by the particular swelling of the collarette tissue.

The ovaries are long, reaching from the neck

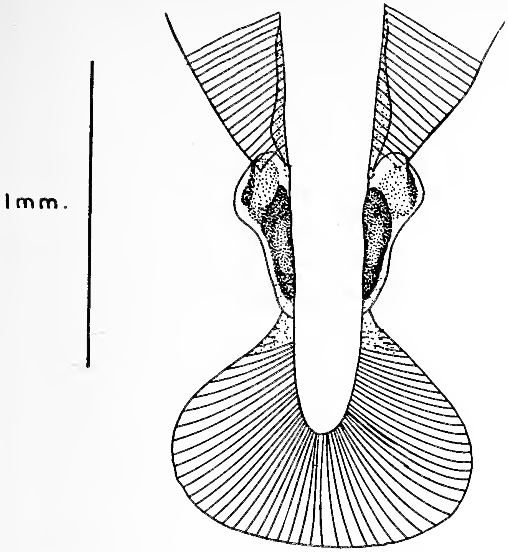

FIG. 3. *S. robusta*, seminal vesicles, ventral view.

to the anterior septum in the fully mature specimens. The ova are round and arranged in one row in the ovaries (Fig. 4).

Hooks 7–8. This notation is unusually constant.

Anterior teeth 6–9.

Posterior teeth 10–15.

The eye pigment is concentrated as in Figure 5. The shape of the pigmented area is similar in both *S. robusta* and *S. ferox* but in *S. ferox* the longitudinal axis of the ellipse is longer in relation to the transverse axis.

S. robusta from the CalCOFI and from part of the Shellback samples mature when 7–8 mm in length. The mature specimens are smaller at the eastern edge of the distributional area, that is, off the southern part of Baja California and the southern part of Mexico. This fact is probably due in many cases to an increase in temperature.

Sagitta ferox Doncaster

Total length when mature, 16–18 mm without tail fin.

Average % of tail segment in relation to total length, 26.5.

The body is rigid, firm, with the same width from the neck to the tail septum. The longitudinal and transverse muscles are strong. The lateral fields are narrow. In general resembles a clove, as does *S. robusta,* but larger in size and with well-defined characteristics which permit easy differentiation of the species (Fig. 6*d*).

The head is large (Fig. 7).

The eyes are as shown in Figure 8.

The collarette is well developed, extending from the head to the anterior end of the anterior fins.

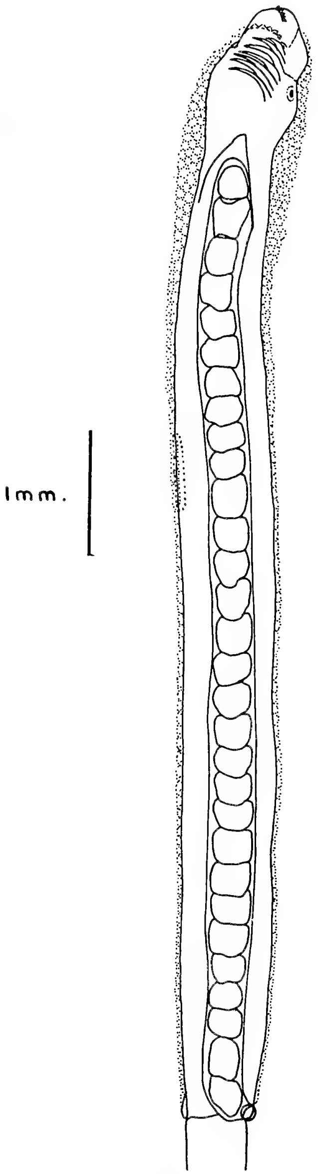

FIG. 4. *S. robusta,* lateral view of left ovary. Detail of the disposition of the ova.

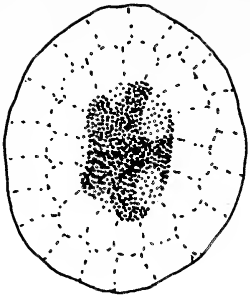

FIG. 5. *S. robusta*, right eye.

Anterior fins reach the level of the middle of the ventral ganglion. They are longer than the posterior fins. No rayless zone is present. They are narrower and longer in comparison to the total size than in *S. robusta.*

The posterior fins are rounded and triangular in shape. They are wider at a point behind the tail septum. They extend approximately the same distance on the trunk as on the tail, or slightly more on the tail. They present an interior rayless zone which extends from the level of the tail septum to the final anterior end of the fins.

Both anterior and posterior fins are rather close laterally.

The seminal vesicles almost touch both the posterior fins and the tail fin, but are not as conspicuous in the early stages as in *S. robusta.* However, they are very noticeable when full or at the last stage of maturity of the male organs. The rupture occurs by a lateral opening (Fig. 9 *a, b*).

The ovaries reach the neck region completely filling the body cavity when fully mature. The ova when ripe, are wider than long and are dorso-ventrally arranged in two or three rows. (Fig. 10.)

Gut diverticula present.

MATURITY STAGES

Fig.	Stage	*Sagitta robusta* Doncaster		*Sagitta ferox* Doncaster	
		male organs	female organs	male organs	female organs
2*a*, 6*a*	I	testes begin to appear; seminal vesicles begin to appear at a precocious age	ovaries as thin tubes, reaching up to the anterior end of posterior fins	testes begin to appear; no trace of seminal vesicles	ovaries as fine tubes, reaching up to the anterior end of the posterior fins
2*b*, 6*b*	II	tail filled with sperm; seminal vesicles conspicuous	ovaries reach anterior end of anterior fins	tail filled with sperm; seminal vesicles begin	ovaries reach anterior end of anterior fins
2*c*, 6*c*	III	seminal vesicles full	ovaries reach up near to the neck	tail partially discharged; seminal vesicles full	ovaries reach to a point between the neck and the ventral ganglion; they are wider; ova large and arranged dorso-ventrally in two or three rows
2*d*, 6*d*	IV	seminal vesicles turgid, discharging and still conspicuous	ovaries reach the anterior septum; ova in one row	tail empty; seminal vesicles discharged	ovaries reach the neck, filling the body cavity

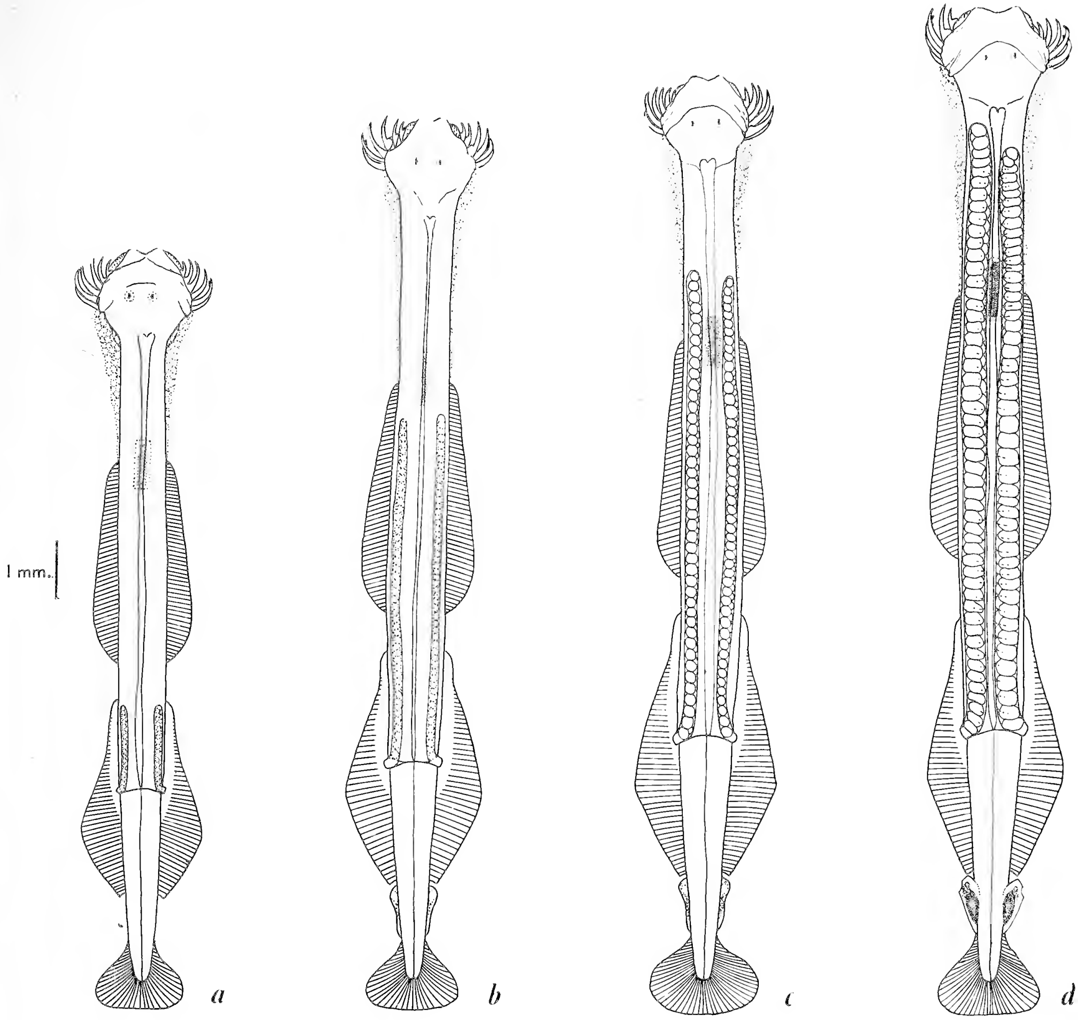

FIG. 6. *S. ferox* Doncaster: *a,* Up to 12 mm long, maturity stage I; *b,* 14 mm long, maturity stage II; *c,* 15 mm long, maturity stage III; *d,* 16 mm long, maturity stage IV.

Hooks 5–6, usually 6, and this notation appears particularly constant.

Anterior teeth 7–10, usually 9.

Posterior teeth 12–14.

Specimens of *S. robusta* from the Naga Expedition are fully mature when 12 mm in length. Specimens from the Equapac Horizon and Stranger are mature when 10 mm, and from the CalCOFI and Shellback area when 7–8 mm. In the measurements the tail fin was not included.

REVISION OF LITERATURE AND DISCUSSION OF TAXONOMY

Doncaster (1903) gives a few well-defined characteristics for *S. robusta* and *S. ferox,* but an incomplete description (Table 1).

Fowler (1906) redescribes both in more detail and also gives their respective distribution areas and temperature ranges on pages 42, 45, 55, 69, 72, 76, 77, and 78. He states for *S. ferox:*

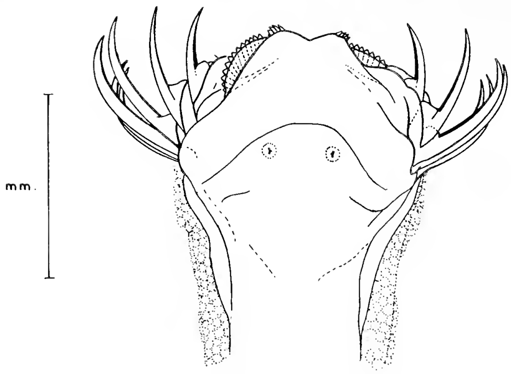

FIG. 7. Head of *S. ferox*.

"it gets mature at 15 mm., while *S. robusta* at about 12 mm. Anterior fins commencing about on a level with the abdominal ganglion. Posterior fins shorter than anterior fins, more on the tail than on the trunk, extending to the seminal vesicles, widest behind the septum. Tail fin generally rounded." And for *S. robusta:* "head fairly large, but smaller than in *S. ferox.* Body proportionally more slender than in *S. ferox.* Anterior fins long, beginning at or just behind the abdominal ganglion. Posterior fins larger than anterior fins (unlike *S. ferox*) more on the tail than on the trunk, widest behind the septum, reaching to the seminal vesiculae when they are bursting." (See Table 2.)

Kofoid (1907) keeps both *S. robusta* and *S. ferox* as valid species.

Michael (1908) identifies both *S. robusta* and *S. ferox* and characterizes *S. robusta* with posterior fins as long or longer than the anterior fins, and *S. ferox* with posterior fins shorter than the anterior fins. The same author in 1911 and 1913

TABLE 1

DIFFERENTIAL CHARACTERISTICS OF *S. robusta* DONCASTER AND *S. ferox* DONCASTER
(from Doncaster 1903)

	Sagitta robusta Doncaster	*Sagitta ferox* Doncaster
Length mature, mm	16	12
Tail	¼ of total length	more than ¼ of total length
Head	broad	
Collarette	epidermis thickening behind head	epidermis slightly thickening behind head
Anterior fins	as long as posterior, but narrower, its front end is opposite posterior end of abdominal ganglion	
Posterior fins	reach seminal vesicles	do not quite reach seminal vesicles
Tail fin	reach seminal vesicles	
Corona ciliata	long, narrow; beginning in front of eyes; in shape of an elongated ellipse	resembles that in *S. robusta*
Intestinal diverticula	pair at beginning of intestine	as in *S. robusta*
Ovaries	extremely long; extend in fully mature specimens to anterior transverse septum, so that coelom of trunk becomes almost obliterated	long as in *S. robusta,* but do not quite reach front end of trunk cavity
Seminal vesicles	touch both posterior and tail fins; project somewhat	project only slightly
Hooks	usually 7 or 8	5 or 6, thick and powerful, never more than 6
Anterior teeth	9	6
Posterior teeth	10–14	10

TABLE 2

DIFFERENTIAL CHARACTERISTICS OF *S. robusta* DONCASTER AND *S. ferox* DONCASTER
(from Fowler 1906)

	Sagitta robusta Doncaster	*Sagitta ferox* Doncaster
Length mature, mm	12	15
Body	more slender than in *S. ferox;* strong longitudinal muscles, small lateral fields	firm, broad, opaque owing to longitudinal muscles, trunk of nearly uniform width from ganglion to tail septum; lateral fields narrow
% tail	25–33	26–36
Head	fairly large, larger than in *S. serratodentata,* smaller than in *S. ferox*	large, in expansion broader than body at its broadest
Collarette	distinct, slightly less in breadth and length than in *S. ferox*	well developed, extends to or nearly to anterior fins, powerfully developed in adult specimens
Corona ciliata		commencing in front of eyes, very long, reaching up to ¾ of distance to ganglion or even closer to abdominal ganglion and anterior fins
Anterior fins	long, beginning at or just behind abdominal ganglion, rounded, narrower and shorter than in *S. ferox*	long, widest posteriorly and narrowing forwards, commencing about on a level with abdominal ganglion
Posterior fins	longer than anterior fins, rounded, more on tail than on trunk, widest behind septum, reaching seminal vesicles	shorter than anterior fins, more on tail than on trunk, extending to seminal vesicles when these are tumid, widest behind septum
Hooks	5, 6, or 7 short, strong, broad, strongly curved	5 or 6 short, strong, broad at the base, strongly curved
Anterior teeth	5–8	4–10
Posterior teeth	11–14	9–14

places *S. robusta* under the *S. hispida* synonymy and keeps *S. ferox.*

Ritter-Zahony (1909*a, b;* 1910; 1911*a, b*) places *S. ferox* under the *S. robusta* synonymy.

Baldasserony (1915) reports *S. robusta* and states: "in some specimens the anterior fins reached the posterior end of the ventral ganglion while in others the anterior fins extended to the middle of the ventral ganglion." Accordingly, he recognizes both *S. robusta* and *S. ferox.*

Michael (1919) redescribes both species and gives taxonomic validity to both (Table 3).

Burfield and Harvey (1926) compare the identities of both species with others and *S. ferox* is included under the *S. robusta* synonymy. Burfield and Harvey's drawings no. 33, 34, 35, 37, and perhaps no. 36 do not correspond to *S. robusta,* but agree with *S. ferox.*

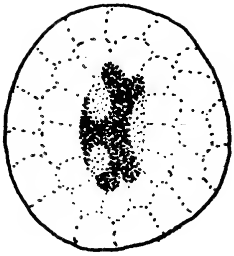

FIG. 8. *S. ferox,* left eye.

In the present article only those publications which give diagnostic details as well as drawings to enforce the identification were considered.

Tokioka (1939) describes *Sagitta ai* as a new species and states at the end of the description:

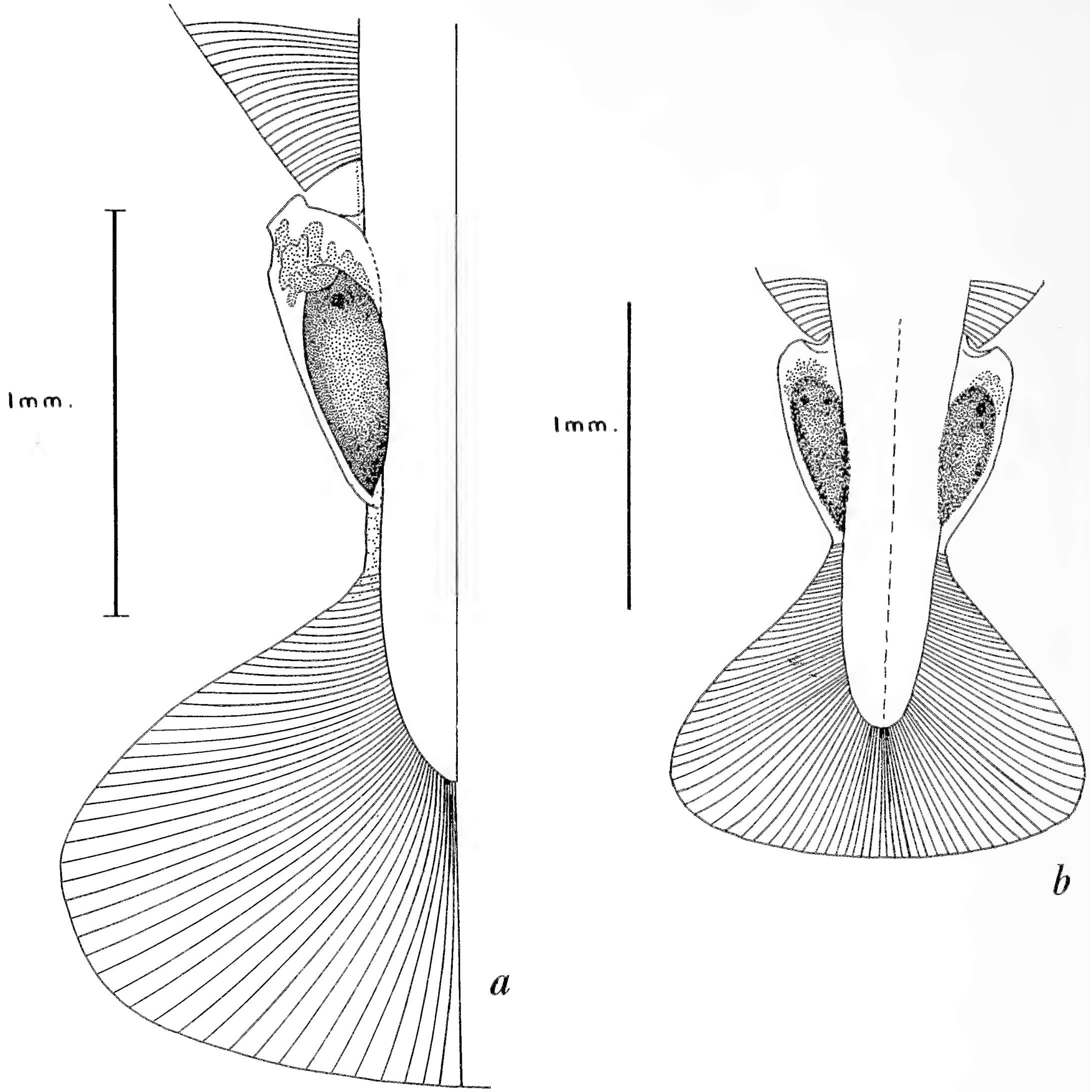

FIG. 9. *S. ferox: a,* Left seminal vesicle, maturity stage IV; *b,* seminal vesicles, dorsal view, maturity stage III.

It is possible that *S. ferox* Doncaster reported by Fowler (1906) from the SIBOGA area is identical with the present species, though there are some differences in the shape of the seminal vesicle, collarette and in some other minute characteristics. However, *S. ferox,* described originally by Doncaster, seems to be not quite identical with the same species reported by Fowler, since there is no characteristic in common to both forms, except for the number of hooks. . . . the present form is fished from the surface waters mingled with *S. robusta* with no intermediate form being found, the former is much fewer than the latter.

Sagitta ai Tokioka has morphological characteristics identical to *S. ferox* Doncaster, according to the original description, redescription (Fowler, 1906), and redescription (Michael, 1919).

The description of *Sagitta ai* Tokioka (1939) agrees with *S. ferox* Doncaster but not as to size. It is also identical to that of *S. ferox* Fowler (1906) and Michael (1919), even to the number of hooks. This meristic characteristic is not very helpful for identification purposes as the number of hooks and teeth vary with the changes in the environment, but, strangely enough, in the case of *S. robusta* and *S. ferox* it remains more constant. Perhaps the factors affecting these numerical changes remain at a constant level in the area they occupy.

Because of the general aspect of the body, length of the ovaries, seminal vesicles, and the important characteristic of longer anterior fins than posterior fins, Delman's (1939) drawing of *S. planctonis* is *S. ferox* and not *S. robusta* as Thomson (1947) states, due to the fact that *S. robusta* has shorter anterior than posterior fins.

Tokioka's (1940*a*: 372) description and drawings of *S. robusta* Doncaster and *Sagitta ai* Tokioka, correspond with the redescription for both *S. robusta* and *S. ferox* as well as with the identifications obtained in the present study.

The disposition and proportion of the fins, more than that of the seminal vesicles, suggest that *Sagitta ai* Tokioka (1942) is more likely to be *S. robusta* than *S. ferox* Doncaster. After comparing the seminal vesicles shown in Tokioka's figure 9 (1942: 540) with those of specimen plate VII, figure 3, the conclusion could be drawn that different specimens are involved.

TABLE 3

DIFFERENTIAL CHARACTERISTICS OF *S. robusta* DONCASTER AND *S. ferox* DONCASTER
(from Michael 1911, 1913, 1919)

	Sagitta robusta Doncaster	*Sagitta ferox* Doncaster
Length mature, mm	10–14	15.6
% tail	25–33	25–36
Body	opaque	opaque, firm, of uniform width from ventral ganglion to tail septum; muscles broad and firm; lateral fields small
Head		large
Collarette	extends about to halfway from neck to ventral ganglion	long and broad, wider than in *S. robusta,* extends beyond anterior end of ventral ganglion into anterior fins
Anterior fins	do not reach ventral ganglion, shorter than posterior fins	extending anteriorly beyond posterior end of ventral ganglion, frequently past its middle; longer than posterior fins
Posterior fins	longer than anterior fins	extending caudally to seminal vesicles; less than 50% of its length in front of tail septum; triangular in shape, greatest width about midway between septum and seminal vesicles
Corona ciliata		long, commencing in front of eyes and terminating near ventral ganglion
Hooks	5–7	4–6
Anterior teeth	5–10	5–9
Posterior teeth	11–14	10–14
		the anterior half of Michael's (1919) drawing of *S. ferox* is accurate, while second half (disposition of posterior fins and seminal vesicles) is not right

TABLE 4

DIFFERENTIAL CHARACTERISTICS OF *S. robusta* DONCASTER, *S. ferox* f. *americana* TOKIOKA AND *S. ai* TOKIOKA

(from Tokioka 1939, 1940*a*, 1959, 1939, 1940*a*, 1942 respectively)

	Sagitta robusta Doncaster (Tokioka 1939, 1940*a*)	*S. ferox* f. *americana* Tokioka (Tokioka 1959)	*Sagitta ai* Tokioka (Tokioka 1939, 1940*a*, 1942)
Length mature, mm	10–13.5	8.3 (medium size)	16–19.5 individuals 10–13.5 immature
% tail	27.9–32.5	27–29	26.3–30.4
Body			very sturdy, widest between caudal end of anterior fin and front end of posterior fin; lateral fields narrow; muscles well developed
Head	large	medium size	very large, larger than in *S. robusta,* broader than widest portion of body
Collarette	continues to seminal vesicles though thickness decreases between ventral ganglion and anterior part of seminal vesicles, swelling again in front of seminal vesicles	fairly conspicuous at neck, reaches anterior end of ventral ganglion, diminishing in thickness posteriorly; there is a swelling in front of seminal vesicles	fairly conspicuous, extends posteriorly as far as corona ciliata
Anterior fins		begin at the posterior end of ventral ganglion. No rayless zone present	elongated, beginning at the level of the middle of the ventral ganglion, broader at the caudal portion. No rayless zone present
Posterior fins		longer than anterior fins, more on tail than on trunk, widest behind tail septum; small rayless area in front of aperture of female organs	rounded-triangular, as long as anterior fins, being broadest behind tail septum and lying more on tail than on trunk; narrow inner rayless zone in front of tail septum
Eye pigment		covers rather large area, slightly elongated and curved	reniform, apparently
Corona ciliata	head length × 2.5, somewhat wavy in its appearance	begins in front of eyes 1.5 times as long as head, both sides are slightly sinuous	begins just behind brain and stretches posteriorly twice head length, without waving, though marked with sinus between eyes
Intestinal diverticula	conspicuous	very distinct	less remarkable than in *S. robusta*
Ovaries	fill body cavity almost completely	reach neck when fully mature	extend to neck
Seminal vesicles	large, round head and narrow trunk; bursting occurs along ventral lateral size of head; maximum size when ovaries reach maturity	have glandular anterior portion and voluminous sperm sac; in outline resemble those of *S. robusta;* rupture occurs at anterolateral side	head is conspicuous, elongated, slightly larger in anterior portions, which is not as conspicuous as in *S. robusta;* it opens on the lateral side of head
Hooks	7–8	7–8 as in *S. robusta*	6
Anterior teeth	5–7	4–14 (fewer than post. teeth)	7–10
Posterior teeth	11–15	10–12 (9–14)	11–15

Thomson (1947: 14) says: "but in Doncaster's original description *S. robusta* was given as reaching 16 mm. and *S. ferox* only about 13 mm." He, too, is aware of some error in the original description by Doncaster.

Burfield (1950) records only *S. robusta* although *S. ferox* could also be found in that area.

Tokioka (1952) in the list of Chaetognatha includes under the synonymy of *S. ferox* "(*S. hispida* of some authors, *S. japonica* Galzow, *S. robusta* of many authors)," but *Sagitta ai* is placed under the *S. robusta* synonymy. However, the same author (1940*b*) speaks of both *S. robusta* Doncaster and *Sagitta ai* Tokioka.

Tokioka (1955) states: "front end of the anterior fins reaches the middle of the ganglion in *S. robusta*." This statement does not agree with Tokioka (1940*a*: 372, fig. 5, A) or with Doncaster (1903), Fowler (1906), or Michael (1919).

It is likely that specimens of 22 mm in length are *S. planctonis* or *S. zetesios,* rather than *S. robusta* or *S. ferox* as Thomson (1947) reports.

According to the drawings given by Rao and Ganapati (1958) their *S. robusta* is probably *S. ferox.*

In the Shellback stations where Tokioka (1959) reports *S. ferox* f. *americana,* specimens with the characteristics of *S. robusta* are recorded in this study. It is obvious that Tokioka's description of *S. ferox* f. *americana* agrees with the definition here obtained of *S. robusta* as well as with Tokioka's description of *S. robusta* (1940*a*), but is somewhat smaller. Tokioka (1959) gives for his *S. ferox* f. *americana* a medium size of 8.3 mm long and states that "fully swollen seminal vesicles are found in 6.2 mm. long individuals" (Table 4).

In the present study it was found that *S. robusta* appears with the seminal vesicles well developed when the individuals are still small, and that the species is very protandrous. The seminal vesicles are conspicuous from an early stage to the most advanced stage in the animal's life, unlike those of *S. ferox,* and much like *S. serratodentata* Krohn, *S. pseudoserratodentata* Tokioka, and *S. pacifica* Tokioka.

The specimens recorded from the Shellback Expedition, where Tokioka reports *S. ferox* f. *americana,* have characteristics that agree completely with the previous descriptions of *S. robusta.*

In order to follow as accurately as possible the taxonomic descriptions by the original authors as well as the redescriptions, it was decided that this revision should name *S. robusta* and *S. ferox* the species with the characteristics iden-

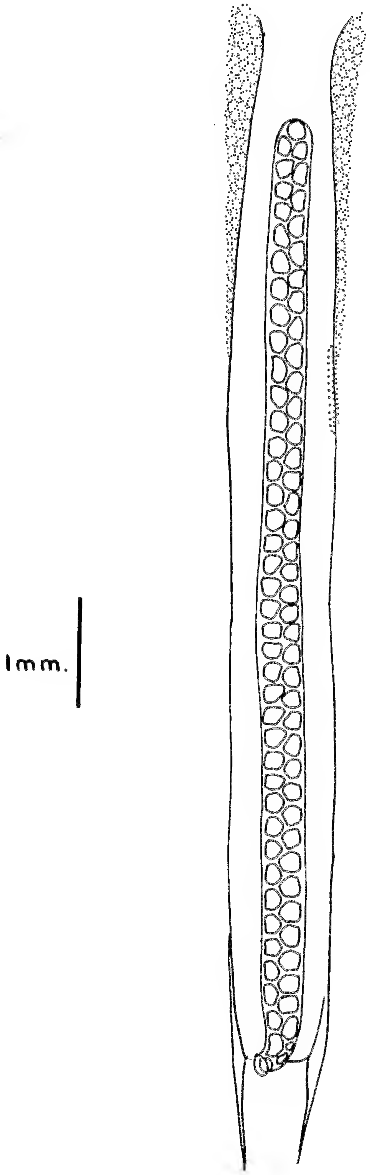

FIG. 10. *S. ferox,* lateral view of right ovary. Detail of disposition of the ova.

TABLE 5

DIFFERENTIAL CHARACTERISTICS OF *S. robusta* DONCASTER AND *S. ferox* DONCASTER FROM THE PRESENT STUDY

	Sagitta robusta Doncaster	*Sagitta ferox* Doncaster
Length mature, mm	8–12	16–18
Average % tail	27.5	26.5
Head	broad	broad
Collarette	well developed, from head to posterior end of ventral ganglion, extending to tail as thin layer thickening in front of anterior end of seminal vesicles	extends from head to anterior end of anterior fins
Anterior fins	shorter than posterior fins, wider than in *S. ferox,* without rayless zone, extending up to level of posterior end of ventral ganglion	reach level of middle of ventral ganglion; they are longer than posterior fins, narrower and longer than in *S. robusta;* no rayless zone present
Posterior fins	rounded, lying more on tail than on trunk, about ⅔ of their length on tail segment; wider at slightly behind or in front of tail septum with small rayless zone in front of tail septum	rounded triangular; wider at a point behind tail septum; they cover same extension on trunk than on tail, or slightly more on latter; a rayless zone extends from tail septum to anterior end of fins
Intestinal diverticula	very conspicuous	conspicuous
Ovaries	long tubes, reaching anterior septum and filling completely body cavity; ova round and arranged in one row	reach neck region, filling completely body cavity; ova arranged in two or three rows
Seminal vesicles	very conspicuous, even in young specimens; they touch both tail and posterior end of posterior fins; a swelling of collarette tissue in tail appears in front of anterior end of seminal vesicles	not so conspicuous as in *S. robusta;* very close to both tail fin and posterior fins
Hooks	7–8	5–6
Anterior teeth	6–9	8–9
Posterior teeth	10–15	12–14

tical to those given to the same species by Fowler (1906) and Michael (1919), and that *Sagitta ai* Tokioka should be classed with *S. ferox,* and *S. ferox* f. *americana* with *S. robusta.*

Tables 1–5, with the respective differential in characteristics for the species from Doncaster, Fowler, Michael and Tokioka's *S. ai* and *S. ferox americana,* give complementary and comparative information.

DISTRIBUTION

S. robusta is equatorial in distribution, extending more to the east than *S. ferox.* It spreads north in the eastern part of the tropical region, invading the waters off Mexico, from the southern part of Baja California southward. The distribution of *S. robusta* (Fig. 11) is more patchy and not as continuous as *S. ferox. S. robusta* was observed mainly in the deeper tows, whereas *S. ferox* appears more often in the upper layers. A difference in the distribution in depth might be the reason for this uneven distribution.

S. ferox occurs along the equatorial and tropical regions of the Pacific, extending northwestwards into the central waters (Fig. 12).

The distribution of *S. robusta* and *S. ferox* reported by Bieri (1959) corresponds respectively to *S. ferox* and *S. robusta.*

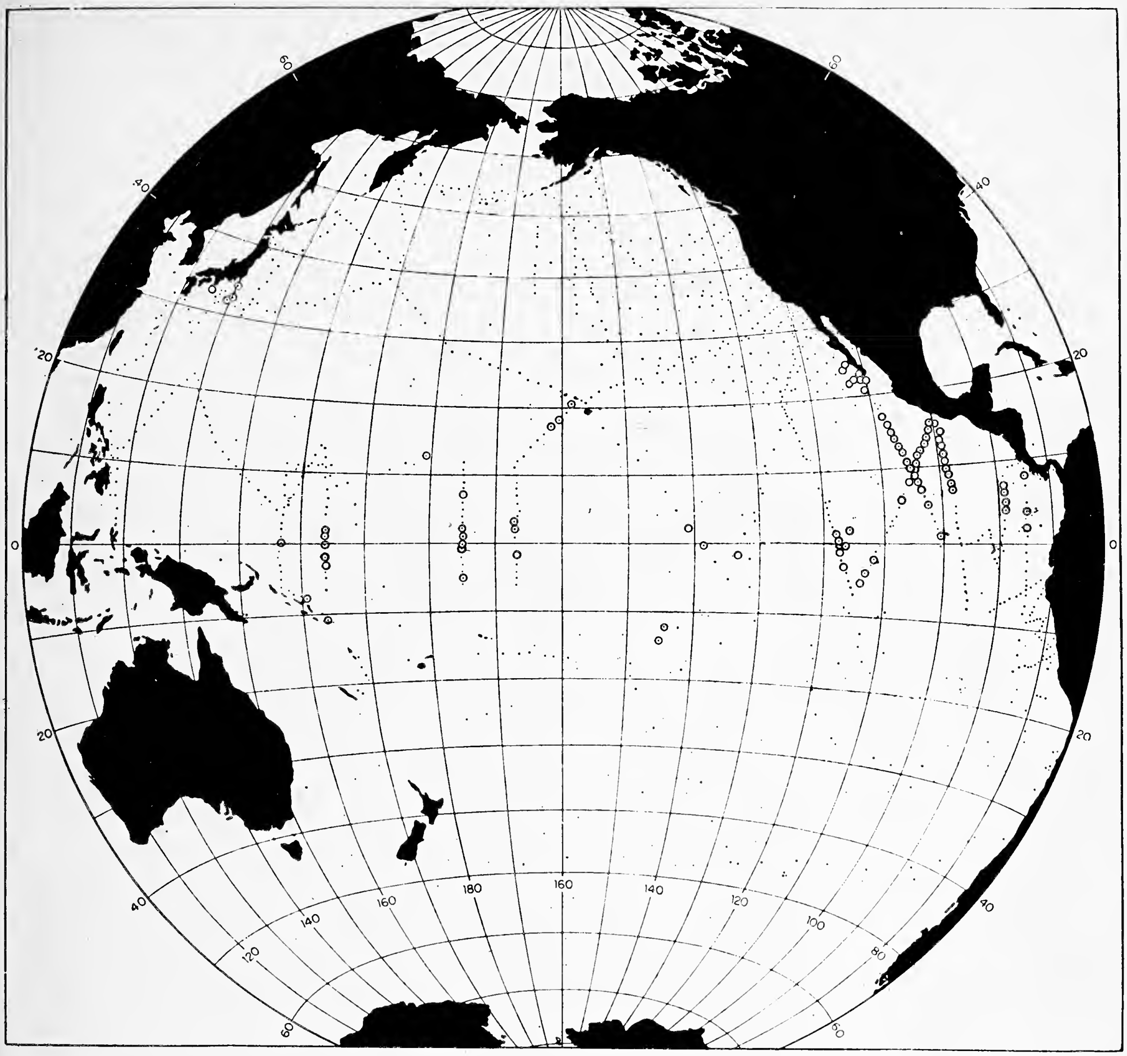

FIG. 11. Distribution of *S. robusta* in the Pacific Ocean. Positive stations O, negative stations ⊙.

REFERENCES

BÉRANECK, E. 1895. Les Chétognathes de la baie d'Amboine. Rev. Suisse Zool. 3: 137–159.

BIERI, R. 1957. The Chaetognatha fauna off Peru in 1949. Pacif. Sci. 9(3): 255–264.

——— 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnol. Oceanogr. 4(1): 1–28.

BURFIELD, S. T. 1950. Chaetognatha. Great Barrier Reef Exped. Sci. Rept. 5(8): 459–473.

BURFIELD, S. T., and E. J. W. HARVEY. 1926. The Chaetognatha of the Sealark Expedition. Trans. Lin. Soc. London, ser. 2, zool. 19(5): 93–119.

DELSMAN, H. C. 1939. Preliminary plankton investigations in the Java Sea. Treubia 17(2): 139–181.

DONCASTER, L. 1903. Chaetognatha, with a note on the variation and distribution of the group. Fauna Geog. Maldive Laccadive Arch. 1(14): 209–218.

FOWLER, G. H. 1906. The Chaetognatha of the Siboga Expedition. Siboga-Exped. Monog. 21: 1–86.

KOFOID, Ch. A. 1907. The coincident distribution of related species of pelagic organisms as illustrated by the Chaetognatha. Amer. Naturalist 41(484): 241–451.

MICHAEL, E. L. 1908. Notes on the identification of the Chaetognatha. Biol. Bull. 15(2): 67–84.

——— 1911. Classification and vertical distribution of the Chaetognatha of the San Diego region. 8(3): 21–186.

——— 1913. Vertical distribution of the Chaetognatha of the San Diego region in relation to the question of isolation vs. coincidence. Amer. Naturalist 47: 17–49.

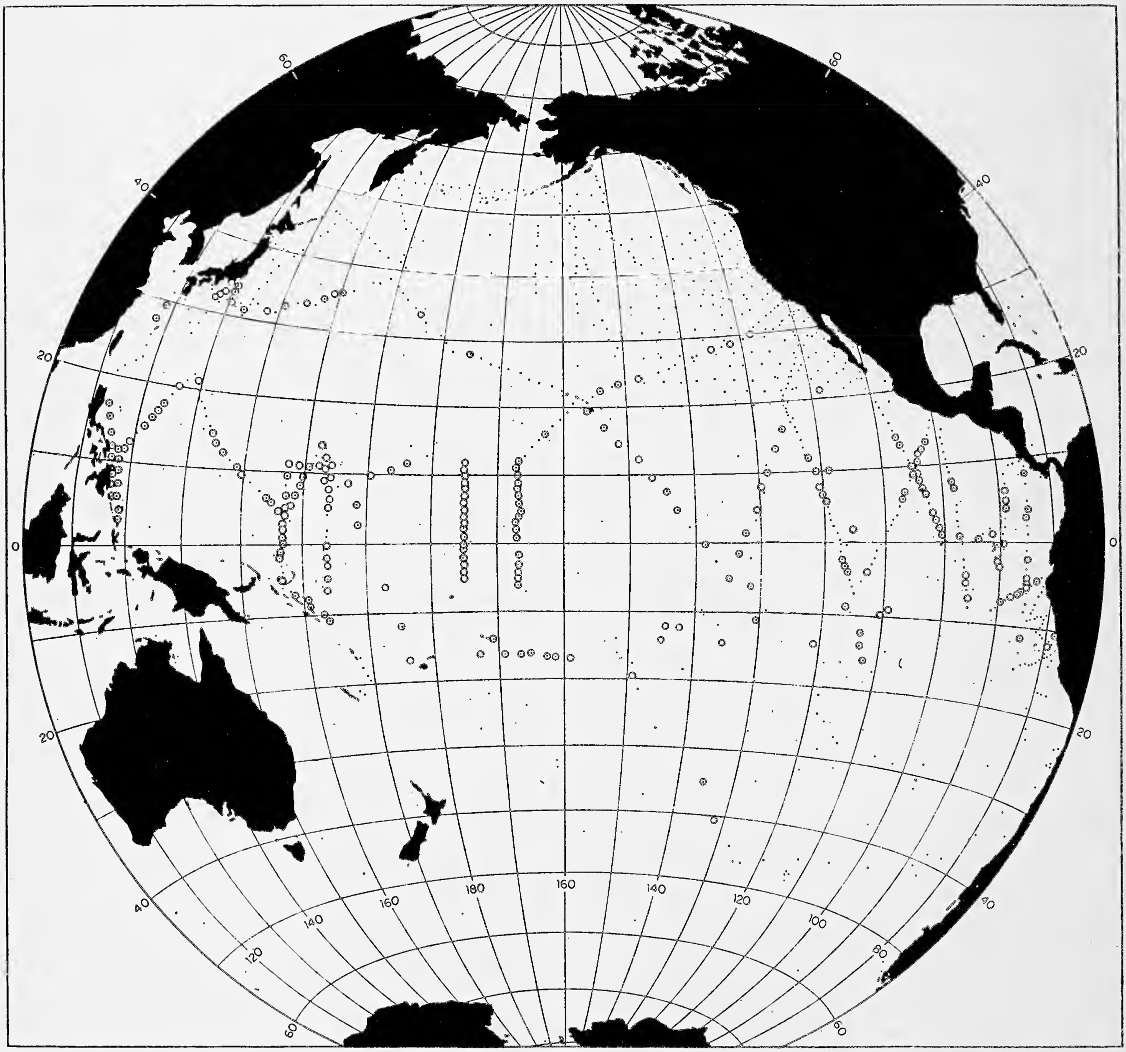

FIG. 12. Distribution of *S. ferox* in the Pacific Ocean. Positive stations ○, negative stations ⊙.

——— 1919. Report on the Chaetognatha collected by the U. S. Fisheries steamer Albatross during the Philippine Expedition, 1907–1910. U. S. Natl. Mus. Bull. 100, 1(4): 235–277.

RAO, T. S. S., and P. N. GANAPATI. 1958. Studies on the Chaetognatha in the Indian Seas, Part III. Systematics and distribution in the waters off Visakhapatnam. Andhra Univ. Mem. Oceanogr. 1: 147–163.

RITTER-ZAHONY, R. 1909*a*. Chätognathen. In, Zool. Ergbn. Exped. S.N.S. Pola in das Rote Meer, Nördliche und Südliche halfte, 1895–1898. Berichte der Komm. fur Ozeanogr. Forsch. 84: 43–54.

——— 1909*b*. Die Chaetognathen der Gazelle Expedition. Zool. Anz. 34(26): 787–793.

——— 1910. Chaetognatha. Die Faune Südwest-Australiens. Erg. Hamburger Südwest-Austral. Forsch. 1905, 3(3): 125–126.

——— 1911*a*. Revision der Chätognathen. Deutsche Südpolar-Exped. 13(5): 1–71.

——— 1911*b*. Die Chätognathen der plankton Expedition. Plankton Exped. der Humbolt-Stiftum 2, H.e., pp. 3–33.

SUND, P. N., and J. A. RENNER. 1959. The Chaetognatha of the Eastropic expedition, with notes as to their possible value as indicators of hydrographic conditions. Inter-Amer. Trop. Tuna Comm. Bull. 3(9): 395–436.

THOMSON, J. M. 1947. The Chaetognatha of South-eastern Australia. Council Sci. Indus. Res. Bull. 222. Div. Fisheries Rept. 14: 4–43.

TOKIOKA, T. 1939. Chaetognaths collected chiefly from the bays of Sagami and Suruga, with some notes on the shape and structure of the seminal vesicles. Rec. Oceanogr. Works Japan 10(2): 123–150.

——— 1940*a*. A small collection of Chaetognaths from the coast of New South Wales. Rec. Austral. Mus. 20(6): 367–379.

——— 1940*b*. The Chaetognatha fauna of the waters of western Japan. Rec. Oceanogr. Works Japan 12(1): 1–22.

——— 1942. Systematic studies of the plankton organisms occurring in Iwayama Bay, Palao, III. Chaetognaths from the bay and adjacent waters. Seto Mar. Biol. Lab. Cont. 104. Palao Trop. Biol. Sta. Studies 2(3): 527–548.

——— 1952. Chaetognaths of the Indo-Pacific. Annot. Zool. Japonenses 25(1,2): 307–316.

——— 1955. Notes on some Chaetognaths from the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribbean 5(1): 52–65.

——— 1959. Observations on the taxonomy and distribution of Chaetognaths of the North Pacific. Seto Mar. Biol. Lab. 7(3): 350–456.

Some Aspects of the Feeding Behavior of *Remora remora*

Donald W. Strasburg[1]

For several years the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, has been interested in holding captive tuna in ponds, and in 1958–59 conducted a series of tests of salt well-water as a medium for these fish. Preliminary experiments took place in a concrete cylinder 8 ft in internal diameter and 5 ft high, in which were confined a variety of reef and semipelagic fish, the latter being important because of our need to anticipate difficulties to be expected with the truly pelagic tunas.

Perhaps the most pelagic of these experimental fish was *Remora remora* (Linnaeus). Two specimens of this species were removed from tiger sharks, *Galeocerdo cuvieri* (Lesueur), on Jan. 16, 1959, and placed in the tank, which already contained several kinds of reef fish. The larger remora measured 170 mm in standard length, the smaller one 76 mm. The fish were fed every day, or every 2 days, and the remoras began eating bread on Jan. 23, continuing to take this and other foods throughout a 1-month observational period. The larger remora succumbed to an eroding infection of the head on Feb. 18, and the smaller one escaped through a drain on Feb. 23.

As soon as they were placed in the tank the remoras exhibited their characteristic attaching behavior. Both fish attached vertically with the head up, the larger fish in a small clearing in the algae coating the tank, the smaller fish to a concrete block placed on the tank's bottom. The larger fish continuously occupied its clearing for the month it lived, and during this period the algae encroached so that the clear space was the size and shape of the remora's disc. The smaller remora's habits were more variable, for it alternated between attaching to the concrete block, swimming freely at the surface, and attaching to the sides of black triggerfish (*Melichthys buniva* (Lacépède)) and parrotfish (*Scarus* sp.).

When first inducing the remoras to feed, food was dropped into the water as near as possible to them. It was soon discovered that they would detach to seize stray bits of food but would immediately reattach after eating, and the question then arose as to what competitive interaction existed between the attaching and feeding acts. A logical second question dealt with their sensory perception, for obviously they would not detach for undetected food. Another variable was the presence of other species, either the host which bore the remora or competitors for food. As these questions arose experiments were undertaken, and records were kept of the kind, quantity, and manner of presentation of food, as well as the behavior of the remoras and the other species. These records form the basis for the present report.

No unusual equipment or methods were employed, but the kinds of food should be listed. Bread was presented in the form of moistened compressed balls varying from ⅛ to ½ inch in diameter, depending on which remora was being fed. Fish consisted of freshly-killed tilapia (*Tilapia mossambica* (Peters)) and swordtails (*Xiphophorus helleri* Heckel) cut into transverse slices or cubes. Shrimp was offered in the form of small cubes cut from commercial frozen shrimp.

FEEDING VERSUS ATTACHING

Prior to examining the relative strength of the feeding and attaching urges in remoras it is necessary to say something about their sensory acuity toward food. Only the larger remora was observed for this, largely because of its single attached position. Food was offered to this animal from two directions: ventrally (toward the tank's center) or laterally (around the periphery of the tank). By starting with food presented

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close to the fish and progressing to offerings spaced increasingly distant it was found that the remora could detect food for at least 48 inches ventrally and 15 inches laterally. It is not known which sense was the most important in this detection, for the more distant offerings were tossed, striking the water with a splash which the fish undoubtedly heard. The water was clear, however, and this, together with the fact that *R. remora* normally feeds selectively on small zooplankters (Strasburg, 1959), may indicate that it could also see ¼-inch pieces of shrimp and bread.

The larger remora was increasingly reluctant to detach and feed when its food was offered from greater distances. Evidence for this is given in Figure 1, which shows the rapid decline in successful feedings with distance (excluding cases where food was approached by another fish). The longest feeding sally was 36 inches, although the fish made short ventures toward food dropped at 42 and 48 inches. The difference in behavior between ventral and lateral food presentations is not understood, but is possibly related to the concomitant binocular and monocular visual situations and the remora's relative ability to evaluate the distance to the food. Both eyes enter into the ventral profile and presumably provide the fish with binocular vision in this direction. All lateral food presentations were from such a direction that they could be seen only by the fish's left eye.

The extent of the larger remora's desire to attach is further manifested in its behavior when simultaneously confronted with two pieces of food. Food was presented ventrally in 25 double feedings at a distance from the remora of 1 to 15 inches. In 17 cases the fish detached, seized one piece of food, and dashed back to reattach to the tank wall, ignoring the second food fragment. In 6 trials the remora did this but immediately after reattaching sallied forth for the second piece of food. Once it ignored both foods and another time it ate both (at a distance of 8 inches) without attaching between feedings. For feedings involving three to eight pieces of food, behavior was much the same, the fish usually venturing out for a single particle, seizing it, returning to the tank wall to reattach, then venturing out again. Toward the end of its confinement it grew rather tame and would eat as many as five food fragments, without reattaching, if they were only a few inches from the attachment site. In general it would seem that the urge to attach is nearly as important as that to feed.

While attached to the concrete block on the tank's bottom, the smaller remora's behavior was much like the larger one's. It ventured after food offered at distances up to 14 inches and usually reattached immediately after seizing it. On three occasions this fish became temporarily free-swimming when food was presented, this occurring when numerous small food particles drifted close by. At such times the remora cruised back and forth through the showers of food at speeds of 0.2–0.4 ft per second, pursuing particles detected as far away as 24 inches. On four other days this fish was unattached throughout the observation period, swimming and feeding at the surface as described above.

The smaller remora spent a total of 11 days attached to triggerfish and 2 days to a parrotfish. The former hosts alternated between circling about the tank at 0.4–0.6 ft per second and wedging themselves into crevices between concrete blocks on the bottom. The remora did not feed when its hosts were in the wedged position. The parrotfish was demersal while it bore the remora, resting quietly on the bottom most of the time but occasionally dashing across the tank, rubbing its side against the bottom in an attempt to dislodge the remora. It appeared that the remora knew this host was a reluctant one, for it was unusually wary of becoming separated. On one occasion the remora had detached and was 2 inches from the parrotfish when the latter flexed its body; the remora, although within an inch of a piece of food, abandoned it to reattach to the host. Another time the remora had loosely attached to the parrotfish while masticating a large lump of bread. Its convulsive chewing and swallowing movements caused it to be displaced an inch or so from its attachment site. The remora's actions apparently disturbed the parrotfish, which tensed and shifted position each time the remora moved. This in turn affected the remora, which ceased chewing and clamped more tightly to the host each time it moved.

While attached to the triggerfish the small remora never ventured more than 6 inches in

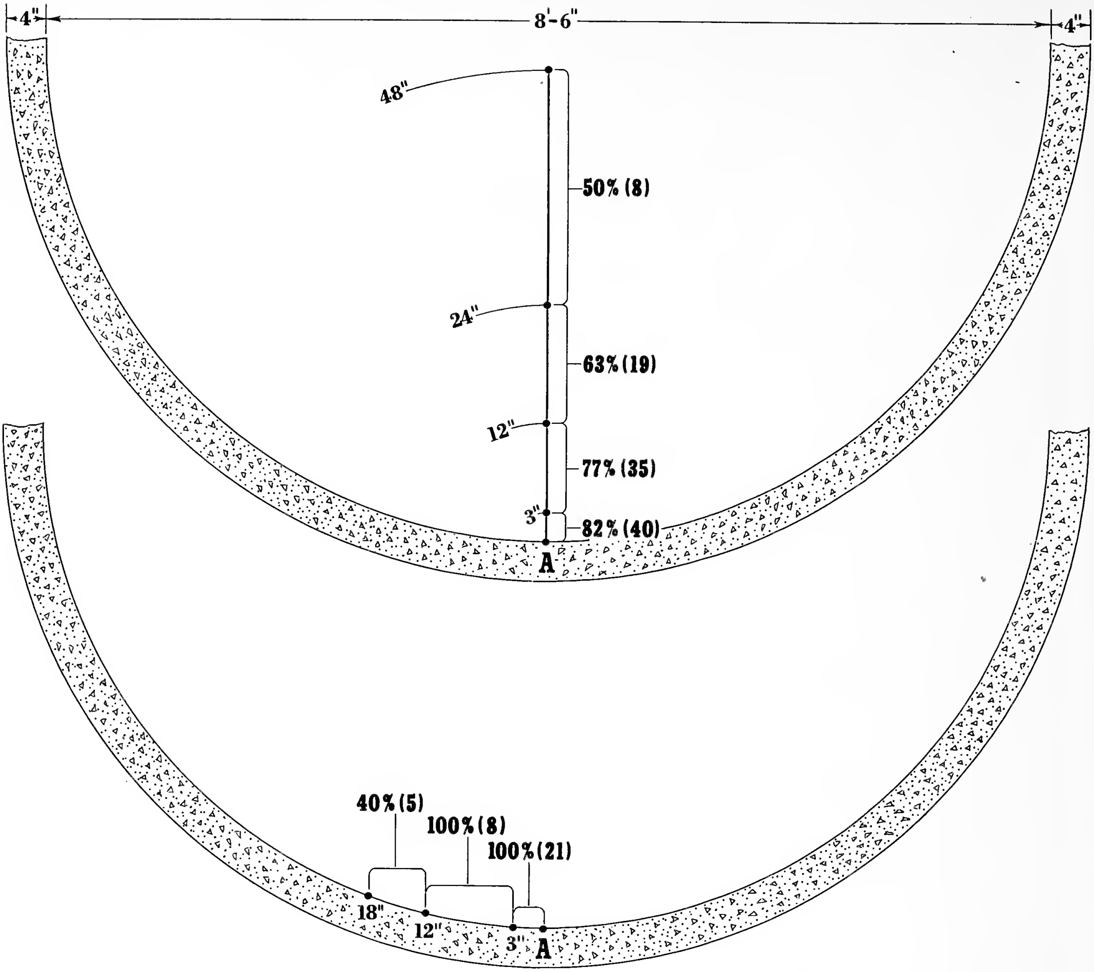

FIG. 1. Percentage occurrence of successful feedings when the larger remora was attached at point *A* and food was offered at successively greater distances. Figures in parentheses represent the total number of food presentations.

pursuit of food, although it reacted to food (by detaching and swimming a short distance) as far away as 12 inches. Of 44 food presentations made within 6 inches, 22 were culminated by the remora's making a successful feeding sally and 20 by an excursion part way to the food. All ventures were immediately followed by reattachment, and when large pieces of food had been seized, by leisurely mastication and swallowing. As noted above, the ingestion of food was often convulsive, resulting in a displacement of the remora by as much as 2 inches along the host's side. It appeared that large items could not be swallowed without loosening the grip on the host, while clamping more firmly to the host often meant losing food from the mouth.

Whenever a food particle fell near the host, the remora undertook a different type of movement in order to feed. The fish slid rapidly over the host's skin, moving forward, backward, or sideways with equal facility, and remaining so close to the host as to appear semi-attached. The extent of contact could not be determined, but probably the disk rim and the dorsal fin actually touched the host. These moves were used in going from the host's sides to the dorsal, anal, and caudal fins, and also in shifting from one side of the host to the other. Ten sliding movements were observed in detail: in six the remora did not feed, its actions only allowing it to keep the food in view; twice the remora was able to seize food practically touching the host, and twice the remora first slid, then detached and swam to the food. This behavior again emphasizes the strength of the attaching urge in these fish.

RECOGNITION OF ATTACHMENT SITE

As noted earlier, the larger remora was a continuous occupant of a small clearing in the algae coating the tank wall. This was an oval space 3 inches high by 1 inch wide, located 11 inches beneath the surface. The surrounding alga was the diatom *Melosira,* which occurred as a dense growth up to 2 inches in thickness. The remora's disk fitted the clear space remarkably well, the disk being oval and 2¾ inches long by 1 inch wide. After each sally for food the remora returned directly to this site, centering its disk precisely in the clearing, and requiring no shifting of position because of misalignment. Its disk was never seen to overlap the clearing's edge nor were algal filaments ever seen to be drawn into the space beneath the disk. Despite the presence of numerous other alga-free spots in the tank, the larger remora restricted its attaching to this one.

A simple experiment was conducted to see whether this remora could be lured to a new attachment site. Two oval clearings were scraped in the algae, 6 and 12 inches to the left of the original site but identical in size and shape to it. Pieces of food were presented to the remora in such a way that it swam past the new clearings in order to feed. Many times the remora would seize its food within 2 inches of one of the new areas, but in no case could it be induced to attach in them.

The smaller remora was also able to recognize its precise point of attachment, at least when on its triggerfish host. This species, *Melichthys buniva,* is largely jet black in color, but when viewed in certain lights on some occasions it has a brilliant metallic green cast. When the remora detached from a triggerfish the skin to which it had been adhering was a much brighter green than the surrounding area, appearing as a horizontal oval spot on the host's side. When closely scrutinized, this spot was found to contain outlines of the disk laminae and rim, all visible as bright green marks against a black background. Each time the remora detached, it returned precisely to this spot, orienting itself to the spot's shape and position. Judging from preserved specimens, remoras have little or no dorsal vision, and it therefore seems that positioning is accomplished by some other sense. It is suggested that this is tactile and that the texture of soft attachment surfaces, such as a host's skin, becomes altered through long contact with the disk, enabling the remora to reestablish its position by touch.

EFFECT OF OTHER SPECIES

Among the factors affecting the feeding behavior of remoras are the presence of hosts, potential hosts, competitors, and predators. The host's role as a vehicle is obvious, and as such the rider is carried from place to place, provided with a respiratory flow of water (Strasburg, 1957), and furnished food in the form of ectoparasites (Strasburg, 1959) or scraps. These favorable characteristics are in part offset by the host's tendency to consume any remoras venturing near its mouth, and an inclination to dislodge or injure others by rubbing against hard objects. The beneficial aspects of the host outweigh the negative qualities, however, as is evidenced by a remora's conspicuous urge to attach.

The feeding experiments provided an opportunity to study the relation between an unattached remora and a potential host. This was done only for the smaller remora, because the larger one never attempted to attach to any of the relatively small hosts available to it. The smaller remora was free-swimming or attached to concrete blocks for 8 days following its capture. At this time two large triggerfish were added to the tank, and the remora attached to one or the other of these for the next 11 days, by which time both hosts had died. The next day the remora was attached to the next-largest available host, a parrotfish, the latter making vigorous efforts to rid itself of its adherent by scraping its sides against the bottom. The remora-parrotfish partnership was apparently mutually displeasing, for the remora left this host the same day, and during a 50-minute observation period was seen to make six passes at other fish. Each pass consisted of the remora's swimming rapidly toward the other fish (*Acanthurus, Chaetodon,* and *Parupeneus*), increasing its speed as it went. The other fish allowed the remora to approach to about a foot, then made a violent turn and fled rapidly. While it is impossible to be certain, it is likely that these maneuvers were attempts to attach. After experiencing several such passes the other fish would no longer let the remora approach them, keeping about 18 inches away from it. This situation prevailed for the remainder of the period of captivity, during which the remora was only once successful in attaching to a fish. This occurred with the parrotfish and lasted for 1 day.

Although the smaller remora was bold when approaching another species, both remoras were very timorous when other species approached them. In 14 feeding experiments it happened that some other tank denizen was attracted to food meant for a remora. Usually the remora had detached and was part way to the food when it realized that another fish was approaching. This resulted in a rapid dash to the attachment site on the part of the remora, and a seizure of the food by the other species (*Parupeneus* and *Abudefduf*). On three occasions the two remoras competed with each other for food. Twice the larger remora abandoned the food to the smaller one, and once it waited until the smaller fish had passed the food before venturing toward it.

SATIATION

An incidental by-product of the feeding experiments was an estimate of the stomach capacity of the two remoras. Although most feedings were not conducted with this in mind, there were a few tests in which the fish were presented with known quantities of food until further offerings were ignored. Where the food was whole fish, volumes were ascertained by water displacement; where balls of bread or blocks of flesh were used, volumes were calculated on the assumption that the balls were spheres and the blocks cubes.

It was found that satiation in remoras resembled that in humans in that the fish not only had favorite foods but also tired of a particular item only to resume eating when a new course was offered. The larger remora became satiated with bread when it had consumed 0.4–2.0 cc; when fed bread until further offerings were ignored and then fed tilapia, satiety occurred with 4.1–4.3 cc; when fed tilapia alone the fish ceased feeding after eating 4.6 cc; and when given shrimp it ate 8.7 cc. A similar but less marked situation was found for the smaller remora. For it, satiety with bread occurred after eating 0.2–0.5 cc; for bread followed by tilapia it happened at 0.7 cc; for fish alone (*Xiphophorus*) it occurred at something less than 1 cc (consumption could not be completely witnessed); and for shrimp at 0.3 cc.

The volume of the 170 mm remora was 56 cc and of the 76 mm fish 4 cc. The largest meal eaten by each was 8.7 and 0.7 cc, respectively, giving a food volume per fish volume ratio of 16–17%. This seems to be typical for a regularly feeding predator, for Nakamura (Ms) found oceanic skipjack (*Katsuwonus pelamis*) consuming about 10% of their own weight at a single feeding, and Hatanaka et al. (1957) found mackerel (*Pneumatophorus japonicus*) consuming 12.5% of their own weight. If *R. remora* were dependent on scraps from its host, one would expect it to be able to ingest large meals and then forego feeding for some time. That it probably eats frequent small meals is suggested by its stomach capacity as well as by the observations of Strasburg (1959), who showed this species to subsist largely on zooplankters. These organisms are captured piecemeal and there is no need for ingesting a single large meal.

REFERENCES

HATANAKA, M., K. SEKINO, M. TAKAHASHI, and T. ICHIMURA. 1957. Growth and food consumption in young mackerel, *Pneumatophorus japonicus* (Houttuyn). Tohoku Jour. Agric. Res. 7(4): 351–368.

NAKAMURA, E. L. Ms. Establishment of skipjack tuna in captivity. Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

STRASBURG, D. W. 1957. Notes on the respiration of small *Remora remora*. Copeia 1957: 58–60.

——— 1959. Notes on the diet and correlating structures of some central Pacific echeneid fishes. Copeia 1959: 244–248, 1 fig.

Systematic Position and Relationships of the Percesocine Fishes[1]

WILLIAM A. GOSLINE[2]

THE FISH FAMILIES Sphyraenidae, Mugilidae, and Atherinidae have been assigned to the percesocine fishes by all authors, and many would include only these (e.g., Berg, 1940: 368). Others have expanded the group in various ways (e.g., Boulenger, 1904: 636). Most commonly, however, such expansion has extended only to the family Polynemidae (e.g., Regan, 1912: 846) or, in recent years, to the polynemid and phallostethoid fishes (e.g., Myers, 1935: 6).

Generally, the percesocine fish groups have been placed at the front of or just ahead of the order Perciformes. The major question in this regard is whether they represent derivatives of a percoid or of a pre-percoid stock.

In the present investigation some attempt has been made to determine the interrelationships and systematic position of the Sphyraenidae, Mugilidae, Atherinidae, and Polynemidae. For this purpose Hawaiian specimens of *Sphyraena barracuda* (Sphyraenidae), *Mugil cephalus* (Mugilidae), *Pranesus insularum* (Atherinidae), and *Polydactylus sexfilis* (Polynemidae) have been stained with alizarin and dissected. To base conclusions regarding families on such limited material is obviously a treacherous undertaking. However, the Sphyraenidae, Mugilidae, and Polynemidae are rather closely-knit families and it is assumed that, for these, any species is fairly representative. For the Atherinidae the situation is quite different. Indeed, Jordan (1923: 177) split the Atherinidae as usually conceived into four separate families. It is therefore highly possible that the structures described for *Pranesus* would be quite different in atherinid genera such as *Craterocephalus* or *Melanotaenia*.

No phallostethoid fishes have been available. However, a considerable literature exists on the anatomy of these forms (Regan, 1916; Bailey, 1936; Villadolid and Manacop, 1934; Aurich, 1937; Hubbs, 1944). On the basis of this, some discussion of phallostethoid relationships has been included.

The conclusions reached here are not new, but it is hoped that the material presented will help to establish them on a somewhat sounder basis than heretofore.

PELVIC STRUCTURE

As a group, the four families Polynemidae, Mugilidae, Sphyraenidae, and Atherinidae have been separated from the typical percoid fishes almost solely on the basis of the subabdominal pelvic position (Regan, 1929). Some attempt to evaluate the systematic significance of this character seems in order.

Regarding the Atherinidae, Boulenger (1904: 639) stated: "Pelvic bones connected with the clavicular [cleithral] symphysis by a ligament." Gregory (1933: 262) wrote: ". . . at least in *Sphyraena ideastes,* a long ligament runs from the pelvis to the cleithral symphysis (as I noted in dissecting a fresh specimen)." Dollo (1905) used Boulenger's statement as a basis for the hypothesis that the abdominal or subabdominal position of the pelvic fins in various families including the four under consideration was a result of secondary regression from the percoid-type pelvic location.

Efforts by the present author to find a ligament between the pelvic girdle and the cleithral symphysis in *Polydactylus, Mugil, Sphyraena,* and *Pranesus* have been unsuccessful. There are ligaments running forward from the bases of the pelvic rays to the pelvic musculature. There are also ligaments running back from the cleithral symphysis to the musculature of the body (Fig. 1*a*). These two sets of ligaments do not meet, however, in any of the four species examined. (The ligament that runs between the anteroventral tip of the pelvic girdle and the lower portion of the pectoral girdle in *Holocentrus* (Fig. 1*a*) seems to be completely lacking in all percesocine fishes investigated.)

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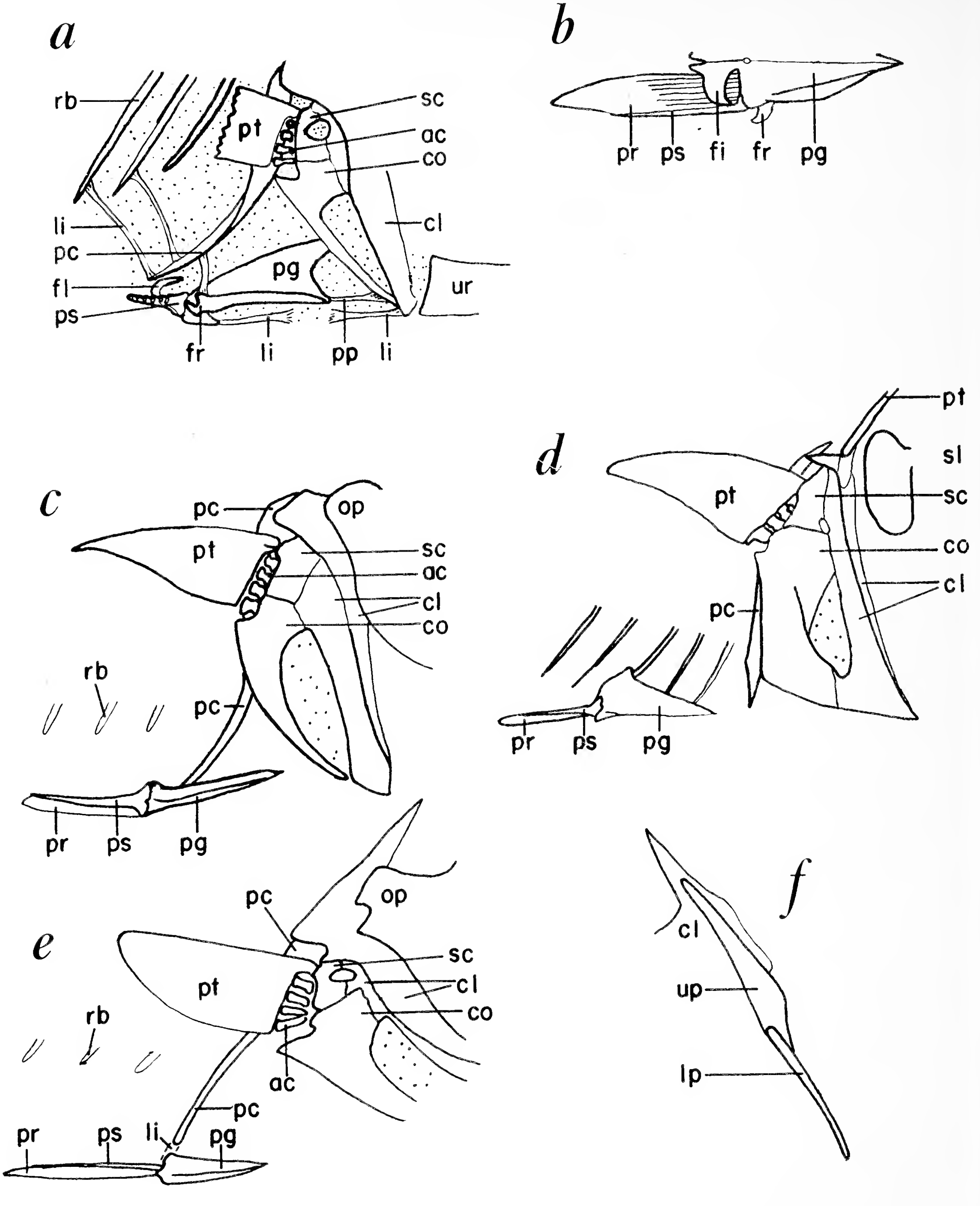

FIG. 1. Pelvic-pectoral relationships, semidiagrammatic. *a, b, Holocentrus lacteoguttatus; c, Mugil cephalus; d, Pranesus insularum; e, f, Sphyraena barracuda. a, c, d, e,* Right side in lateral view; *b,* right half of pelvic girdle from above; *f,* right postcleithral strut from inside. *ac,* Actinost; *cl,* cleithrum; *co,* coracoid; *fl,* flange that abuts against tip of postcleithrum; *fr,* flange for attachment of ligament from postcleithrum; *li,* ligament; *lp,* lower postcleithrum; *pc,* postcleithrum; *pg,* pelvic girdle; *pp,* pelvic-pectoral ligament; *pr,* pelvic rays; *ps,* pelvic spine; *pt,* post-temporal; *rb,* rib; *sc,* scapula; *sl,* supracleithrum; *up,* upper postcleithrum; *ur,* urohyal.

Boulenger (1904: 641, and fig. 391) also points out that in the Polynemidae the pelvic bones are suspended from the postclavicles, i.e., postcleithra. Among the four families under consideration postcleithral struts supporting the pelvic girdle on either side are found in *Polydactylus, Mugil* (Fig. 1*c*), and *Sphyraena* (Figs. 1*e*, *f*) but not in *Pranesus*. In *Pranesus* (Fig. 1*d*) the pelvic girdle may be supported to some extent by the tips of the first three pairs of ribs (i.e., the pleural ribs of vertebrae three, four, and five), but of the three only the third has any strong ligamentous attachment between its tip and the pelvic girdle.

No such postcleithral or rib abutment against the pelvic girdle was found in any of the perciform genera examined: *Epinephelus, Apogon, Priacanthus, Caranx, Mulloidichthys, Chaetodon, Acanthurus,* and *Eleotris*. In the deep-bodied genera *Priacanthus, Caranx, Chaetodon,* and *Acanthurus,* the postcleithra are long and strong but pass down behind the pectoral girdle. This last type of postcleithrum occurs in the zeiform genus *Antigonia,* which has the anterior portion of the pelvic girdle attached to the cleithral symphysis as in the percoids. Judging from an X-ray photograph of the lampridiform genus *Metavelifer,* its pelvic girdle has the same relationships as in the percoids and *Antigonia.*

A postcleithral abutment against the pelvic girdle is not unique, however, to the Polynemidae, Mugilidae, and Sphyraenidae. It occurs again (among the fishes examined) in the berycoid genera *Holocentrus* (Fig. 1*a*) and *Myripristis*. However, in the polynemids, mugilids, and sphyraenids the postcleithra are attached directly or indirectly to the outer rim of the pelvic girdle ahead of the fin articulation, whereas in *Holocentrus* and *Myripristis* the postcleithral abutment is against an expanded flange behind the pelvic ray articulation (Fig. 1*b*). Furthermore, the front of the pelvic girdle of *Holocentrus* is firmly wedged into the musculature between the lower ends of the pectoral girdle and attached to it by both muscles and a ligament (Fig. 1*a*), whereas the pelvic girdle of the percesocine fishes is not. In view of the above and of Regan's statement (1912: 839) that in the berycoid *Trachichthys* the pelvics are directly attached to the pectoral girdle, it would appear that the holocentrids could provide better examples than the percesocine fishes for Dollo's hypothesis of a secondary backward movement of the pelvics.

A rather casual search of the literature has shown that a postcleithral support for the pelvics also occurs in the syngnathiform genus *Centriscus* (Jungersen, 1908: 88, and pl. 2, fig. 2; see also his footnote 14 on p. 105). However, in the other syngnathiform genera studied by the same author (Jungersen, 1908, 1910) there is no attachment of any sort between the pelvic and pectoral girdles.

In view of the above discussion it seems somewhat unsatisfactory, or at least questionable, to postulate a secondarily abdominal position for the pelvic fins of the percesocine fishes. A different and, to the present writer, preferable explanation is that the support provided for the pelvic fins by the postcleithra represents a level of structural stabilization in the general trend toward forward movement of the pelvics in teleostean evolution. To accept such an explanation, as will be done here, does not imply (1) that the various groups with a postcleithrum-pelvis abutment has developed only once, (2) that the pelvic fins have never moved back in the course of teleostean evolution, or (3) that the development of the postcleithral pelvic support has provided an especially successful or stable stage of structural organization.

Only one working hypothesis with regard to the above thesis will be discussed here. So long as the pelvic fins have no pungent defensive spines, attachment to a pelvic girdle that lies free in the body wall would seem to be a satisfactory arrangement. When, however, the pelvics develop pungent spines, a more secure emplacement of the pelvic girdle would appear advantageous. There is some evidence to bear out this hypothesis. Among the fishes investigated, *Polydactylus* and *Mugil* (Fig. 1*c*) have stiff, sharp pelvic spines and firm postcleithral abutments against the girdles. In *Sphyraena* (Fig. 1*e*) and *Pranesus* (Fig. 1*d*) the outer pelvic rays, by contrast, are relatively slender and somewhat flexible. In *Sphyraena* the postcleithrum does not abut directly against the pelvic girdle but is merely attached to the girdle by ligamentous tissue; in *Pranesus* the girdle is held in place, as already noted, merely by the tips of abdominal ribs.

There appear to be only three ways in which fishes have attained a firm emplacement for pungent pelvic spines. One is the extension of the pelvic girdle over the body wall as a large dermal plate, as in *Gasterosteus*. The second is the abutment against a postcleithral strut. The third is direct attachment anteriorly to the cleithral symphysis. Presumably, once a fish with pungent pelvic spines has developed one of the above three types of pelvic support, it will retain it. For such fishes, any of the three types would seem to provide a level of structural stabilization in evolution. However, for those fishes without pungent pelvic spines none of the three types of girdle support would seem to be of any great value, and it is presumably in such fishes that changes in pelvic position have evolved.

POLYNEMIDAE, MUGILIDAE, SPHYRAENIDAE, AND ATHERINIDAE

The polynemids have usually been separated from the mugilids, sphyraenids, and atherinids on the basis of pectoral peculiarities (Regan, 1929; Berg, 1940). The last three families have long been placed together. Nevertheless they differ widely from one another. Starks (1899: 1), in a report on the osteology of several members of these families, remarked:

> In examining the crania of these species, attention is attracted at once to the fact that in all of them the epiotics are developed into long, thin processes which divide into more or less bristle-like filaments.
>
> There is little else in purely internal characters whereby to differentiate these families as a group from other Acanthopteri. In order to so differentiate them we must turn to the well-known external characters—a spinous dorsal in conjunction with the abdominal ventral fins, high pectoral fins, and unarmed opercles.

With regard to the characters listed, *Pranesus* has no epiotic processes, and *Sphyraena* has a moderately low pectoral and a more or less "armed" opercle (Fig. 1*e*). Inasmuch as no new distinguishing characters held in common by sphyraenids, mugilids, and atherinids seem to have been discovered since Starks wrote, the three families form a group for which no very clear-cut definition is available.

As to the interrelationships of the three families, Starks (1899: 1) stated:

> If, however, we eliminate the Sphyraenidae (which, on account of its fanglike teeth, set in deep sockets, its separate superior pharyngeals of third and fourth branchial arches, its lack of parapophyses on anterior vertebrae, and other characters, we may well be justified in doing) and place it in a separate superfamily coordinate with that in which we place the Mugilidae and Atherinidae, we shall then have a more compact group, notwithstanding the great difference in number of veterbrae in the two families of which it is composed.

Of the sphyraenid peculiarities mentioned, the teeth are certainly a specialization related to the predaceous habits of the barracudas. However, Jordan and Hubbs (1919: 6, footnote 3) have pointed out that some of the larger atherinids have strong teeth in shallow sockets, thus approaching the sphyraenids in this feature. In most other characters, however, *Sphyraena* "seems to be a much more generalized form than other members of the Percesoces" (Starks, 1902: 622, footnote 1).

With regard to the relationships of the Polynemidae, Regan (1912: 846, 847) included them with the other three families in an order Percesoces with the statement:

> Contrary to what has usually been supposed, the Polynemidae are more closely related to the Sphyraenidae than to the Mugilidae, as is shown in the subjoined synopsis of the families.
>
> I. A lateral line; pectoral fins placed low. Cranial crests well developed (Polynemidae) or vestigial (Sphyraenidae). Exoccipitals meeting above basioccipital; alisphenoids meeting. Supra-clavicle moderate. Parapophyses, when developed, downwardly directed. Twenty-four vertebrae.
>
> Pectoral fin normal; parapophyses on posterior praecaudals only.. 1. Sphyraenidae
>
> Pectoral fin of two parts, the lower of detached filamentous rays; pterygials represented by a plate attached to the edge of the scapula and coracoid; parapophyses from the third vertebra .... 2. Polynemidae
>
> II. Lateral line incomplete or absent; pectoral fins usually placed high. No cranial crests; exoccipitals separate; alisphenoids separate. Supraclavicle small. Parapophyses well developed, anteriorly nearly horizontal.

24 to 26 vertebrae.................3. Mugilidae
32 to 60 vertebrae..............4. Atherinidae

It seems unnecessary to discuss the above arrangement since in his later work Regan (1929) returned to the more usual system of recognizing the Polynemidae on the one hand and the Sphyraenidae, Mugilidae, and Atherinidae on the other as two separate suborders of the order Percomorphi (= Perciformes).

In the following paragraphs certain hitherto neglected structural systems will be described and others will be discussed. Suffice it to say in advance that in most of these the Atherinidae (at least as represented by *Pranesus*) appears to have diverged farther from the basal percesocine stock than the Polynemidae, Sphyraenidae, or Mugilidae.

BODY AND HEAD SHAPE: *Polydactylus,* like most fishes, has a rather high back and head. *Sphyraena, Mugil,* and *Pranesus* and most members of their families are, by contrast, flat backed and flat headed. Several morphological characters, in all of which *Polydactylus* is the more generalized, would seem to be associated with this difference.

Polydactylus also differs from the others in the decidedly inferior mouth. This has led to some osteological peculiarities in the snout region. However, these features will not be stressed, since other genera of polynemids have a far less inferior mouth than *Polydactylus.*

SKULL: The crania of sphyraenids, mugilids, and atherinids have been dealt with at some length by Starks (1899); and Gregory (1933) gives a rather unsatisfactory figure of the head skeleton of *Polydactylus.* The only aspect of the crania that will be discussed here is one presumably associated with differences in the body shape previously noted.

In *Polydactylus* the skull has the usual percoid-type supraoccipital and frontal-parietal crests. These provide extensive surfaces for the attachment of the body muscles, which run forward over the rear of the skull. In the flat-headed *Sphyraena, Mugil,* and *Pranesus* the supraoccipital does not rise above the surface of the skull and the frontal-parietal crests are at best represented by vestigial ridges (Regan, 1912: 846). The body musculature does not extend forward over the rear of the skull, and its total area of attachment is provided by the rear face of the skull and such bony areas as may extend back from it. Presumably it is the need for areas of muscular attachment which has led to the development of backwardly projecting bony, brush-like extensions from the head in large species of mugilids and atherinids, but most notably in *Sphyraena* (Starks, 1899: 1, pls. 1, 2).

JAW STRUCTURE AND TEETH: The jaw structure and teeth of the fishes under consideration vary considerably, presumably in association with differences in feeding habits. The large, socketed teeth of *Sphyraena* have already been noted.

Eaton (1935) drew attention to the similarity in jaw structure between *Fundulus* and the atherinids. Gosline (1961) subsequently pointed out that the jaws of *Fundulus* and atherinids have a very different structural organization, that of the atherinids, mugilids, and sphyraenids being derivable from a typically percoid type. Of the four fishes dissected, *Sphyraena* is the only one that retains a supramaxillary.

SUPERFICIAL BONES OF SNOUT AND CHEEK REGION: Probably in relation to the inferior position of the mouth, the whole anteroventral end of the snout of *Polydactylus sexfilis* appears to have been rolled back under the orbit. Thus the front of the lacrimal does not even reach the anterior rim of the orbit (Fig. 2*b*), whereas the nasal bone not only forms a cup over the front of the nasal capsule but has a flat flange extending downward from the lower rim of the cup. The anterior end of the supraorbital canal is carried on the outer surface of the cup to a point somewhat below the olfactory organs. (In *Polydactylus sexfilis* both the nasal bone and the anterior end of the lacrimal are deeply embedded in adipose tissue, which is in turn covered by scales.) The lacrimal, which bears the anterior end of the infraorbital canal in the fishes under consideration, extends back along the whole lower border of the orbit in *Polydactylus* (Fig. 2*b*), and rather broadly overlaps all but the posterior portion of the maxillary when the mouth is closed. The anterior end of the lacrimal fits over and articulates with the tip of the lateral ethmoid. The lacrimal is, however, a very thin bone without serrated edges. Behind it are five circumorbitals that carry the infraorbital canal to its junction with the supraorbital canal. The lowermost of the five has a rather regular, tri-

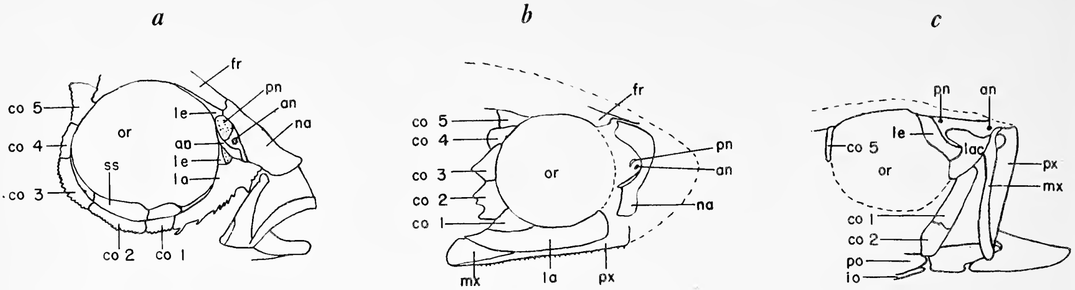

FIG. 2. Bones of the sides of the head in *a, Holocentrus lacteoguttatus, b, Polydactylus sexfilis,* and *c, Pranesus insularum,* all semidiagrammatic. *an,* Anterior nostril; *ao,* antorbital; *co 1–5,* circumorbital bones (not including the lacrimal or antorbital); *fr,* frontal; *io,* interopercle; *la,* lacrimal; *le,* lateral ethmoid; *mx,* maxillary; *na,* nasal; *or,* orbit; *pn,* posterior nostril; *po,* preopercle; *px,* premaxillary; *ss,* subocular shelf.

angular shape, but the upper three have irregular, flap-like posterior extensions. A subocular shelf (not shown in Fig. 2*b*) is represented in *Polydactylus* by a small strut from the second circumorbital extending in along the posteroventral border of the orbit.

The circumorbital bones of *Polydactylus* differ in a number of ways from those of the other three species examined. Among the latter, *Sphyraena* is the only genus with a complete circumorbital series—lacrimal plus five circumorbitals—and the only one in which the infraorbital sensory canal extends continuously from the lacrimal back to its junction with the supraorbital canal. In *Mugil* the lacrimal is completely separated from the small ossicles around the rear of the orbit that make up the rest of the series. In *Pranesus* (Fig. 2*c*) the lacrimal and first two circumorbital bones are widely separated from the other small circumorbitals along the rear border of the orbit. In none of these three percesocine fishes is there any sign of a subocular shelf.

Probably in relation to the inferior mouth of *Polydactylus,* it is the anterior (rather than the posterior) end of the lacrimal that wedges against the lateral ethmoid. In the other three genera investigated, the lacrimal is held in position in different ways. In *Mugil* and *Sphyraena* the rear of the lacrimal is wedged under the lateral ethmoid and the front under the nasal. In *Sphyraena,* the lacrimal is a long triangular bone; in *Mugil cephalus* it is short and stout, with a serrated posteroventral border. The anterior circumorbital bone arrangements of *Pranesus* are most unusual. The lacrimal forms a plate over the lateral ethmoid; extending obliquely down and back from the lacrimal are the two anterior circumorbitals. The posterior end of the second overlaps and has a firm ligamentous attachment to the anteriormost point on the preopercle. Here, as in the scorpaeniform and gasterosteiform fishes, there is a suborbital stay, but in *Pranesus* this runs down to the *front* of the preopercle. The peculiar axis of this suborbital stay is doubtless associated with the obliquity of the mouth in *Pranesus.* (To what extent it occurs in other atherinids I have not the material to determine.)

The nasal bones of *Sphyraena, Mugil,* and *Pranesus* do not form a cup around the front of the nasal capsule as in *Polydactylus,* but extend for the most part straight forward along the superolateral border of the snout region.

NASAL ORGAN AND NOSTRILS: The nasal organ of *Polydactylus sexfilis* is seated deep in the adipose tissue of the snout directly ahead of the middle of the eye. The two nostrils are close together, the anterior a little lower than the posterior (Fig. 2*b*). The front nostril is a roundish hole with a flap on its rear border that partially covers the posterior nostril, which is somewhat elongated vertically. Both nostrils extend in through the adipose tissue to the nasal sac. The nasal rosette has a central rachis that runs downward and forward. In a 110 mm specimen there are about a dozen lamellae extending out from either side of the rachis.

In the other genera the two nostrils of each side are high on the head and well separated from one another (Fig. 2*c*). The three available genera differ widely from one another, however, in the structure of the nasal rosette. In *Mugil cephalus* it has an elongate rachis with numerous well-developed lamellae extending out to either side; in *Sphyraena* the nasal rosette is reduced, with a few rudimentary lamellae on either side; and in *Pranesus* the nasal organ seems to be represented by four longitudinal flaps that lie beside one another.

OPERCULAR BONES: The opercular bones of *Polydactylus* are sufficiently shown in Gregory's figure (1933: 268, fig. 144). Though the preopercle of *Polydactylus,* unlike that of the percesocine fishes (sensu stricto), is serrate, that of the related *Pentanemus* is said to be entire. There seem to be no other major differences between the opercular bones of *Polydactylus* and those of the percesocine fishes.

PHARYNGEAL TEETH: According to Starks (1901: 2, 3), in the Atherinidae and Mugilidae the third and fourth upper pharyngeals are anchylosed; in the Sphyraenidae they are not. *Polydactylus sexfilis* is like *Sphyraena* in this respect.

PECTORAL GIRDLE: According to Starks (1899: 2, 3) the lower limb of the post-temporal is attached to the opisthotic [= intercalar] by a dentate suture in the Mugilidae, but not in the Sphyraenidae and Atherinidae. Stated in slightly different terms, the post-temporal is rigidly attached to the skull in the Mugilidae (by both the upper and lower limb), but is movably attached in the Atherinidae, Sphyraenidae, and also in the Polynemidae. The fusion of the post-temporal to the skull in *Mugil* is perhaps related to the development of the peculiar pharyngial apparatus that occupies the space below and between the post-temporals in that genus.

The divided pectoral fin and associated girdle features (Starks, 1926: 194, fig. 18) of polynemids are unique, and form the usual basis for separating the Polynemidae from the other three families. Among the latter, Starks (1926: 193) notes that in the atherinid *Atherinopsis* the uppermost actinost may become completely fused to the scapula. (The reduction in the number of actinosts ascribed to the phallostethids by Bailey (1936) may have occurred in the same fashion.)

FIN STRUCTURE AND FIN SUPPORTS: Hubbs (1944) has provided a detailed comparison between the fin structure of the phallostethids, atherinids, mugilids, sphyraenids, and polynemids, pointing out the rather striking resemblances between the fins of the five groups. Hollister (1937) has described the caudal skeleton of certain sphyraenids, mugilids, and atherinids. Gosline (in press) has suggested that the caudal skeletons of these families plus the polynemids could be interpreted as increasing structural specialization away from the basic percoid type in the series *Polydactylus-Sphyraena-Mugil-Pranesus.* Bridge (1895) has described the dorsal and anal fins and fin supports in *Sphyraena* and *Mugil.* He points out that the endoskeletal supports of certain of the soft dorsal and anal rays of *Sphyraena* are trisegmental, a characteristic feature of lower teleostean fishes found for the last time in a few basal percoids. The present account deals only with the relationship between the endoskeletal supports of the spinous dorsal and the vertebral column.

DORSAL ENDOSKELETAL STRUCTURES: In all four fishes investigated there are two sorts of dorsal endoskeletal structures: those that support dorsal fin rays and those that do not. Structurally the two types seem to grade into one another. Nevertheless, for purposes of description the endoskeletal elements supporting fin rays will be called pterygiophores and those that do not supraneurals, following Eaton's (1945) terminology.

In *Polydactylus* (Fig. 3*a*) there are three supraneurals above the first three vertebrae. Following this there are seven pterygiophores (bearing eight spines), which hold a one-to-one relationship with the vertebrae below them. Behind the last of these there is a gap one vertebra in width, followed by the first pterygiophore of the second dorsal. (The anteriormost ray in this fin is a spine.) This arrangement of endoskeletal supports closely parallels that of the lower percoid fishes (Katayama, 1959: 148–149, figs. 24–28). The one peculiarity seems to be the absence of a supraneural between the two dorsal fins; in this feature *Polydactylus* parallels *Mulloidichthys* (Mullidae) but not *Apogon* among percoids with separate dorsals. In *Mugil* (Fig. 3*c*), *Sphyraena* (Fig. 3*d*) and *Pranesus* (Fig. 3*b*) there are supraneurals between the two dorsal fins, but those of *Sphyraena* are rudimentary.

In *Sphyraena, Mugil,* and *Pranesus* there has been a condensation of the spinous dorsal base resulting in two or more pterygiophores over each vertebra. In *Mugil* (Fig. 3*c*) the pterygiophores still interdigitate between the tips of the neural spines, but in *Pranesus* (Fig. 3*b*) the pterygiophores form a discontinuous plate of bone that lies entirely above the neural spines. *Sphyraena* (Fig. 3*d*) is intermediate between *Mugil* and *Pranesus* in this respect.

With regard to position, the first pterygiophore of *Polydactylus* lies over the 3rd neural spine, that of *Sphyraena* over the 4th, of *Mugil* over the 7th and 8th, and of *Pranesus* over the 15–18th.

Mugil and *Sphyraena* retain the three supraneurals ahead of the spinous dorsal, but in *Pranesus* they are gone.

VERTEBRAL COLUMN AND RIBS: In the specimens of *Polydactylus, Mugil,* and *Sphyraena* dissected the total number of vertebrae is 24. Jordan and Hubbs (1919: 6) give a vertebral range of 24–26 for the Mugilidae. In the Atherinidae (Jordan and Hubbs, 1919: 7) the vertebral count is always more than 30.

In *Polydactylus* and *Sphyraena* all of the neural spines taper dorsally to a point, as is usual in fishes. In *Mugil* and *Pranesus,* however, some of the anterior neural spines are flattened and blade-like (Fig. 3*c*), as was noted for the Mugilidae and Atherinidae by Starks (1899: 2).

The articulation between the skull and the first vertebra is quite different in *Polydactylus* and *Sphyraena* on the one hand and in *Mugil* and *Pranesus* on the other. In the skull itself this difference is reflected in the separation of the exoccipitals noted by Regan (1912: 846). So far as the first vertebra is concerned, its neural arch and centrum are separately movable in *Polydactylus* (Fig. 3*a*) and *Sphyraena* (Fig. 3*d*), fused in *Mugil* and *Pranesus.*

Starks also used the absence of parapophyses on the anterior vertebrae of *Sphyraena* as a basis of differentiating this genus from the atherinids and mugilids. However, *Sphyraena* does have parapophyses on vertebrae 5 through 9 (Fig. 3*d*), though these are not nearly so well developed as in the other fishes examined.

One final vertebral feature may be noted because of its bearing on phallostethid structures. In *Polydactylus, Sphyraena, Mugil,* and *Pranesus* the first pleural rib is that on the third vertebra, with which it articulates firmly. This is the typical condition for the basal percoid fishes (Boulenger, 1895: 2–5, 114–115).

PHALLOSTETHOID FISHES

Since their discovery in 1913 the phallostethoid fishes have received a good deal of attention. Much of this has been directed toward elucidating the structure of the unique clasping organs of the males. With regard to systematic position Regan (1913, 1916) originally included the phallostethoids among the cyprinodont fishes. Myers (1928, 1935) subsequently placed them among the percesocine fishes nearest the Atherinidae. Finally, Berg (1940: 465) recognized the phallostethoids as a separate order.

Judging from the literature, the phallostethoids cannot possibly be placed among the cyprinodont fishes. For one thing some phallostethoids have a small, separate spinous dorsal. For another they have the typical berycoid-percesocine-percoid type of upper jaw protrusion rather than the peculiar type that seems to have been developed within the cyprinodonts (Gosline, 1961). The conclusion seems inescapable that the phallostethoids have been derived from some percesocine or percoid stock.

So far as pelvic structure is concerned, the pelvic fins are either absent or rudimentary. I can find no mention of a pelvic girdle in female phallostethoids, but in the adult males the girdle is said to form part of the clasping organ (priapium). This is attached anteriorly to the tip of one or both forwardly-extended cleithra and is supported posteriorly by the two anterior ribs. The structure of the complicated priapium has been variously interpreted. Bailey (1936) tried to show a possible derivation from a pelvic girdle supported by a postcleithrum, as in *Polydactylus.* This interpretation seems incorrect because the phallostethoid structure which Bailey interpreted as a homologue of the postcleithrum is almost assuredly the modified rib of the third vertebra[3] and not part of the pectoral girdle.

Now, the adult male priapium consists of a number of specialized ossifications. Nevertheless, that part that is generally agreed to represent

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[3] The third vertebra of females bears the usual, normally developed rib (Aurich, 1937: 265).

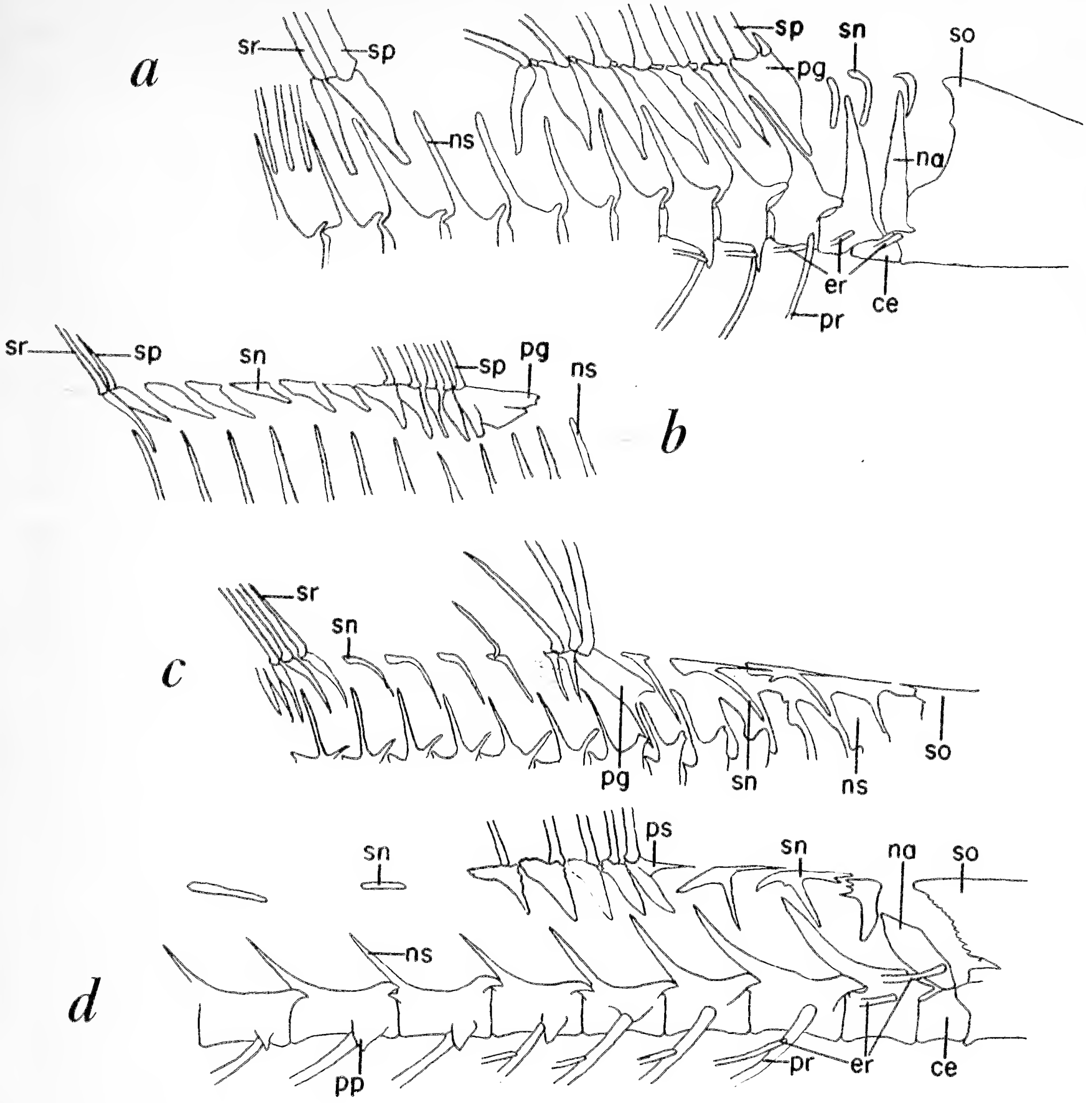

FIG. 3. Anterior dorsal fin supports and part of vertebral column of *a, Polydactylus sexfilis, b, Pranesus insularum, c, Mugil cephalus,* and *d, Sphyraena barracuda. ce,* Centrum; *er,* epipleural rib; *na,* neural arch; *ns,* neural spine; *pg,* pterygiophore; *pp,* parapophysis; *pr,* pleural rib; *sn,* supraneural; *so,* supraoccipital; *sp,* dorsal spine; *sr,* dorsal soft ray.

the pelvic girdle is supported by the modified ribs of the 3rd and 4th vertebra and does not extend forward to the cleithra.[4] The pelvic supports of the phallostethoid priapium would thus seem to show a considerably greater similarity to the rib supports of the pelvic girdle of atherinids than to either the polynemid or percoid condition.

Other similarities between the phallostethoids and atherinids are the small, anteriorly placed spinous dorsal (when present), which has already been mentioned, the upwardly directed mouth, and the fact that both groups lay eggs with adhesive filaments (Villadolid and Manacop, 1934). There thus seems every reason to accept Myers' (1928) original placement of the phallostethoids next to the Atherinidae.

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[4] It is the specialized pulvinular structure of uncertain origin that articulates with the cleithra.

DISCUSSION AND CONCLUSIONS

The present author would agree with Myers (1935) and Hubbs (1944) that the Polynemidae, Sphyraenidae, Mugilidae, Atherinidae, and Phallostethoidei are more closely related to one another than to other fish groups. Nevertheless these five groups have diverged widely, and distinctive characters held in common by all of them are lacking. Apparently the best that can be done by way of defining the group as a whole is as follows:

Fishes that are basically percoid except in pelvic structure; pelvics never thoracic, either subabdominal with a spine and five soft rays, vestigial, or lacking; pelvic girdle never attached to the cleithral symphysis directly or by ligament. Spinous dorsal fin, if present, well separated from the soft dorsal.

Reasons have been given for believing that the pelvic morphology in these fishes is one that has never reached the percoid level of evolution. Whether or not this is so, a series of other structural features, e.g., the supramaxillary and the trisegmental dorsal ray supports in the Sphyraenidae indicate that they must have been derived from a very low level of percoid, if not of prepercoid, evolution. To state this conversely, the polynemids and sphyraenids cannot possibly have arisen from any advanced percoid groups. This being so, the whole series should stand before or at the bottom of the Perciformes in any teleostean classification.

Because of the great divergence among the groups under consideration, and because of the already tremendous size of the order Perciformes, it is perhaps most convenient to consider these fishes as a separate order Mugiliformes = Percesoces sensu Myers, 1935. The alternative is to consider the Mugiliformes as a suborder of the Perciformes. If this were done, it would seem necessary to include other groups such as the Scorpaeniformes as well, thus enlarging the Perciformes still further.

If the Mugiliformes is considered as an order, there is no particular objection to dividing it into three suborders in the way Myers proposed in 1935, namely Polynemoidei, Mugiloidei, and Phallostethoidei. Other ways of expressing the interrelationships might be equally good, but there seems no reason for merely substituting one equally good classification for another.

The following diagnosis attempts to express increasing levels of divergence from what is presumed to be the basal stock (peculiarities developed within groups are omitted here).

1a. Pelvic girdle supported by a postcleithral strut; vertebrae 24–26; eggs not adhesive.
    2a. Supraoccipital and frontal-parietal crests present. First dorsal spine over the 3rd vertebra; third and fourth upper pharyngeals separate; infraorbital canal complete; pectorals low or median .... Polynemidae
    2b. No crests on top of skull.
        3a. Supramaxillary present; first dorsal spine over the 4th vertebra; third and fourth upper pharyngeals separate; infraorbital canal complete; pectorals on middle of sides .... Sphyraenidae
        3b. No supramaxillary; first dorsal spine over the 7th vertebra; third and fourth upper pharyngeals fused; infraorbital canal interrupted; pectorals high on sides...... .... Mugilidae
1b. Pelvic girdle not supported by postcleithral strut; vertebrae more than 26; eggs usually adhesive. Spinous dorsal, if present, placed well back on body; pectoral fins high on sides.
    4a. Pelvic fins present, with a spine and five soft rays; spinous dorsal present. Third and fourth upper pharyngeals fused; infraorbital canal interrupted .... Atherinidae
    4b. Pelvic fins absent or rudimentary; spinous dorsal absent or reduced........ .... Phallostethoidei

In whatever way the members of these groups are classified, certain aspects of interrelationship deserve reiteration. First, the Polynemidae and Sphyraenidae retain more generalized features than the others. Conversely, the Atherinidae, at least as represented by *Pranesus,* appears to be more generally divergent from the basal stock than the Polynemidae, Sphyraenidae, and Mugilidae. Finally, the phallostethoid families seem to have been derived from an atherinid-like ancestor, as Myers (1928) originally suggested.

REFERENCES

AURICH, H. 1937. Die Phallostethiden. Internationale Rev. gesamten Hydrobiol. Hydrogr. 34: 263–286, 14 figs.

BAILEY, RALPH J. 1936. The osteology and relationships of the phallostethid fishes. J. Morph. 59: 453–483, pls. 1–4, 1 text fig.

BERG, L. S. 1940. Classification of fishes, both recent and fossil. Trav. Inst. Zool. Acad. Sci. URSS 5: 87–517, 190 figs.

BOULENGER, G. A. 1895. Catalogue of the Fishes of the British Museum. 2d ed. Volume 1. London. xix+391 pp., 15 pls., 27 text figs.

——— 1904. Teleostei. In: Cambridge Nat. Hist. 7: 541–727, figs. 325–440.

BRIDGE, T. W. 1895. The mesial fins of ganoids and teleosts. J. Linnean Soc. London, Zool. 25: 530–602, pls. 21–23.

DOLLO, L. 1909. Les téléostéens à ventrales abdominales secondaires. Verh. Zool.-Bot. Gesell. Wien 59: 135–140.

EATON, T. H. 1935. Evolution of the upper jaw mechanism in teleost fishes. J. Morph. 58: 157–162, 2 pls.

——— 1945. Skeletal supports of the median fins of fishes. J. Morph. 76: 193–212, 5 figs.

GOSLINE, W. A. 1961. Some osteological features of modern lower teleostean fishes. Smithsonian Misc. Coll. 142(3): 1–42, 8 figs.

——— In press. The perciform caudal skeleton. Copeia. (Now: 265–270, 3 figs.)

GREGORY, W. K. 1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Amer. Philos. Soc. (n. s.) 23: 75–481, 302 figs.

HOLLISTER, G. 1937. Caudal skeleton of Bermuda shallow water fishes, II. Order Percomorphi, Suborder Percesoces: Atherinidae, Mugilidae, Sphyraenidae. Zoologica 22: 265–279, 14 figs.

HUBBS, C. L. 1944. Fin structure and relationships of the phallostethid fishes. Copeia 1944: 69–79.

JORDAN, D. S., and C. L. HUBBS. 1919. Studies in ichthyology. A monographic review of the family of Atherinidae or silversides. Leland Stanford Jr. Univ. Publ. (Univ. Ser.), pp. 1–87, pls. 1–12.

JUNGERSEN, H. F. E. 1908. Ichthyotomical contributions, I. The structure of the genera *Amphisile* and *Centriscus*. Mém. Acad. Roy. Sci. Let. Danemark (ser. 7, sect. sci.) 6: 41–109, pls. 1, and 2, 33 text figs.

——— 1910. Ichthyotomical contributions, II. The structure of the *Aulostomidae, Syngnathidae* and *Solenostomidae*. Mém. Acad. Roy. Sci. Let. Danemark (ser. 7, sect. sci.) 8: 269–364, pls. 1–7.

KATAYAMA, M. 1959. Studies on the serranid fishes of Japan. (1). Bull. Faculty Educ., Yamaguchi Univ., 8: 103–180, 39 figs.

MYERS, G. S. 1928. The systematic position of the phallostethid fishes, with diagnoses of a new genus from Siam. Amer. Mus. Novitates 295: 1–12, 2 figs.

——— 1935. A new phallostethid fish from Palawan. Proc. Biol. Soc. Washington 48: 5, 6.

REGAN, C. T. 1912. Notes on the classification of the teleostean fishes. Proc. Seventh Internat. Congr. Zool., Boston (1907): 838–853.

——— 1916. The morphology of the cyprinodont fishes of the subfamily Phallostethinae, with descriptions of a new genus and two new species. Proc. Zool. Soc. London 1916: 1–26, pls. 1–4, 15 text figs.

——— 1929. Fishes. In: Encyclopaedia Britannica. 14th ed. 9: 305–328.

SCHULTZ, L. P. 1948. A revision of six families of atherine fishes, with descriptions of new genera and species. Proc. U. S. Nat. Mus. 98: 1–48, pls. 1–2, 9 text figs.

STARKS, E. C. 1899. The osteological characters of the fishes of the suborder Percesoces. Proc. U. S. Nat. Mus. 22: 1–10, 3 pls.

——— 1902. The shoulder girdle and characteristic osteology of the hemibranchiate fishes. Proc. U. S. Nat. Mus. 25: 619–634, 6 figs.

——— 1930. The primary shoulder girdle of bony fishes. Stanford Univ. Publ., Univ. Ser., Biol. Sci. 6: 149–239, 38 figs.

VILLADOLID, D. V., and P. R. MANACOP. 1934. The Philippine Phallostethidae, a description of a new species, and a report on the biology of Gulaphallus mirabilis Herre. Philippine J. Sci. 55: 193–220, pls. 1–5, 3 text figs.

Revision of the Genus *Pandanus* Stickman

HAROLD ST. JOHN

Part 11, New Species from Malaya

R. E. HOLTTUM[1] and HAROLD ST. JOHN[2]

DURING 1948–49 Mr. Holttum, of the Singapore Botanic Garden, studied the species of *Pandanus* of Malaya and Singapore. At this time he distinguished the following species and left them in manuscript. During 1960–61 Mr. St. John revised the Malayan species of *Pandanus,* illustrated them, and prepared expanded descriptions to include more of the diagnostic characters. Mr. Holttum has consented to the publication here of these new species under joint authorship.

SECTION *Acrostigma*

Pandanus alticola Holttum & St. John, sp. nov. (sect. *Acrostigma*)

Figs. 98–99

DIAGNOSIS HOLOTYPI: Planta fruticosa epiphytica, caulibus 15–20 cm longis ramosis in apice 13 mm diametro in basi cum restis foliorum vetustiorum marcescentium obtectis, foliis 1.3 m longis 13–15 mm latis coriaceis supra viridibus infra pallidioribus 1-sulcatis 2-plicatis in sectione mediali cum 13–14 nervis secundariis in quoque latere proxime basem infra nervis tertialis reticulis oblongis formantibus, supra ad apicem plicis cum serris paucis remotis in apice subulato deltoideo 5 cm longo 1.5–2 mm lato sensim diminuentibus basi dilatata inermi amplexicauli sed ex 9–10 cm marginibus cum dentibus 1–1.5 mm longis 5–15 mm distantibus deltoideis salientibus luteis, midnervo ex basi ad mediam et ultra inermi, in sectione mediali marginibus cum serris crenatis 0.4–0.6 mm longis 3–6 mm distantibus, proxima apicem marginibus et midnervo infra cum serris 0.3–0.5 mm longis 2–6 mm distantibus et supra in plicis cum serris simulantibus sed paucis et remotioribus, inflorescentia foeminea terminali, pedunculo 6 cm longo folioso cum syncarpio unico 4.3 cm longo 3 cm diametro ellipsoideo cum circa 832 drupis eis 7–8 mm longis 2–2.5 mm latis et crassis 6-angulosis parte ½ supera libera corpore 4.5 mm longo ellipsoideo, pileo 4–5 mm longo anguste elliptico-pyramidali laevi 6-anguloso, apice obliquo et proximale inclinato in stylo abrupte diminuento, stylo 1 mm longo cornoso proximale curvato, stigmate 1 mm longo sublineari brunneo fere ad apicem extenso, endocarpio in parte 2/5 infera lateribus 0.1 mm crassis stramineis, semine 3 mm longo ellipsoideo, mesocarpio apicali cavernoso cum membranis paucis, mesocarpio basali in lateribus fibroso intra carnoso.

DIAGNOSIS OF HOLOTYPE: Plant bushy, epiphytic; stems 15–20 cm long, branched, at tip 13 mm in diameter, clothed with marcescent, shredded, old leaf bases; leaves 1.3 m long, 13–15 mm wide, coriaceous, green above, paler green below, 1-ribbed, 2-pleated, at midsection on each side with 13–14 parallel secondary nerves, and near the base on the lower side the tertiary cross veins form oblong meshes, above the apical pleats with a few remote serrae, the tip gradually narrowed into a 5 cm subulate, deltoid apex 1.5–2 mm wide, just above the base dilated and widening to the amplexicaul, unarmed base, beginning 9–10 cm up the margins with deltoid, salient teeth 1–1.5 mm long, 5–15 mm apart, yellowish; the midrib below unarmed to well beyond the middle; at midsection the margins with crenate serrations 0.4–0.6 mm long, 3–6 mm apart; on the subulate apex the margins and midrib beneath with serrae 0.3–0.5 mm long, 2–6 mm apart, and the pleats on the upper surface with similar serrations but these fewer and more distant; pistillate inflorescence terminal, peduncle 6 cm long, leafy bracted, bearing a single syncarp, this 4.3 cm long, 3 cm in

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[1] 80 Mortlake Road, Kew Gardens, Richmond, Surrey, England.

[2] B. P. Bishop Museum, Honolulu 17, Hawaii, USA. Manuscript received April 18, 1961.

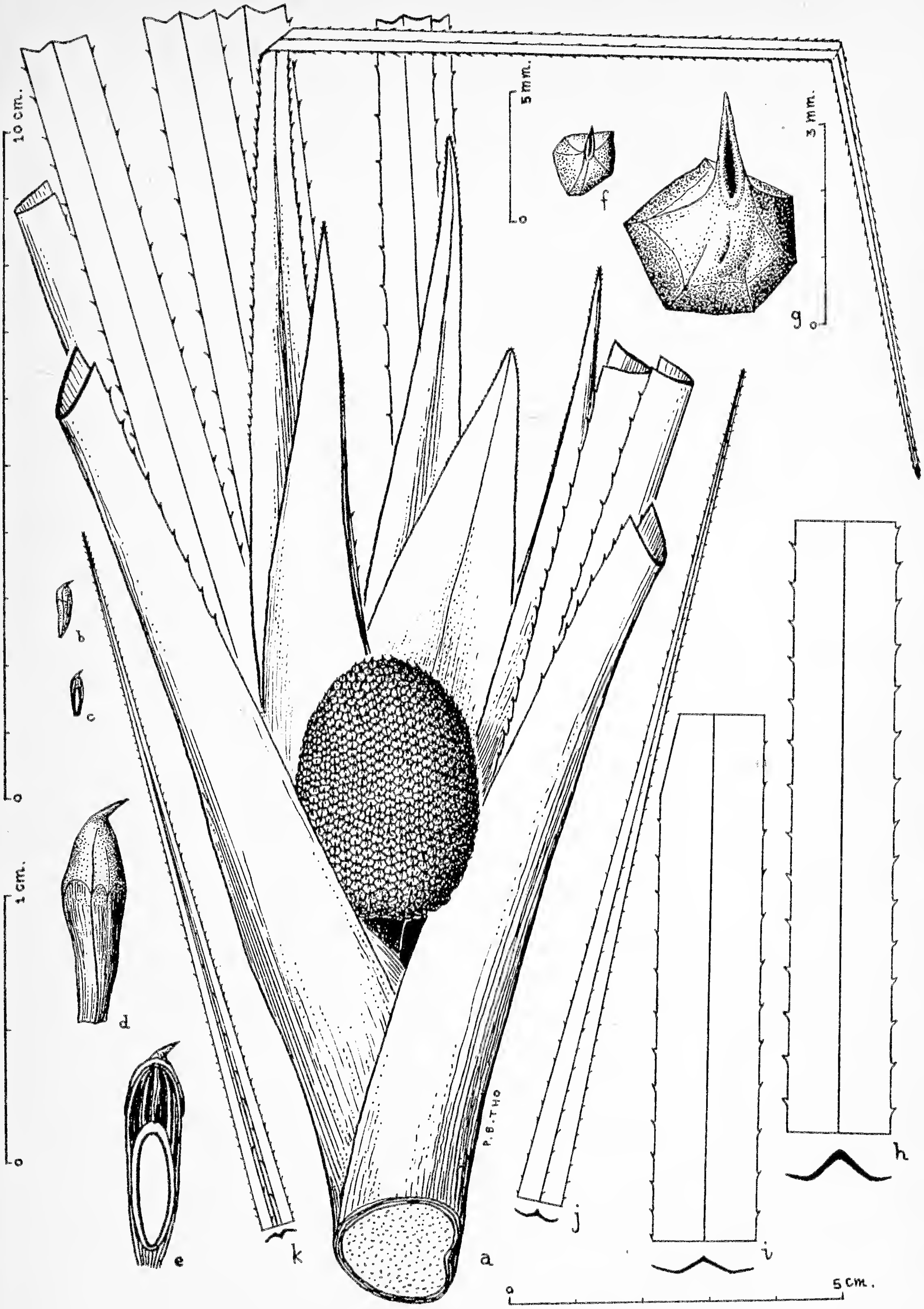

FIG. 98. *Pandanus alticola,* holotype. *a,* Leafy branch with syncarp, × 1; *b,* drupe, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d,* drupe, lateral view, × 4; *e,* drupe, longitudinal median section, × 4; *f,* drupe, apical view, × 4; *g,* drupe with stigma, apical view, × 10; *h,* leaf base, lower side, × 1; *i,* leaf middle, lower side, × 1; *j,* leaf apex, lower side, × 1.

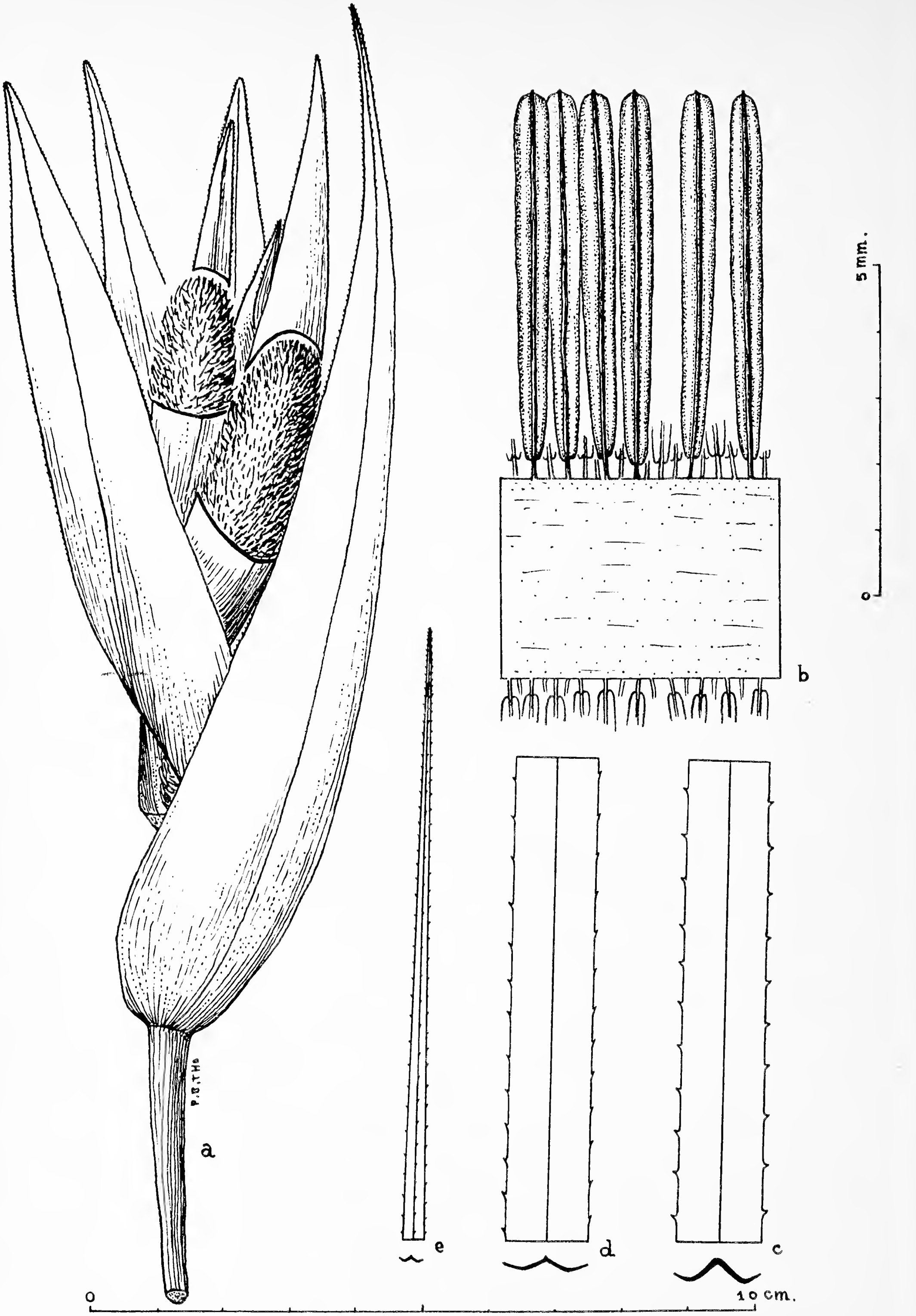

FIG. 99. *Pandanus alticola*, paratype, staminate, from S[ungei] Sedili, 28.7.37, Corner. *a*, Staminate inflorescence, × 1; *b*, stamens, × 10; *c*, leaf base, lower side, × 1; *d*, leaf middle, lower side, × 1; *e*, leaf apex, lower side, × 1.

diameter, ellipsoid, bearing about 832 drupes, these 7–8 mm long, 2–2.5 mm wide and thick, 6-angled, upper ½ free, the body 4.5 mm long, ellipsoid, pileus 4–5 mm long, narrowly elliptic pyramidal, smooth, 6-angled, the tip oblique and proximally inclined, abruptly narrowed to the style, this 1 mm long, horn-like, proximally curved; stigma 1 mm long, almost linear, brown, extending almost to the tip; endocarp in lower 2/5, the walls 0.1 mm thick, stramineous; seed 3 mm long, ellipsoid; apical mesocarp a cavern with a few membranes; basal mesocarp sparse, fibrous up the sides, fleshy within.

DESCRIPTION OF STAMINATE PLANT (from *Corner,* S. Sedili, 28.7.37): Leaves 1.15 m long, 9–12 mm wide, the pleats above unarmed; staminate inflorescence 13–16 cm long, the bracts creamy white, the median one 8–8.5 cm long, 3 cm wide, lanceolate, the margin at the midsection denticulate, beyond it serrulate; the 4–5 spikes 2.5–4 cm long, 8–10 mm in diameter, yellow, heavily scented; stamens yellow, numerous, crowded on the rhachis; filaments 2–2.5 mm long; anthers 5.5 mm long, 0.5 mm wide, linear-oblong, obtuse, terminating in a 0.2 mm umbonate projection of the connective.

HOLOTYPUS: Malaya, Johore, S[ungei] Kayu, Mawai-Jemaluang Road, Feb. 1935, *E. J. H. Corner* (SING).

SPECIMENS EXAMINED: Malaya, Johore, Sungei Sedili, then cult. in Singapore Botanic Garden, staminate, flowered 28.7.37, and 1.10.37, *E. J. H. Corner* (SING); from Johore, Ulu Tiram in 1932, then cult. in Singapore Botanic Garden, flowered 31 May 1936, *E. J. H. Corner 31,443* (SING); Trengganu, Sungei Tong Forest Reserve, off 23rd mile, Kuala Trengganu-Besut road, epiphytic, *J. Sinclair & Kiah bin Salleh 40,482* (SING).

DISCUSSION: *P. alticola* is a member of the section *Acrostigma.* There also is its closest relative, the Malayan *P. collinus* Ridl., which species is autophytic, and has the leaves 25–45 cm long, 8–11 mm wide, with 10–11 secondary veins on a side, the subulate tip 1.5–2 cm long, 0.6–0.8 mm wide, the margins beginning at 2 cm from the base with prickles 0.7–1 mm long, 3–7 mm apart, subulate; syncarp subglobose, 3 cm long, 2.5 cm in diameter; drupes 5–7 mm wide, the body obovoid; and the style 4–5 mm long. *P. alticola* is an epiphyte with leaves 1.1–1.3 m long, 9–15 mm wide, with 13–14 secondary veins on a side, the subulate tip 5 cm long, 1.5–2 mm wide, the margins beginning 9–10 cm from the base with deltoid teeth 1–1.5 mm long, 5–15 mm apart; syncarp ellipsoid, 4.3 cm long, 3 cm in diameter; drupes 2–2.5 mm wide, the body narrowly ellipsoid; and the style 1 mm long.

The new epithet is coined from the Latin, *altum,* height; *cola,* dweller in, and given in reference to its epiphytic habitat. This species has long been known in the sterile condition. Only recently have flowers and fruit been discovered.

Pandanus undulifolius Holttum & St. John, sp. nov. (sect. *Acrostigma*)

Fig. 100

DIAGNOSIS HOLOTYPI: Frutex 4 m alta pauce ramosa, apice caulinis 13 mm diametro brunneo laevi, internodis 3–5 mm longis, foliis multis 45–75 cm longis 7.8–9.1 cm latis subcoriaceis supra pallide viridibus infra minime pallidioribus sed non glaucis 1-sulcatis et paene 2-plicatis marginibus partim undulatis, apice pendenti 5 cm longo 1.5–2.5 mm lato subulato deltoideo, basi amplexicauli alba, in sectione mediali cum 36–39 nervis secundariis 1–1.5 mm distantibus conspicuis in quoque latere, nervis tertialis supra indistinctis sed infra distinctis et reticulis oblongis vel rhombicis brevibus formantibus, basi inermi sed ex 5 cm marginibus cum aculeis 0.5–0.8 mm longis 2.5–6 mm distantibus subulatis adscendentibus apicibus brunneis, midnervo infra ex 15–22 cm cum papillis deinde aculeis 0.2 mm longis 4–14 mm distantibus breve subulatis adscendentibus, in sectione mediali marginibus cum serris 0.7–1 mm longis 1–3 mm distantibus apicibus subulatis, midnervo infra plerumque inermi, in sectione apicali rotundato marginibus cum aculeis simulantibus sed approximatioribus, midnervo infra cum aculeis 1–1.3 mm longis tenuiter subulatis salientibus vel subadscendentibus, apice caudato cum marginibus et midnervo infra cum aculeis 0.5–0.7 mm longis 0.2–1 mm distantibus subulatis adscendentibus congregatis solitariis vel compositis, pedunculo foemineo 14 cm longo 8 mm diametro erecto trigono bracteoso, in flore floribus sub bracteis foliosis occultatis, syncarpio solitario 6.5 cm longo 4.5 cm diametro erecto

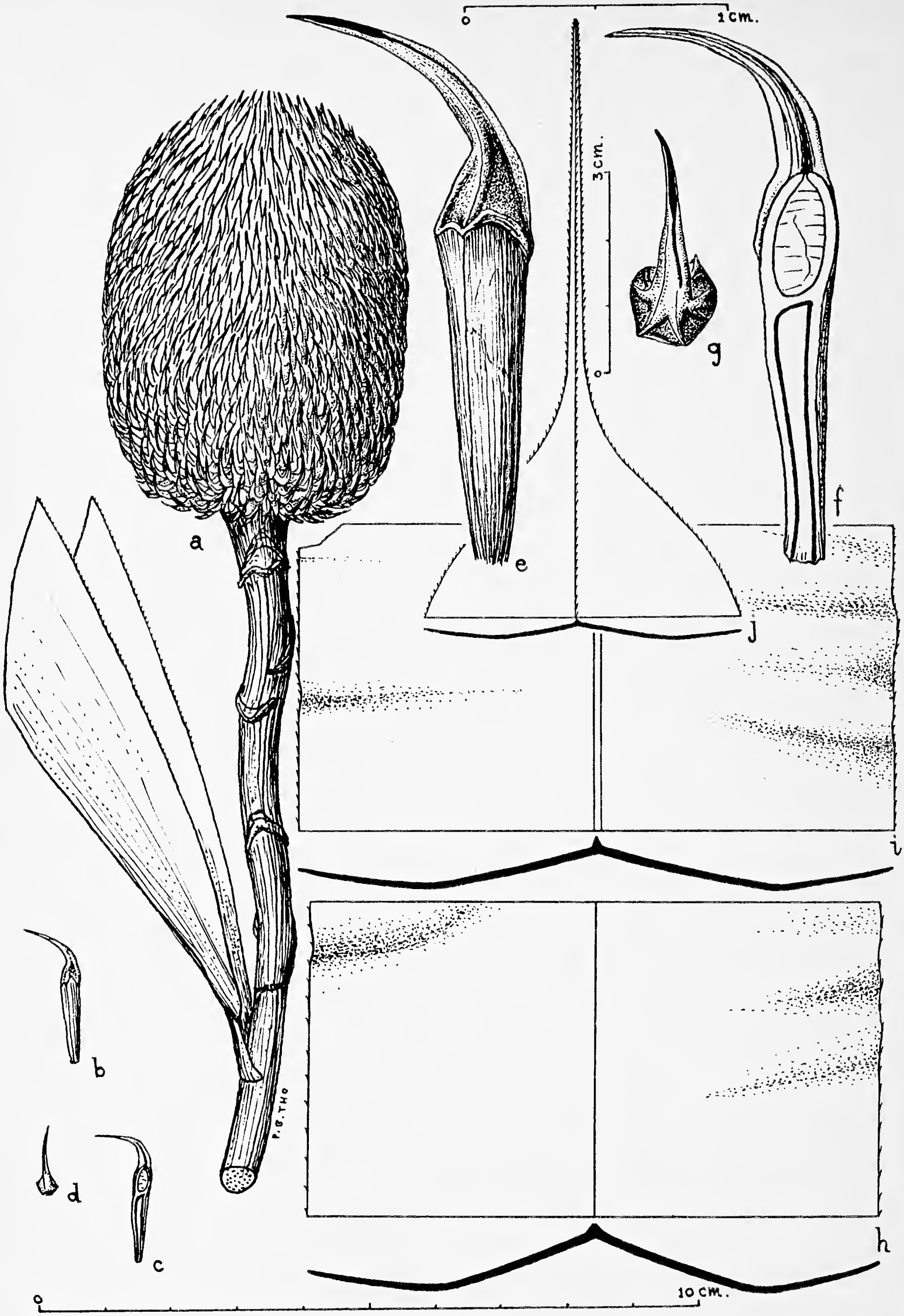

FIG. 100. *Pandanus undulifolius,* holotype. *a,* Syncarp and peduncle, × 1; *b,* drupe, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d,* drupe, apical view, × 1; *e,* drupe, lateral view, × 4; *f,* drupe, longitudinal median section, × 4; *g,* drupe with stigma, apical view, × 4; *h,* leaf base, lower side, × 1; *i,* leaf middle, lower side, ×1; *j,* leaf apex, lower side, × 1.

cylindrico-ellipsoideo subtrigono cum circa 1,120 drupis eis 22–23 mm longis 2.5–3 mm latis et crassis valde adpresse adscendentibus corpore 13 mm longo cuneato-oblongo obtuso, pileo 12 mm longo basi pyramidali acuiter 5-anguloso sed ad basem angulis ceteris 1–2-divisis in stylo sensim diminuentibus, stylo 8–9 mm longo crassiter subulato valde proxime curvato dimidia infera acuiter 5-anguloso dimidia supera tereti osseoso, stigmate 4–5.5 mm longo lineari distali brunneo papilloso ad apicem extensa, endocarpio in parte 2/5 infera stramineo lateribus 0.1 mm crassis, semine 5–6 mm longo cylindrico sed infra cuneato, mesocarpio apicali cavernoso cum membranis medullosis paucis, mesocarpio basali 3 mm longo in lateribus fibroso intra carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Shrub 1–4 m tall; stem slender, grayish white, simple or with 1–2 branches, at apex 11–15 mm in diameter, brown, smooth; internodes 3–10 mm long; leaves 45–85 cm long, 7.5–9.1 cm wide, subcoriaceous, appearing pale, light green above, paler below, and towards the base greenish white, 1-ribbed, and with 2 faint pleats, the lamina arching outwards, not broken, but the subulate apex pendent, the margins somewhat wavy, the broad apex shallow cucullate, the ultimate caudate tip 4.5–5 cm long, 1.5–2.5 mm wide, trigonous, the base amplexicaul, whitish, ascending and somewhat sheathing, the longitudinal parallel secondary tertiary veins conspicuous and 1–1.5 mm apart, 36–39 on each side at midsection, the cross veins scarcely visible above, but below clearly so and forming a pattern of oblongs or rhombics shorter than wide, the base unarmed, but beginning at 5 cm up the margins with prickles 0.5–0.8 mm long, 1–6 mm apart, subulate, ascending, with brownish tips; the midrib below beginning at 15–22 cm up with first papillae, then prickles 0.2 mm long, 4–14 mm apart, short, subulate, ascending; at midsection the margins with subulate-tipped serrae 0.5–1 mm long, 1–3 mm apart; the nearby midrib below mostly glabrous; where the blade rounds off the margins with prickles similar to those of the middle but more crowded; the midrib below with prickles 1–1.3 mm long, slender subulate, salient or slightly ascending; the caudate tip with margins and midrib below with prickles 0.4–0.7 mm long, 0.2–1 mm apart, subulate, ascending, crowded, single or multiple; pistillate peduncle erect, 10–14 cm long, 8 mm in diameter, 3-sided, bracted, in anthesis the foliaceous bracts hiding the flowering head; syncarps 1–2, erect, 6–6.5 cm long, 4.1–4.5 cm in diameter, cylindric-ellipsoid, slightly 3-sided, bearing about 1,120 drupes, these strongly appressed ascending, 22–23 mm long, 2.5–3 mm wide and thick, the body 11–13 mm long, cuneate oblong, obtuse; the pileus 12 mm long, the base 3 mm long, pyramidal, sharply 5-angled, but near the base some the angles 1–2-divided, tapering gradually into the heavy subulate style 8–9 mm long, this sharply curved proximally, the lower half sharply 5-angled, the upper half terete, bony; stigma 4–5.5 mm long, linear, distal, brown, papillose, running to the apex; endocarp centering in lower 2/5, stramineous, the walls 0.1 mm thick; seed 5–6 mm long, cylindric; apical mesocarp cavernous, with a few medullary membranes; basal mesocarp 3 mm long, fibrous up the sides, fleshy within.

HOLOTYPUS: Malaya, Johore, S[ungei] Kayu, Mawai-Jemaluang Road, locally not uncommon in swampy forest, like a big stalked *Aspidistra,* 11 Oct. 1936, *E. J. H. Corner 32, 477* (SING).

SPECIMENS EXAMINED: Malaya, Johore, Sungei Kayu, 22 Oct. 1936, *Kiah bin Haji Satleh* (SING); S[ungei] Buloh Kasap, Mawai-Jemaluang Road, 4th mile, 5 Jan. 1936, *E. J. H. Corner 29,996* (SING).

DISCUSSION: *P. undulifolius* is a member of the section *Acrostigma.* In that section is its closest relative, *P. glaucophyllus* Ridl. of Perak in Malaya, a species with the stem internodes brown to yellowish; leaves 5.7–6.7 cm wide near the apex which is the broadest part, flaccid, without tertiary cross veins, midrib below beginning 4–9 cm from the base with prickles 0.8–1 mm long, 0.5–6 mm apart; syncarp with about 320 drupes; drupes 16–18 mm long, 5–6 mm wide; and the style 5–6.5 mm long. *P. undulifolius* has the contrasting characters: stem internodes grayish white; leaves 7.5–9.1 cm wide near the middle, the broadest part, subcoriaceous, with conspicuous tertiary cross veins, the midrib beginning at 15–22 cm up with first papillae, then prickles 0.2 mm long, 4–14 mm apart; syncarp with about 1,120 drupes; drupes 22–23 mm long, 2.5–3 mm wide; and the style 8–9 mm long.

The new epithet is from the Latin *undulatus,* wavy; *folium,* leaf, in reference to the partly wavy leaf margin.

Bidens, St. John, sect. nov.

Carpellis (1)–2–3 connatis, stylis corniformatis bifurcatis, stigma lanceolato bifurcato proximali, seminibus in 1–2 lineis transversis, plantis masculis incognitis.

Carpels (1)–2–3 connate; styles hornlike, bifurcate; stigma lanceolate, bifurcate, proximal; seeds in 1–2 transverse rows; staminate plants unknown.

HOLOTYPUS: *Pandanus piniformis* Holttum & St. John, here described.

Pandanus piniformis Holttum & St. John, sp. nov. (sect. *Bidens*)

Fig. 101

DIAGNOSIS HOLOTYPI: Planta fasciculas formans, caulibus 3.3 m altis ramosis, foliis 1.7 m et plus longis proxima basem 7 cm latis coriaceis supra viridibus infra pallide viridibus in sectione mediali cum 50–51 nervis secundariis in quoque latere, nervis tertialis evidentis nullis, lamina in apice circa 4–5 cm longa subulata trigona abrupte diminuenti, basi crassa dura apparente cupracea amplexicauli inermi sed ex 15–16 cm marginibus cum spinis 5–8 mm longis 18–28 mm distantibus validis compressis subulatis rectis subadscendentibus nigris, midnervo infra ex 15 cm cum spinis circa 4–5 mm longis 19–32 mm distantibus conicis divergentibus (apices desunt), in sectione mediali marginibus cum serris 1 mm longis 15–18 mm distantibus apicibus nigris, midnervo infra angusto salienti cum serris 1.5 mm longis 20–28 mm distantibus, in sectione apicali marginibus et midnervo infra cum aculeis 0.5–0.8 mm longis 1–2 mm distantibus subulatis adscendentibus, inflorescentia foeminea spicata cum 7 syncarpiis maximo infero alteris minoribus, pedunculo 14 cm et ultra longo 2 cm diametro folioso bracteato, syncarpio infero 11 cm longo 7.5 cm diametro cum circa 70 drupis eo supero 8.5 cm longo 7 cm diametro ellipsoideo, drupis 3.2–3.4 cm longis 1–2 cm latis 1–1.8 cm crassis cuneatis obtusis 6-angulosis parte ¼ supera libera lateribus minute papillosis viridibus apice obtuso 6-subangulato, drupis (1–)2–3-loculatis, stylis 5–8 mm longis obscure brunneis lucidis complanatis cornosis acute ⅓ bifurcatis valde proxime inclinatis, stigmatibus 4–6 mm longis lanceolatis bifurcatis brunneis papillosis proximis ad apicem non extensis, endocarpio mediali obscure brunneo vel nigro osseoso solido lateribus 2–3 mm crassis, seminibus 8–11 mm longis in 1–2 seriebus anguste ellipsoideis, mesocarpio apicali cum fibris longitudinalibus fortibus multis et membranis medullosis multis, mesocarpio basali fibroso et medulloso.

DIAGNOSIS OF HOLOTYPE: Plant forming clumps; stem 3.3 m tall, branched; leaves more than 1.7 m in length, 7 cm wide near the base, coriaceous, green above, pale green below, at midsection with 50–51 secondary parallel veins on each side, no visible cross veins, narrowed rather abruptly to a subulate, trigonous apex estimated to be 4–5 cm long, the base thick, hard, apparently copper-colored, amplexicaul, unarmed; beginning 15–16 cm up the margins with thorns 5–8 mm long, 18–28 mm apart, stout, flattened subulate, straight, only slightly ascending, black; the midrib below beginning at 15 cm with thorns about 4–5 mm long, 19–32 mm apart, conical, divergent (the tips broken off, but apparently divergent); at midsection the margins with serrae 1 mm long, 15–18 mm apart, black-tipped; the midrib below narrow, salient, with subulate-tipped serrae 1.5 mm long, 20–28 mm apart; on the subulate tip the margins and midrib below with subulate prickles 0.5–0.8 mm long, 1–2 mm apart, ascending; pistillate inflorescence a spike of 7 syncarps, the largest below, the smaller ones above; peduncle more than 14 cm in length, 2 cm in diameter, leafy bracted; lowest syncarp 11 cm long, 7.5 cm in diameter, the upper ones 8.5 cm long, 7 cm in diameter, ellipsoid, the larger one with about 70 drupes, these 3.2–3.4 cm long, 1–2.4 cm wide, 1–1.8 cm thick, cuneate obtuse, 6-angled, upper ¼ free, the surface minutely papillose, green, the apex obtuse, faintly 6-angled; drupes (1–)2–3-celled; styles 5–8 mm long, bony, dark brown, shining, flattened, hornlike, sharply bifurcate for about ⅓ their length, sharply bent proximally; stigma 4–6 mm long, lanceolate, bifurcate, brown, papillose, proximal, not reaching the tip; endocarp median, dark brown to black, bony, massive, the lateral walls 2–3 mm thick; seeds in 1–2 rows, 8–11 mm long, narrow ellipsoid; apical mesocarp continuous, with strong longitudinal fibers and many medullary membranes; basal mesocarp fibrous and with pithy membranes.

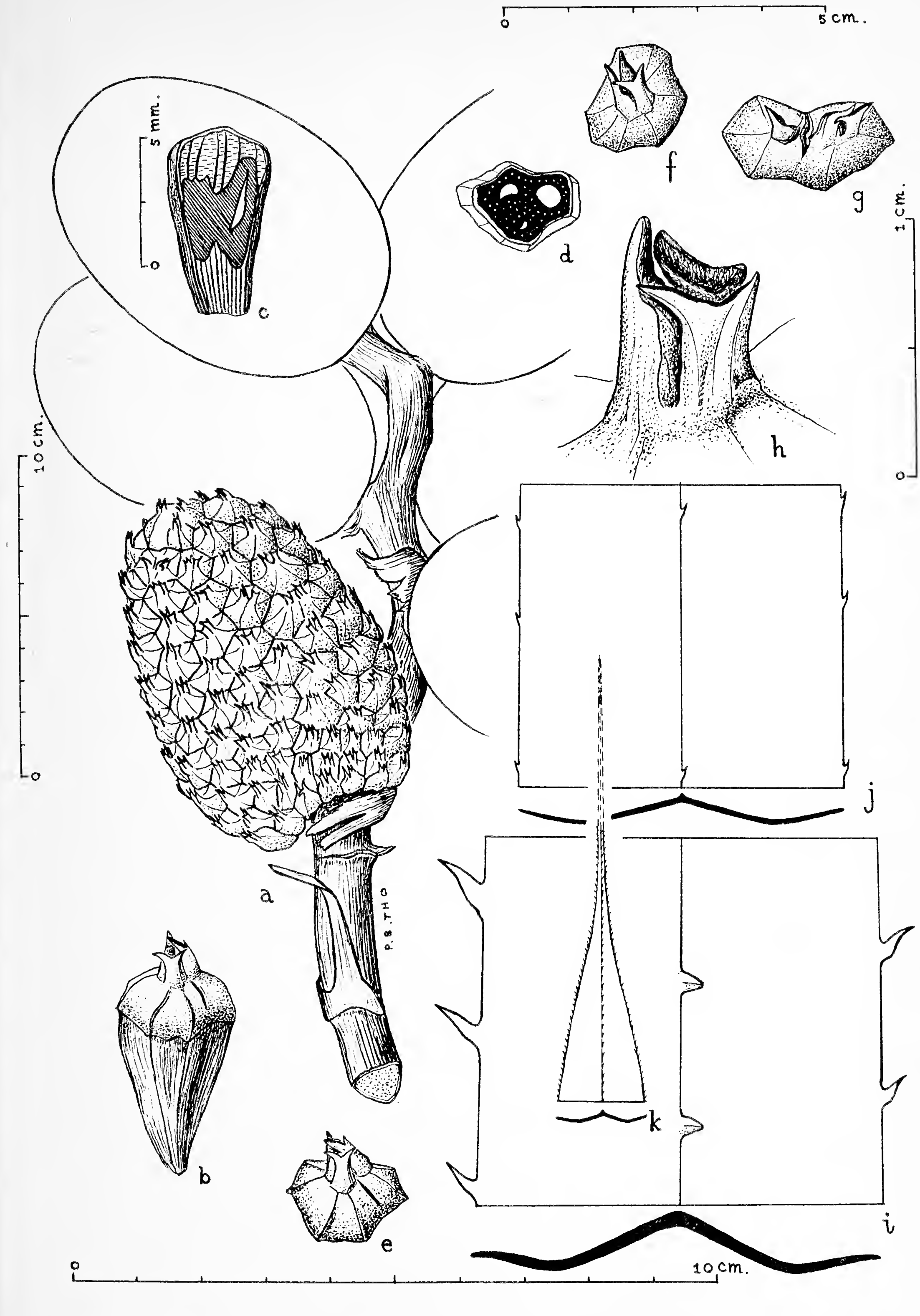

FIG. 101. *Pandanus piniformis,* holotype. *a,* Infructescence with syncarp, × ½; *b,* drupe, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d,* drupe, transverse median section, × 1; *e, f, g,* drupes, apical view, × 1; *h,* styles and stigmas, oblique view, × 4; *i,* leaf base, lower side, × 1; *j,* leaf middle, lower side, × 1; *k,* leaf apex, lower side, × 1.

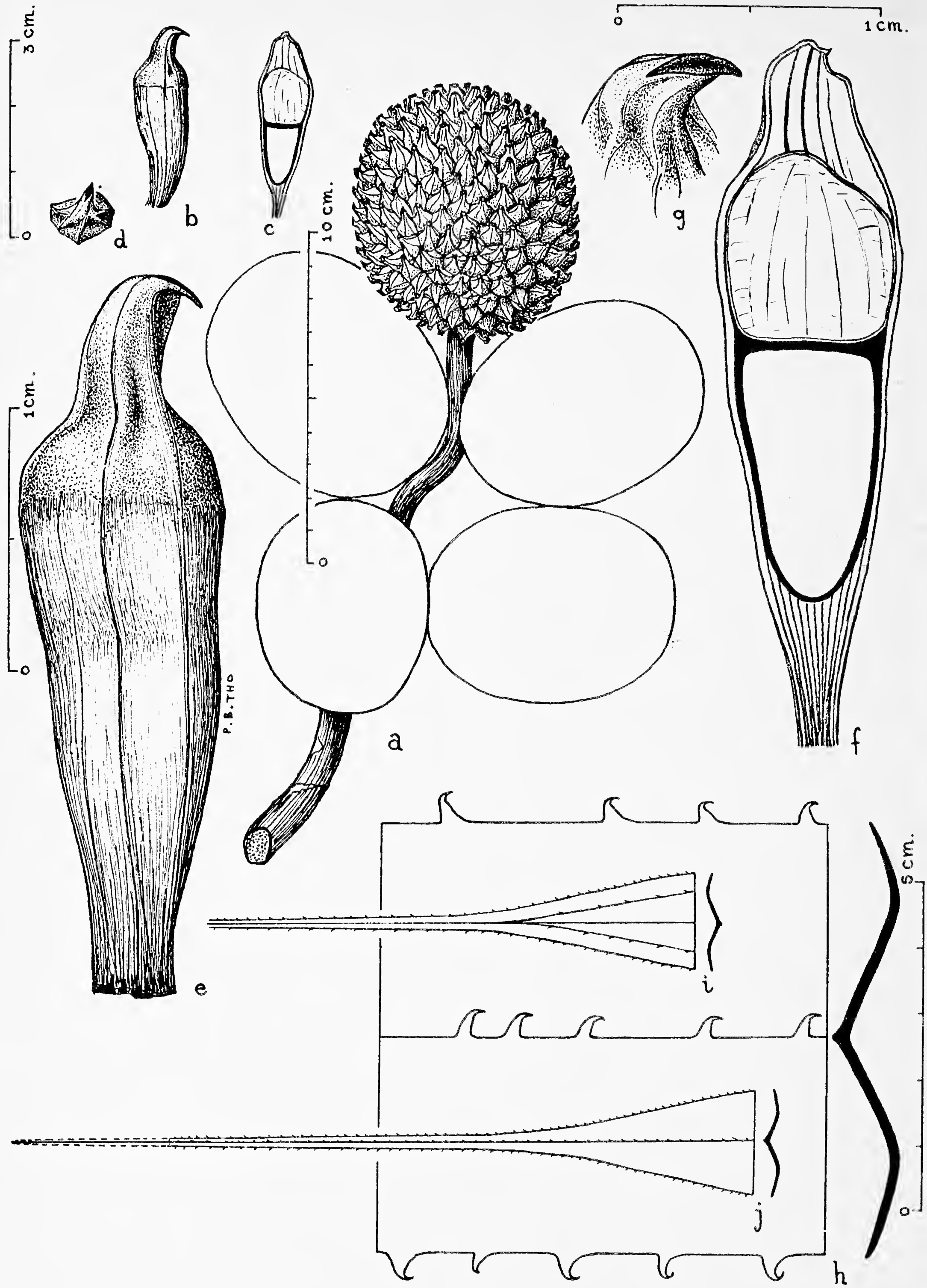

FIG. 102. *Pandanus dumetorum,* holotype. *a,* Infructescence and syncarp, × ½; *b,* drupe, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d,* drupe, apical view, × 1; *e,* drupe, lateral view, × 4; *f,* drupe, longitudinal median section, × 4; *g,* drupe apex with stigma, × 4; *h,* leaf base, lower side, × 1; *i,* leaf apex, upper side, × 1; *j,* leaf apex, lower side, × 1.

HOLOTYPUS: Malaya, Perak, Pulai limestone, not very abundant on cliffs, 400 ft. alt., 2 June 1930, *M. R. Henderson 23,759* (SING).

DISCUSSION: *P. piniformis* is here made the holotype of the new section *Bidens.* The species is distinctive in having styles and stigmas that resemble those of the section *Rykia,* but the drupes are (1–)2–3-celled.

The collector noted that the leaves were glaucous, but this coating does not show on the dried specimen.

The new epithet is from the generic name *Pinus;* and the Latin *formis,* shaped, as the syncarps resemble small, closed pine cones.

Fusiforma, St. John, sect. nov.

Carpellis distinctis 1-loculatis fusiformibus, stylo nullo, stigmate lanceolato vel elliptico distali subapicali.

Carpels distinct, 1-celled, fusiform; style none; stigma lanceolate or elliptic, subapical, distal.

HOLOTYPUS: *Pandanus dumetorum* Holttum & St. John.

Pandanus dumetorum Holttum & St. John, sp. nov. (sect. *Fusiforma*)

Fig. 102

DIAGNOSIS HOLOTYPI: Acaulescens viridaria formans, foliis 3–4 m longis 6–8 cm latis ad basem crassiter coriaceis ad apicem exilibus et subcoriaceis vel chartaceis apice pendente 1-sulcatis 2-plicatis in sectione M-formatis in quoque latere cum 50–51 nervis secundariis evidentis et infra cum nervis tertialis transversis, lamina ligulata subabrupte diminuentibus et apice cucullato et per 7–8 cm caudato et 1–2 mm lato basi amplexicauli inermi sed ex 8–20 cm marginibus cum spinis 4–5 mm longis 8–20 mm distantibus crassiter subulatis arcuato-recurvatis pallidis, midnervo infra ex 5 cm cum spinis simulantibus reflexis sed brevioribus, in sectione 80 cm ex apice marginibus cum serrulis 0.1–0.3 mm longis 15–31 mm distantibus obtusis, infra midnervo exili salientibusque cum serrulis 0.5–0.8 mm longis 7–14 mm distantibus subulatis, per 30 cm ex apice plicis binis supra cum aculeis 0.4–0.5 mm longis 3–18 mm distantibus subulatis rigidis adscendentibus, proxima apicem marginibus et midnervo infra cum serrulis 0.3–0.5 mm longis 2–5 mm distantibus, inflorescentia foeminea in foliis subclausa cum 2–5 syncarpiis, pedunculo 25 cm longo 8–10 mm diametro trigono folioso-bracteato, bracteis in syncarpiis adpressis luteis, syncarpiis ultimis majoribus, infimis 6.5 cm longis 5.5 cm latis 4 cm crassis ellipsoideis compressis cum circa 224 drupis, ultimo 8 cm longo 6.8 cm diametro elliptico-subgloboso cum circa 376 drupis, drupis 25–27 mm longis 6–9 mm latis 5–7 mm crassis oblanceo-fusiformibus 5–6-angulosis corpore 21–23 mm longo oblanceoloideo parte ⅓ supera libera lateribus laevibus, apice late pyramidalibus cum rostro 6–7 mm longo valde 5–6-anguloso obliquo anguste lanceolo-pyramidali, stigmate 2–3 mm longo lanceolato vel elliptico brunneo papilloso apicali sed in latere distali extenso, endocarpio in 2/5 parte infera situato olivaceo osseoso lateribus 0.5 mm crassis, seminibus 10–11 mm longo anguste obconico, mesocarpio supero cavernoso 8 mm longo cum membranis latis albis paucis, mesocarpio basali in lateribus fibroso intra carnoso.

DIAGNOSIS OF HOLOTYPE: Acaulescent, forming small thickets; leaves 3–4 m long, 6–8 cm wide, towards the base thick coriaceous, towards the tip thin and subcoriaceous to chartaceous, eventually half broken near the end and the tip pendent, 1-ribbed and 2-pleated, in section M-shaped, the median section not available but at the region 80 cm from the tip on each side with 50–51 parallel secondary veins, from here to the tip these veins visible on both sides, and on the lower side visible tertiary cross veins slightly oblique, making meshes shorter than wide, the blade ligulate, fairly abruptly obcuneate narrowed and cucullate to a 7–8 cm caudate apex, this 1–2 mm wide, the base amplexicaul, unarmed, but beginning at about 8–20 cm the margins with thorns 4–5 mm long, 8–20 mm apart, heavy subulate, arcuate recurved, pale; the midrib below beginning at about 5 cm up with reflexed thorns like the marginal ones but sharper; at the region 80 cm from the apex the margins with blunt serrulations 0.1–0.3 mm long, 15–31 mm apart; below the slender salient midrib with subulate tipped serrulations 0.5–0.8 mm long, 7–14 mm apart; from the cucullate contraction down for about 30 cm the 2 lateral pleats above with prickles 0.4–0.5 mm long, 3–18 mm apart, subulate, rigid, ascending;

the caudate deltoid apex with the margins and midrib below with serrulations 0.3–0.5 mm long, 2–5 mm apart; pistillate inflorescence partly hidden in the clump of leaves, bearing 2–5 syncarps; peduncle 25 cm long, 8–10 mm in diameter, 3-sided, leafy bracted; bracts surrounding syncarps appressed, clear yellow; syncarps increasing upwards in size, the lowest 6.5 cm long, 5.5 cm wide, 4 cm thick, ellipsoid, compressed; the apical one 8 cm long, 6–8 cm in diameter, elliptic-subglobose, the lowest with about 224 drupes, the apical with about 376 drupes, these 25–27 mm long, 6–9 mm wide, 5–7 mm thick, oblance-fusiform, 5–6-angled, the body 21–23 mm long, oblanceoloid; the exposed apex ⅓ of total length, the sides smooth, this with a broad pyramidal base, prolonged into an oblique, narrow, lance-pyramidal beak 6–7 mm long, sharply 5–6-angled; stigma of the fruit 2–3 mm long, lanceolate to elliptic, brown, papillose, apical but extending down distal side; endocarp centering in lower 2/5, olivaceous, bony, the walls 0.5 mm thick; seed 10–11 mm long, narrowly obconic; upper mesocarp a cavern 8 mm long, with a few broad, white membranes; basal mesocarp fibrous up the margins, fleshy within.

HOLOTYPUS: Malaya, Trengganu, Kemaman, Ulu Bendong, common in hillside forest, 500 ft. alt., 30 Oct. 1935, *E. J. H. Corner 30,066* (SING).

DISCUSSION: Because of its peculiar drupes, ending in narrow pyramidal tip bearing a lanceolate or elliptic stigma, this species is made the basis of a new section of the genus. It differs from the section *Acrostigma* which has a subulate style bearing a linear stigma.

The new epithet is from the Latin noun *dumetorum*, a thicket.

SECTION *Pulvinistigma*

Pandanus echinodermops Holttum & St. John, sp. nov. (sect. *Pulvinistigma*)

Fig. 103

NOM. VERN.: "siakum."

DIAGNOSIS HOLOTYPI: Ramis 2–2.5 cm diametro decumbentibus in paludibus viridaria formantibus, nodis superis stramineis, foliis 93–125 cm longis 3.5–3.6 cm latis subcoriaceis supra obscure viridibus infra pallidis 1-costatis 2-plicatis in sectione M-formatis in sectione mediali cum 30–31 nervis secundariis in quoque latere et eis ubique evidentibus, nervis tertiis paene evidentibus, laminis ligulatis sed subcuneatis et proxima basem 30 mm latis apice acuto basi alba amplexicauli et inermi venulosa et ex 5 cm marginibus cum aculeis 1.5–2 mm longis 3–5 mm separatis valide subulatis adscendentibus pallidis vel cum apicibus rubris, midnervo infra ex 8 cm cum aculeis 1.5–2 mm longis 2–8 mm distantibus simulantibus sed reflexis, in sectione mediali marginibus cum aculeis simulantibus sed gracilioribus et 3–8 mm distantibus adscendentibus, midnervo infra angusto salienti et cum aculeis simulantibus 6–13 mm distantibus, proxima apicem marginibus undulatis et cum serris 1.5–2 mm longis 2–6 mm distantibus apicibus subulatis, midnervo infra cum serris simulantibus 3–7 mm distantibus, supra per 30 cm ultimos plicis cum aculeis acutis 1–1.3 mm longis 4–11 mm distantibus rigidis subulatis adscendentibus, inflorescentia foeminea erecta cum 3 syncarpiis, pedunculo 15 cm longo 7 mm diametro trigono folioso, syncarpio terminali majori 9 cm longo 8 cm diametro viridibus sed auranti-rubescentibus subgloboso-ovoideis cum circa 448 drupis, syncarpiis in spica congregatis, syncarpiis inferis 7–8 cm longis 5.5–6 cm diametro late ellipsoideis cum 208–320 drupis, drupis 27–32 mm longis 6–9 mm latis 4–7 mm crassis oblanceo-fusiformibus 5–6-angulosis parte ⅓ supera libera 5–6-angulosa lateribus laevibus apice recto vel proxime inclinato truncato et cum stigmate 2.5–3 mm lato reniformi vel late cordato pallide brunneo in juvente cum pilis brevibus, endocarpio in parte ⅓ infera lateribus 0.2 mm crassis osseosis pallide brunneis, semine 4 mm longo obovoideo apice truncato, mesocarpio supero cavernam 12–15 mm longam cum membranis paucis formantibus, mesocarpio basali cum lateribus fibrosis et intra carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Stems 2–2.5 cm in diameter, decumbent, forming thickets in fresh water or in swamps, the upper nodes stramineous; leaves 92–125 cm long, 3.3–3.6 cm wide, subcoriaceous, dark green above, pale but not glaucous beneath, 1-ribbed, 2-pleated, in section M-shaped, at midsection on each side with 30–31 parallel secondary veins, these distinct on both sides through-

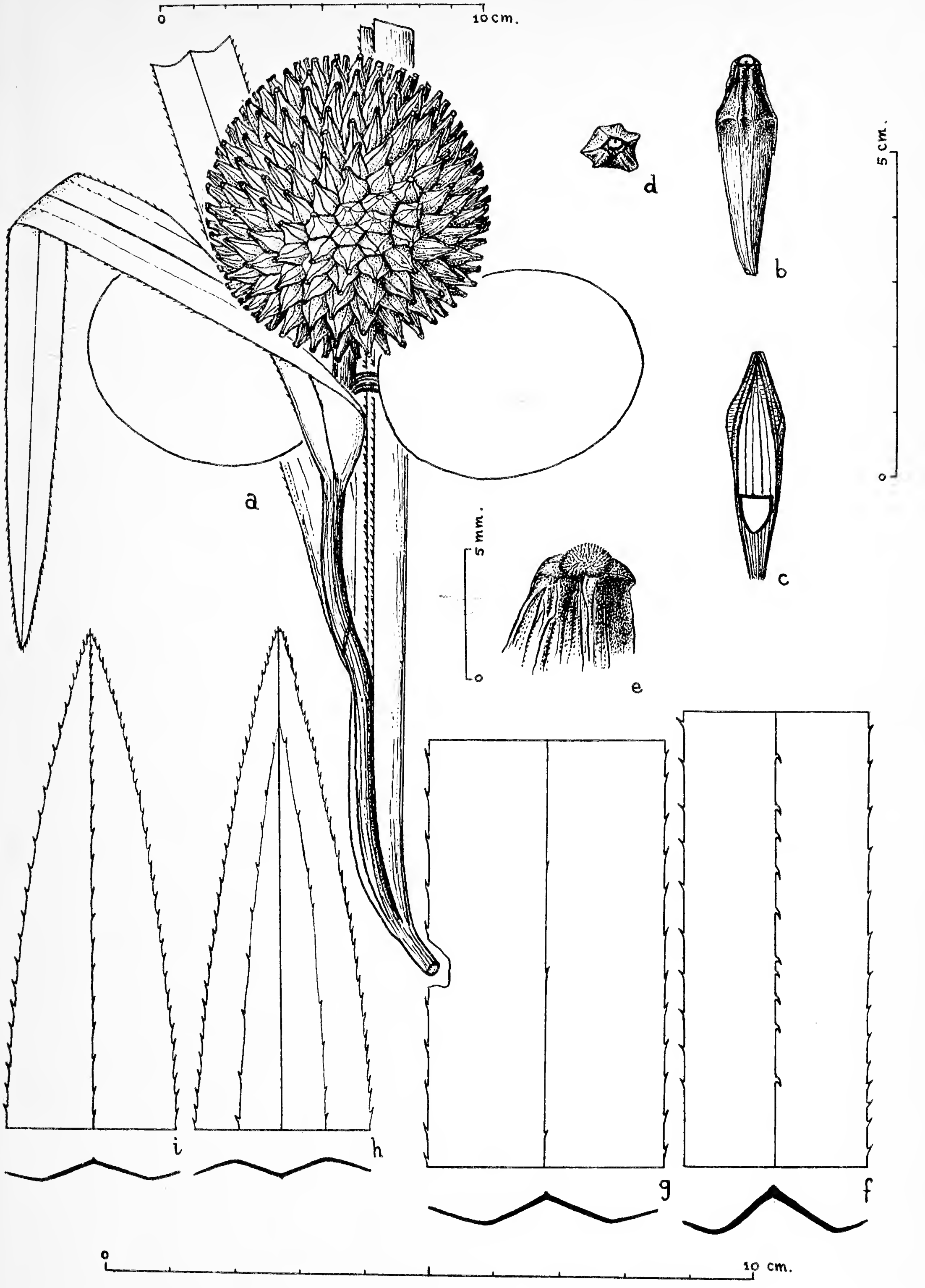

FIG. 103. *Pandanus echinodermops,* holotype. *a,* Infructescence with syncarps, × ½; *b,* drupe, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d,* drupe, apical view, × 1; *e,* drupe apex with stigma, × 4; *f,* leaf base, lower side, × 1; *g,* leaf middle, lower side, × 1; *h,* leaf apex, upper side, × 1; *i,* leaf apex, lower side, × 1.

out; tertiary cross veins almost invisible, the blade ligulate, but slightly narrowed downwards and near the base about 30 mm wide, the apex acute, the base white, amplexicaul and unarmed, veiny, beginning at 5–7 cm the margins with prickles 1.5–2 mm long, 3–5 mm apart, stout subulate, ascending, pale or with dark reddish tips; the midrib below beginning 8 cm up with prickles 1.5–2 mm long, 2–8 mm apart, similar but reflexed; at midsection the margins with similar but more slender prickles 3–8 mm apart, ascending; the midrib below narrow, salient, with similar prickles 6–13 mm apart; near the tip the margins undulate between the subulate tipped serrae 1.5–2 mm long, 2–6 mm apart; the midrib below with similar serrae but 3–7 mm apart; on the upper surface for the last 30 cm of the tip the two lateral pleats with sharp prickles 1–1.3 mm long, 4–11 mm apart, rigid, subulate, ascending; pistillate inflorescence erect, bearing 1–3 syncarps; peduncle 15–20 cm long, 7 mm in diameter, 3-sided, leafy bracted; terminal syncarp the largest, 9 cm long, 8 cm in diameter, green, turning orange-red, subglobose-ovoid, bearing about 448 drupes, the syncarps crowded in a close spike, the lower ones 7–8 cm long, 5.5–6.5 cm in diameter, broadly ellipsoid to subglobose, bearing about 208–320 drupes, these 27–32 mm long, 6–9 mm wide, 4–7 mm thick, oblance-fusiform, 5–6-angled, upper ⅓ free, the tip apparently not detachable, sharply 5–6-angled, the sides smooth, apex straight or proximally inclined, truncate, bearing the stigma which is 2.5–3 mm wide, reniform to broad cordate, pale brown, when young with short hairs; endocarp in lower ⅓, the walls 0.2 mm thick, bony, light brown; seed 4 mm long, obovoid, the apex truncate; upper mesocarp a cavern 12–15 mm long, with a few white, delicate membranes near the sides; basal mesocarp with longitudinal fibers up the sides, fleshy within.

HOLOTYPUS: Malaya, Johore, Kangka Sedili, Ketchil, low elevation, 18 June 1934, *E. J. H. Corner 28,597* (SING).

SPECIMENS EXAMINED: Malaya, Johore, Kangka Sedili Kechil, low elevation, 18 June 1934, *E. J. H. Corner 28,483* (= *28,579*), (SING); Johore, S[ungei] Sedili, Mersing Road, in swampy stream, forming thickets in the water or muddy hollows, 30 Sept. 1936, *E. J. H. Corner 31,948* (SING).

DISCUSSION: *P. echinodermops* is a new member of the small section *Pulvinistigma.* It is closely related to *P. dasystigma* Kanehira of Indonesian Borneo, a species which has the syncarp globose, 8 cm in diameter; the drupes 3.5–4 cm long, the apex acute, and the upper ⅕ free; and the leaves 60 cm long, 2.5–3 cm wide. *P. echinodermops* has the syncarps broadly ellipsoid to subglobose-ovoid, 5.5–8 cm in diameter; drupes 2.7–3.2 cm long, the apex truncate, and the upper ⅓ part free; and the leaves 93–125 cm long, 3.3–3.6 cm wide.

The new epithet is coined from the Greek *echinoderm;* and *ops,* of like appearance, since the fruiting syncarps look much like an echinoderm.

SECTION *Rykia*

Pandanus calcicola Holttum & St. John, sp. nov. (sect. *Rykia*)

Fig. 104

DIAGNOSIS HOLOTYPI: Caule 1 m alto, foliis 3.9 m longis 9 cm latis rigidis crassis coriaceis supra viridibus infra minime pallidioribus 1-sulcatis 2-plicatis in sectione mediali cum 62 nervis secundariis in quoque latere in lateribus ambis excepta in basi nervis tertialis evidentis ex medio ad apicem reticulum ex oblongis formantibus laminis ligulatis ad apicem per 20 cm diminuentibus et cum 12–14 cm apice valido subulato trigono caudato eo 10 cm ex apice 5 mm lato, basi crassa dura rubro-brunnea amplexicauli et inermi sed ex 15 cm marginibus cum spinis 3–4.5 mm longis 9–22 mm distantibus crasse subulatis adscendentibus subarcuatis brunneis in basi crassis, midnervo infra ex 22 cm cum spinis 4–5 mm longis 25–41 mm distantibus crasse subulatis salientibus in basi crassis, in sectione mediali marginibus cum aculeis 1–2 mm longis 18–23 mm distantibus subulatis adpresse adscendentibus, midnervo infra inermi, in apice caudato marginibus et midnervo infra cum serris 0.3–0.6 mm longis 1.5–5 mm distantibus, inflorescentia foeminea terminali et cum 4 syncarpiis, pedunculo 10 cm et ultra longo 2 cm diametro trigono bracteoso, bracteis syncarpiorum 30–40 cm longis 4–6 cm latis lanceolatis striatis per ⅔ parte ultima minute serratis, syncarpio ultimo majore 8 cm longo 3.5 cm diametro ellipsoideo cum circa

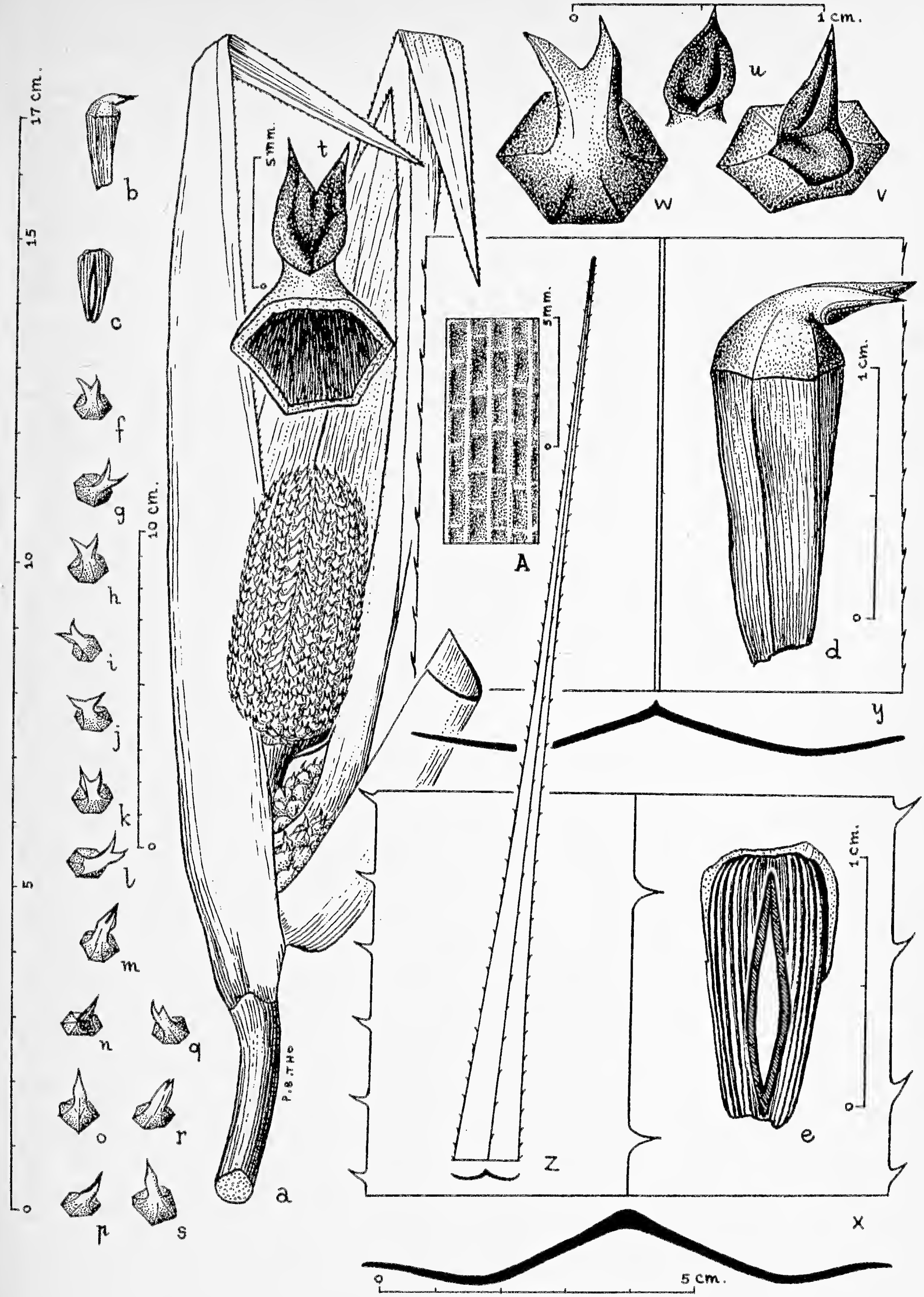

FIG. 104. *Pandanus calcicola,* holotype. *a,* Infructescence with syncarps, × ½; *b,* drupe, lateral view, × 1; *c,* drupe body, longitudinal median section, × 1; *d,* drupe, lateral view, × 4; *e,* drupe body, longitudinal median section, × 4; *f, g,* drupes, apical view, × 1; *h,* drupe with the most typical bifid style, × 1; *i, j, k, l, m,* drupes, all also lateral, showing style forks, × 1; *n, o, p, q, r, s,* drupes all apical, apical view, × 1; *t,* style branches and stigma of lateral drupe, proximal view, × 4; *u, v,* stigmas of apical drupes, lateral view, × 4; *w,* style, apical view, × 4; *x,* leaf base, lower side, × 1; *y,* leaf middle, lower side, × 1; *z,* leaf apex, lower side, × 1; *A,* vein network in leaf midsection, lower side, × 4.

312 drupis, syncarpiis alteris 4 cm longis subglobosis sub bracteis clausis, drupis 15–16 mm longis (immaturis) eis superis 6–7 mm latis et crassis, alteris 5–6 mm latis 4–5 mm crassis parte ⅓ supera libera corpore 12–13 mm longo cuneato 5–6-anguloso obtuso, pileo cum basi 4–5 mm alto pyramidali-semiorbiculari minute papilloso, stylo 5–5.5 mm longo cornoso luteo lucido ½ bifurcato dentibus divergentibus (vel in drupis terminalibus paucis stylo integris), stigmate 3–4 mm longo late lanceolato et bifurcato brunneo ad apicem non extenso, endocarpio in parte ½ infera brunneo lateribus 0.2 mm crassis, semine 6 mm longo anguste ellipsoideo, mesocarpio apicali cavernoso cum membranis paucis, mesocarpio basali in lateribus cum fibris fortibus intra carnoso.

DIAGNOSIS OF HOLOTYPE: Stem 1 m tall; leaves 3.9 m long, 9 cm wide, rigid, thick coriaceous, green above, slightly paler beneath, furrowed above the 1 rib, 2-pleated, at midsection on each side with 62 parallel secondary veins, these visible on both sides except at base; tertiary cross veins visible and from the middle outwards conspicuous on both sides, forming a reticulate surface, slightly oblique, forming short oblong meshes, ligulate, towards the apex within a distance of 20 cm tapering and bearing a 12–14 cm stout subulate, trigonous caudate apex which 10 cm down is 5 mm wide, the base thick and hard, reddish brown, amplexicaul and unarmed, but beginning about 15 cm up the margins with thorns 3–4.5 mm long, 9–22 mm apart, thick subulate, ascending and slightly arcuate, brown, broad based; the midrib below from about 22 cm up with thorns 4–5 mm long, 25–41 mm apart, thick subulate, broad based, salient; at midsection the margins with prickles 1–2 mm long, 18–23 mm apart, subulate, appressed ascending, the midrib below unarmed; on the caudate apex the margins and midrib below with serrae 0.3–0.6 mm long, 1.5–5 mm apart; pistillate inflorescence terminal, a spike bearing 4 syncarps, peduncle more than 10 cm long, 2 cm in diameter, 3-sided, bracteate; each syncarp with a subtending bract 30–40 cm long, 4–6 cm wide, lanceolate, striate veined, minutely serrulate throughout outer ⅔'s; terminal syncarp the largest, 8 cm long, 3.5 cm in diameter, ellipsoid, bearing about 312 drupes; lateral syncarps about 4 cm long, subglobose, all closely enwrapped by the bract bases; drupes 15–16 mm long (following the curve of the style), immature, the uppermost ones 6–7 mm wide and thick, the lateral and lower ones 5–6 mm wide, 4–5 mm thick, upper ⅓ free; the body 12–13 mm long, cuneate, 5–6-angled, obtuse; pileus with the base 4–5 mm high, pyramidal-semiorbicular, minutely papillose; style 5–5.5 mm long, hornlike, yellowish, shining, bifurcate nearly half way, the forks spreading (or a few terminal drupes with the style hornlike, undivided); stigma 3–4 mm long, broad lanceolate and bifurcate, brown, not reaching the tips; endocarp in lower ½, brownish, the walls 0.2 mm thick; seed 6 mm long, narrowly ellipsoid; apical mesocarp a cavern with a few membranes; basal mesocarp with strong fibers up the sides, fleshy within.

HOLOTYPUS: Malaya, Perlis, Kaki Bukit, on limestone, 100 ft. elev., 13 April, 1938, *Kiah 35,285* (SING).

DISCUSSION: *P. calcicola* is a member of the section *Rykia*. Its closest relative, *P. heterostigma* (Martelli) Martelli of Sumatra, has the leaves 2 m and more in length, 10 cm wide; raceme 7–10-headed, spathes papery, lance acuminate at base; syncarps 12–15 mm long, 9–19 cm in diameter; and the style 6–7 mm long. *P. calcicola* has the leaves 3–9 m long, 9 cm wide; spike 4-headed, spathes foliaceous, lanceolate; syncarps 4–8 cm long, 3.5–4 cm in diameter; and the style 5–5.5 mm long.

The new epithet is derived from the Latin *calx,* lime; *cola,* a dweller, and applied in allusion to the calcicolous habitat.

P. calcicola, as well as *P. piniformis* Holttum & St. John and *P. irregularis* Ridl., is confined to the precipitous limestone, elongate ridges so conspicuous in the interior of Malaya.

Pandanus longicaudatus Holttum & St. John, sp. nov. (sect. *Rykia*)

Figs. 105–107A

DIAGNOSIS HOLOTYPI: Caule 1–4 m alto 7.5–9 cm diametro, cortice argento-albo et cum radicillis adventiviis paucis, radicibus fulturosis paucis ad 90 cm longis, foliis 2.4–3.3 m longis proxima basem 5 cm latis in media 6 cm latis obscuro-viridibus non glaucis crassis et coriaceis parte ultima pendente late 1-sulcatis 2-plicatis ligulatis sed sensim in apice subulato 15 cm

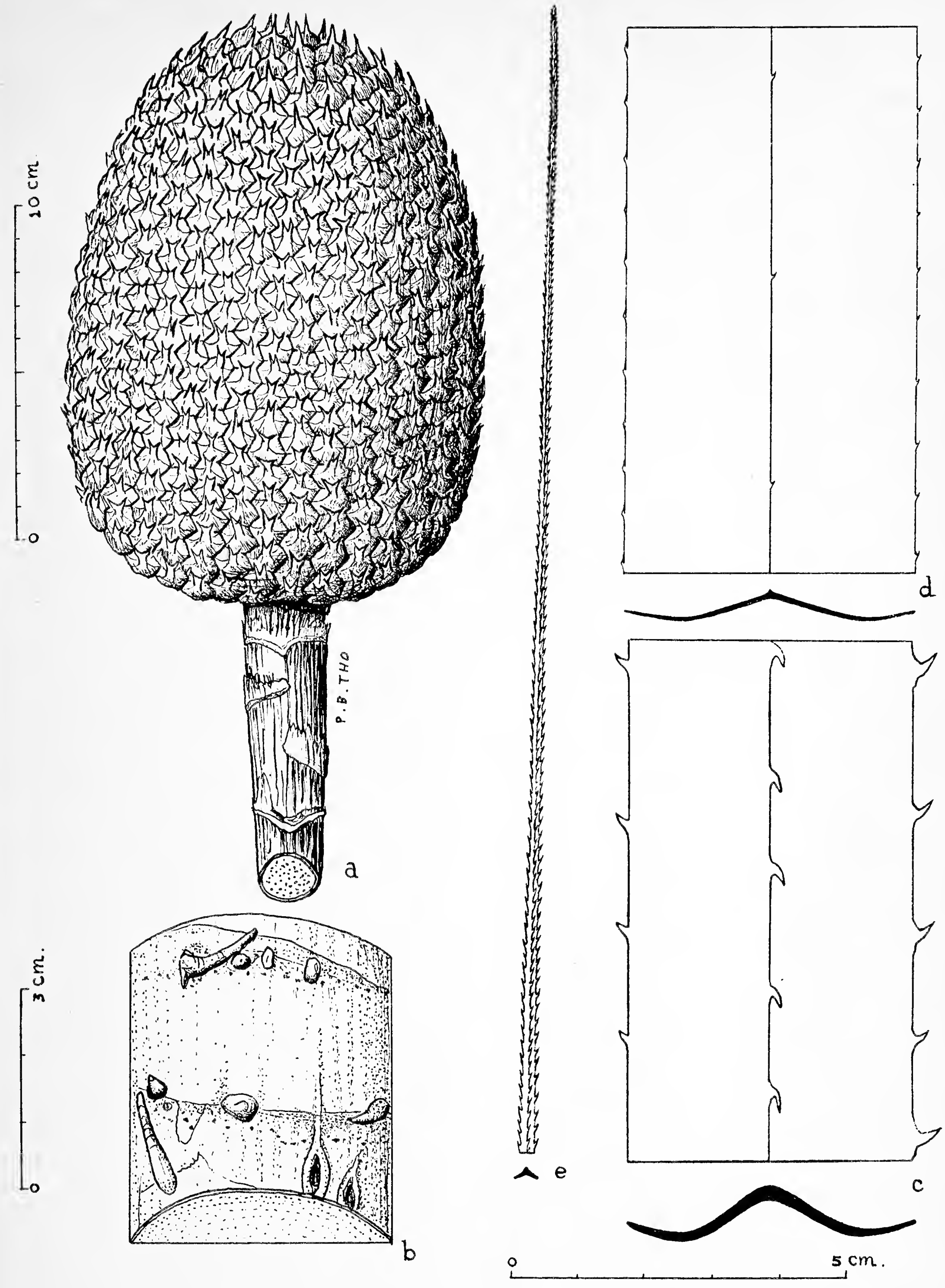

FIG. 105. *Pandanus longicaudatus*, holotype. *a*, Syncarp, × ½; *b*, stem with bark and adventitious rootlets, × 1; paratype, staminate, *Nur 32,632; c*, leaf base, lower side, × 1; *d*, leaf middle, lower side, × 1; *e*, leaf apex, lower side, × 1.

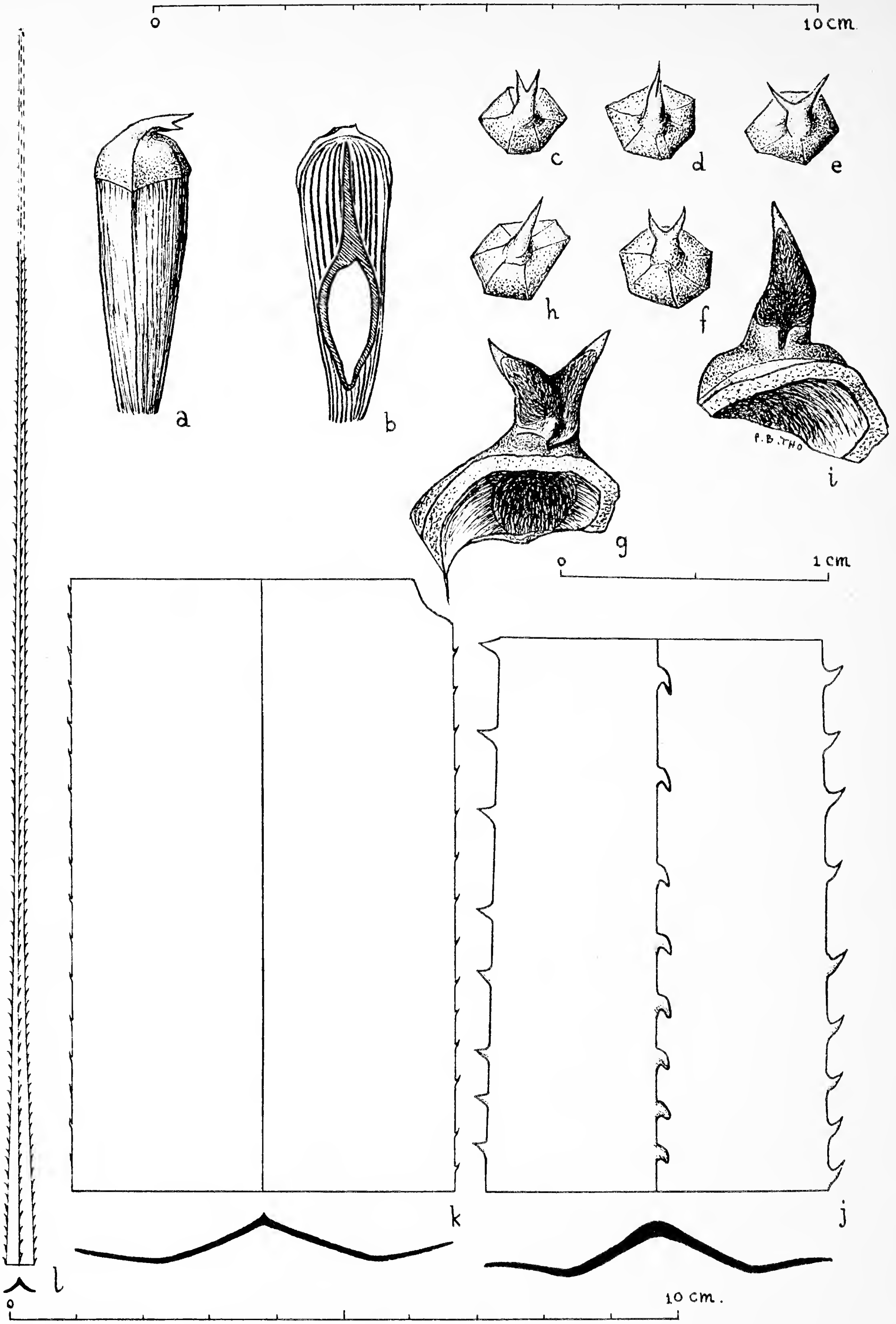

FIG. 106. *Pandanus longicaudatus,* holotype. *a,* Drupe, lateral view, × 1; *b,* drupe, longitudinal median section, × 1; *c, d, e, f,* lateral drupes, apical view, × 1; *g,* style and stigma of lateral drupe, proximal view, × 4; *h,* apical drupe, apical view, × 1; *i,* style and stigma of apical drupe, proximal view, × 4; *j,* leaf base, lower side, × 1; *k,* leaf middle, lower side, × 1; *l,* leaf apex, lower side, × 1.

longo trigono diminuentibus eo 10 cm ex apice 0.7 mm lato, nervis secundariis in dimidia ultima conspicuis in paginis ambis et in sectione mediali 48 in quoque latere, nervis tertialis crassioribus salientibusque et reticulis squarrosis formantibus basi amplexicauli inermi olivaceo-ochracea sed ex 7–15 cm marginibus cum spinis 3–5 mm longis 6–14 mm distantibus deltoideis crasse subulatis basi incrassata et 3–4 mm lata subarcuatis adscendentibus brunneis, midnervo infra cum spinis 4–6 mm longis 7–18 mm distantibus simulantibus crassis sed reflexis, in sectione mediali marginibus cum aculeis 1–2 mm longis 3–8 mm distantibus subulatis rectis vel subarcuatis adscendentibus, midnervo infra angusto salienti inermi, in apice caudato marginibus et midnervo infra cum serrulis 0.4–0.7 mm longis 1–5 mm distantibus, inflorescentia foeminea recta cum syncarpio unico in bracteis siccis pallide brunneis scariosis convolutis, pedunculo 30 cm longo in basi 7 mm diametro in apice 22 mm diametro trigono bracteoso, syncarpio 17 cm longo 10.5 cm diametro elliptico-ovoideo viridi aurantiaco-rosaceo-tincto cum circa 900 drupis eis 41–44 mm longis 8–14 mm latis 7–13 mm crassis eis tertiae superae majoribus cuneato-oblongis corpore 36–38 mm longo, pileo cum basi pyramidali-hemisphaerica 4–6 mm alta 5–6-angulosa laevi, stylo 4–8 mm longo adpresse adscendenti osseoso brunneo lucido eis apicalibus integris et crassiter subulatis omnibus alteris bifurcatis lobis aequalibus sed diversis eis parvis ⅓ lobatis et lobis adscendentibus illis majoribus ½ lobatis et lobis divergentibus, stigmate 3–3.5 mm longo lanceolato vel cum lobis binis lanceolatis brunneis papillosis proximalibus, endocarpio cum corpore ellipsoideo in parte ⅖ infera obscure brunneo summo interiore lucido in apice cum projectione subulata ad stylam, semine 13–15 mm longo 6 mm diametro late ellipsoideo, mesocarpio apicali cavernoso cum fibris fortibus longitudinalibus, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Stem 1–4 m tall, 7.5–9 cm in diameter, the bark dull silvery whitish, with sparse adventitious rootlets, these probably ascending; prop roots few, up to 90 cm long; leaves 2.4–3.3 m long, eventually partly broken and the outer part pendent, 4.7–6 cm wide at the middle, 5 cm wide near the base, dark green, not glaucous, thick and coriaceous, in section with a broad central furrow and on each side one pleat, ligulate, tapering gradually towards the tip and ending in a subulate trigonous caudate apex 15–22 cm long, this at about 10 cm down from the tip 0.7 mm wide, the secondary longitudinal parallel veins obscure towards the base but beyond it conspicuous above and below, at midsection 48 on a side, and the tertiary cross veins still heavier and salient, forming mostly square meshes, the base amplexicaul, unarmed, olive-ochre, beginning at 7–15 cm the margins with thorns 3–5 mm long, 6–14 mm apart, deltoid, heavy subulate, the base much thickened, 3–4 mm wide, slightly arcuate ascending, brown; the midrib below with similar heavy thorns 4–6 mm long, 7–18 mm apart but reflexed; at midsection the margins with prickles 1–2 mm long, 3–8 mm apart, subulate, straight or slightly arcuate, ascending; the midrib below narrow, sharp, salient, unarmed; on the caudate tip the margins and midrib below with serrations 0.4–0.7 mm long, 1–5 mm apart; pistillate inflorescence erect, bearing 1 syncarp enclosed in dry, pale brown, scarious bracts; peduncle 30 cm long, at base 7 mm in diameter, at apex 22 mm, 3-sided, bracted; syncarp 16–17 cm long, 10.5 cm in diameter, elliptic-ovoid, green, flushed with orange-pink, with about 900 drupes 41–44 mm long, 8–14 mm wide, 7–13 mm thick, the larger and fatter ones mostly on the upper third of the syncarp, cuneate oblong, the body 36–38 mm long; pileus with the base pyramidal-hemispheric, 4–6 mm high, 5–6-angled, smooth; style 4–8 mm long, appressed ascending, bony, brown, shining, on the apical ones entire, heavy subulate, on all the rest bifurcate, the lobes subequal, but of various kinds, on the small, narrow drupes the styles lobed about ⅓ way and the lobes ascending, on the larger drupes lobed about ½ way and the lobes widely divergent; stigma 3–3.5 mm long, lanceolate or with two lanceolate lobes, brown, papillose, proximal; endocarp with the main body ellipsoid, centering in the lower ⅖, dark brown, the walls 1.5–2 mm thick, the inner surface shining, bearing a heavy subulate apical prolongation reaching to the style; seed 13–15 mm long, 6 mm in diameter, broad ellipsoid; apical mesocarp a long cavern, traversed by heavy longitudinal fibers; basal mesocarp fibrous and fleshy.

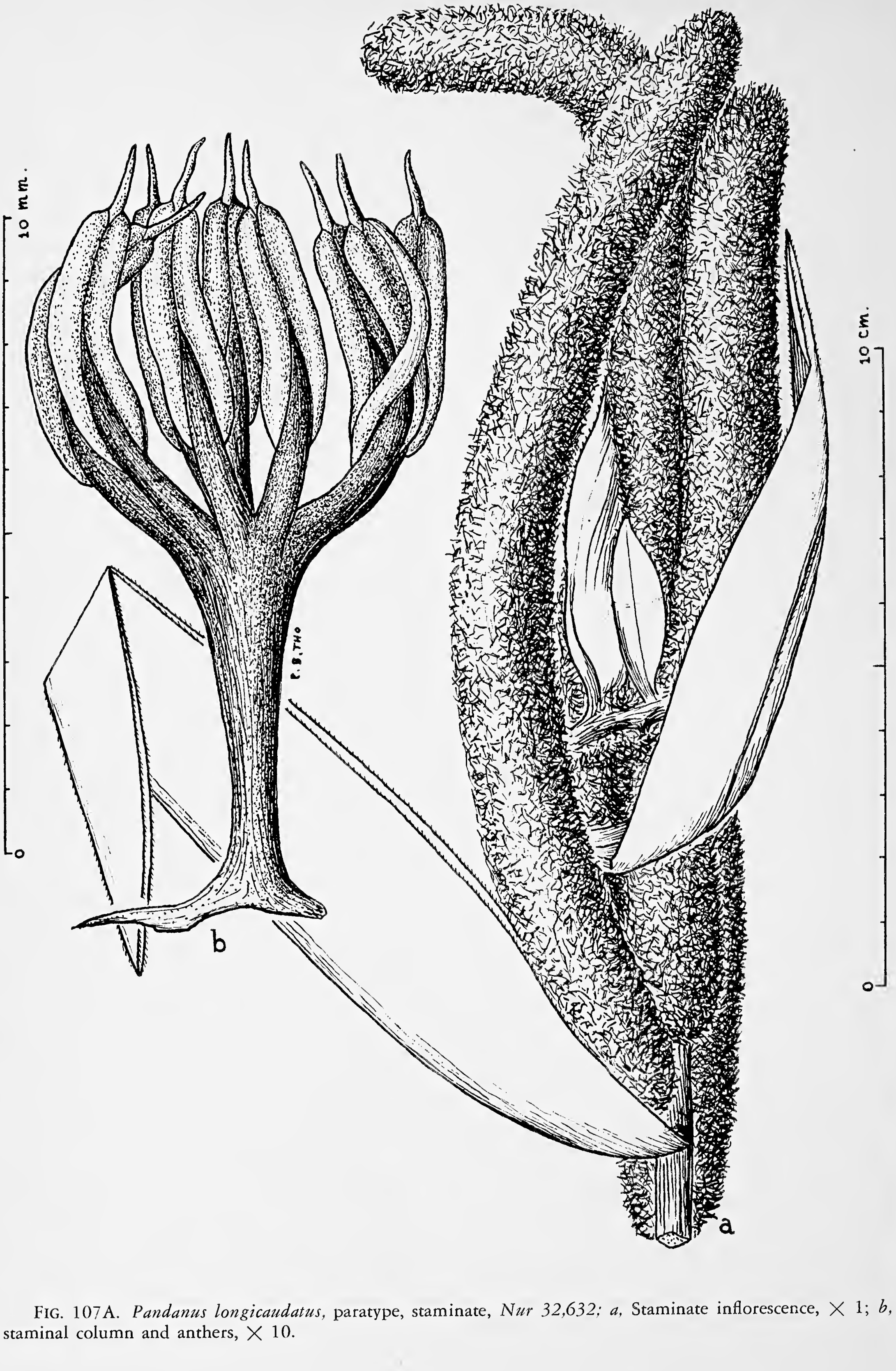

FIG. 107A. *Pandanus longicaudatus,* paratype, staminate, *Nur 32,632; a,* Staminate inflorescence, × 1; *b,* staminal column and anthers, × 10.

DESCRIPTION OF STAMINATE PLANT: Leaves 4–5 m long, 4.5 cm wide at the middle, 4.4 cm wide at the base, at midsection with 35–36 longitudinal parallel secondary veins on each side, near the base the margins with thorns 20–32 mm apart; those of the midrib below 16–25 mm apart; staminate inflorescence with flowering part about 25 cm long, the bracts apparently pale; lowest floral bract 33 cm long, 7.2 cm wide, lanceolate, the margins with subulate teeth less than 1 mm long; median bract 11 cm long, 2.8 cm broad, elliptic lanceolate; spikes 5 or more, 12–20 cm long, 15–17 mm in diameter, dense; staminate flowers very numerous, 9–11 mm long; column 5–5.5 mm long, bearing at the apex 10–11 whorled stamens, the free filament tips 1–2 mm long, rarely 2 of these partly connate; anther body 3–4 mm long, oblong, bearing an apical prolongation of the connective 0.9–1.1 long, subulate, pale.

HOLOTYPUS: Malaya, Pahang, Fraser's Hill, quite a common jungle pandan in forest on ridges and valleys or solitary crests, 4,000 ft. alt., 13 Aug. 1937, *E. J. H. Corner 33,196* (SING).

PARATYPI: Malaya, Pahang, Boh Plantation, Cameron Highlands, 4,000 ft. alt., 12 April 1937, *Md. Nur 32,632,* staminate (SING); Pahang, Fraser's Hill, 4,000 ft. alt., 7 Sept. 1923, *Md. Nur 11,256* (SING); Pahang, Gunong Tahan, 14 Sept. 1937, *E. J. H. Corner* (KEP).

DISCUSSION: *P. longicaudatus* is a member of the section *Rykia* and in that section is its closest relative, *P. bicornis,* a species of Perak in Malaya, one with the stems up to 2 m in height; leaves 1.2 m long; syncarp 7 cm in diameter, subglobose; drupes 3.4 cm long; styles 3 mm long; seed cavity cubical; and the endocarp central. *P. longicaudatus* has the stems 1–4 m tall; leaves 2.4–3.3 m long; syncarp 10.5 cm in diameter, elliptic-ovoid; drupes 4.1–4.4 cm long; styles 4–8 mm long; seed cavity ellipsoid; and the endocarp in the lower 2/5.

The new epithet is coined from the Latin *longus,* long; *caudatus,* tailed, in reference to the long, attenuate leaf apex.

Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean, VIII

Losses of Specimens in the Fire of the Hawaii Marine Laboratory[1]

ALBERT H. BANNER and DORA M. BANNER[2]

IN THE EVENING of 30 December 1961 a fire swept through the wooden main building of the Hawaii Marine Laboratory on Coconut Island, Kaneohe Bay, razing the building and its contents. In this building were stored the collections upon which this series of papers is based. The specimens being actively studied were kept in vials upon the shelves, while the types and the reference specimens were stored in vials either in glass jars or in sealed 1-gal tins. The fire was so intense that it melted the glass containers and burst the sealed tins. A few of the specimens stored in sealed cans were saved; all others were lost. An indication of the total number of species lost is given in Table 1. It would be almost impossible to estimate the number of specimens lost, for many of the species now represented by one or several burned and broken specimens were previously represented by dozens to hundreds of specimens.

TABLE 1

LOCATION	SPECIES PREVIOUSLY IN COLLECTION	SPECIES NOW REPRESENTED BY AT LEAST ONE SPECIMEN
Marianas Islands	49	12
Marshall and Caroline Islands	55	39
Canton and Johnston islands	39	6
Fiji	31	5
Tonga	31	3
Samoa	44	4
Cook Islands	41	5
Society Islands	30	11
Gulf of Thailand	55	0

More serious are the losses of the type specimens of species already described in published papers. The vials containing these were stored in glass jars on open shelves and all were totally destroyed. We had wished to assign these valuable specimens to the Bernice P. Bishop Museum, where they would be available to Pacific workers, but we were holding them in the laboratory pending the final decision of the Museum officials as to whether they would continue to use the Museum as a repository for marine collections. The specimens lost are listed in Table 2.

Attempts will be made to obtain specimens to establish as neotypes. We plan to obtain the two from the Hawaiian Islands. If the opportunity arises, others will be collected from their original type localities but it is unlikely that it will be possible for us to visit again most of the islands so widely scattered over the Pacific.

Also lost were parts of a number of manuscripts. The next one of this series, dealing with the alpheid fauna of Canton and other Phoenix and Line islands, fortunately is at the Bishop Museum awaiting publication. The study scheduled to follow that, on alpheids from the Fijian, Tongan, and Samoan archipelagoes, had been finished in final form the day before the fire and was lying on top of our desk. Nothing of it remains; however, portions of it might possibly be re-created from early notes that had been

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[1] Contribution No. 164 Hawaii Marine Laboratory. Manuscript received February 1, 1962.

[2] Department of Zoology and Entomology, University of Hawaii, Honolulu.

TABLE 2

SPECIES	REFERENCE	TYPE LOCALITY
Athanas dubius	Pacific Sci. 10(3):322–325, fig. 2	Saipan
Alpheopsis diabolus	Pacific Sci. 10(3):325–328, fig. 3	Saipan
A. tetrarthri	Pacific Sci. 10(3):328–329, fig. 4	Saipan
Synalpheus charon obscurus (subspecies only)	Pacific Sci. 10(3):329–331, fig. 5	Saipan
S. anceps	Pacific Sci. 10(3):334–337, fig. 8	Saipan
Alpheus collumianus probabilis (subspecies only)	Pacific Sci. 10(3):338, fig. 10	Saipan
A. collumianus medius (subspecies only)	Pacific Sci. 10(3):340, fig. 11	Saipan
A. collumianus inermis (subspecies only)	Pacific Sci. 10(3):342, fig. 12	Saipan
A. perplexus	Pacific Sci. 10(3):347–349, fig. 13	Saipan
A. chamorro	Pacific Sci. 10(3):349–351, fig. 14	Saipan
Alpheus sp. 2	Pacific Sci. 10(3):351–352, fig. 15	Saipan
A. cloudi	Pacific Sci. 10(3):352–354, fig. 16	Saipan
Alpheus sp. 3	Pacific Sci. 10(3):358–360, fig. 19	Saipan
A. ladronis	Pacific Sci. 10(3):360–362, fig. 20	Saipan
A. dolorus	Pacific Sci. 10(3):362–363, fig. 21	Saipan
Thunor sp	Pacific Sci. 10(3):367–371, fig. 23	Saipan
Alpheus arnoa	Pacific Sci. 11(2):199–200, fig. 5	Arno, Marshall Islands
Salmoneus tricristata	Pacific Sci. 13(2):131–133, fig. 1	Yap, Caroline Islands
Synalpheus tuthilli	Pacific Sci. 13(2):133–136, fig. 2	Yap, Caroline Islands
Alpheus lanceostylus	Pacific Sci. 13(2):136–138, fig. 3	Pearl and Hermes Reef, Hawaiian Arch.
A. malabaricus mackayi (subspecies only)	Pacific Sci. 13(2):149–151, fig. 12	Wailupe Fish Pond, Oahu, Hawaii
Athanas rhothionastes	Pacific Sci. 14(2):142–146, fig. 3	Canton Island, Phoenix Arch.
A. verrucosus	Pacific Sci. 14(2):147–149, fig. 4	Eniwetok, Marshall Islands
Metabetaeus lohena	Pacific Sci. 14(3):299–302, fig. 1	South Point, Island of Hawaii
Prionalpheus triarticulatus	Pacific Sci. 14(3):293–296, fig. 1	Korolevu, Fiji Islands
Prionalpheus sp	Pacific Sci. 14(3):296–298, fig. 2	Arue, Tahiti, Society Islands

filed away in a tightly packed drawer, the contents of which were burned only on the edges. The next two papers in the same drawer, both in draft form, one based on collections from the Cook and Society islands, the other based on collections from Eniwetok in the Marshalls, were saved, but unfortunately the plates and the specimens figured in the plates were lost. The most complete loss was a draft of a study dealing with the shrimps in the Gulf of Thailand and adjacent waters; for this study the entire manuscript, all figures (about 50 sets of drawings), and all specimens were lost. Also lost were all original field notes, giving the ecological conditions for each exact collecting area.

An attempt will be made to rebuild the study collections and to salvage information that may be available in the remaining drafts and notes.

This short report is offered in apology to the several individuals, institutions, and foundations that cooperated with us and supported us in our work. We particularly wish to express to the following institutions our regret for the loss of their specimens which they so helpfully loaned us: Raffles Museum, Singapore; Bernice P. Bishop Museum, Honolulu; Allan Hancock Foundation, Los Angeles; and the Smithsonian Institution, Washington, D. C. And we wish to offer our regrets that we cannot present studies as complete and as documented as we had

planned to the institutions and foundations that have supported our work financially: Bernice P. Bishop Museum and Yale University for the grant that permitted the collections to be made through Polynesia in 1954; the National Science Foundation, Division for Systematic Biology, for a series of grants[3] from 1955 to the present, which supported both the laboratory work and part of the expenses of the trip by Mrs. Banner to Thailand; the Fulbright Foundation and Chulalongkorn University, Bangkok, which permitted us to make our study of the shrimp of the Gulf of Thailand and adjacent waters. Our friends, who have helped us in the studies and who have sent their condolences, are too numerous to list here; these we will thank individually.

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[3] Grant nos. NSF-G-1754, 3863, 9937, 13,401.

NOTE

Myrtomera, A New Generic Name for *Spermolepis* Brongn. & Gris (Myrtaceae)

IN THE VAST REALM of generic names almost inevitably there occur many unwitting duplications, despite the various attempts at indices that have been made in the course of botanical history.

The present case concerns a genus of Myrtaceae which bears a name already preëmpted by a genus of Umbelliferae. New names are proposed as follows:

Myrtomera B. C. Stone, nom. nov.

Spermolepis Brongniart & Gris in Bull. Soc. Bot. France 10: 577. 1863; in Ann. Sci. Nat. V, 2: 136. 1864. Myrtaceae.

Not *Spermolepis* Rafinesque in Neogenyt. 2. 1825. Umbelliferae. Based on *Spermolepis divaricata* (Walt.) Raf.

1. ***Myrtomera gummifera*** (Brongn. & Gris) B. C. Stone, comb. nov. *Spermolepis gummifera* Brongn. & Gris l.c. Type.
   New Caledonia.
2. ***Myrtomera rubiginosa*** (Brongn. & Gris) B. C. Stone, comb. nov. *Spermolepis rubiginosa* Brongn. & Gris l.c.
   New Caledonia.

These two species are endemic to New Caledonia.

The generic name *Myrtomera* is coined *de novo,* from *Myrtus* and the suffix indicating "part," *meros.—Benjamin C. Stone, Department of Botany, U. S. National Museum, Smithsonian Institution, Washington 25, D. C.* *Manuscript received August 7, 1961.*

News Note

THE ART CENTER in La Jolla, California, has been selected as the site for a World Scientific Meeting on the Biology of Tuna and Related Species.

Scheduled for July 2–14, 1962, the meeting is sponsored by the Food and Agriculture Organization of the United Nations. It is being held in the United States at the invitation of the U. S. Government and with the cooperation of the State of California and Scripps Institution of Oceanography.

Southern California, center of the important U. S. tuna fishing industry, is a natural location for the meeting. Annual landings of tuna in this area are valued at more than $40 million at the dockside.

The world tuna catch in 1960, produced by fishermen of 50 nations, amounted to about 1½ billion pounds. By 1970 it is predicted that the world demand for tuna will be double this amount. Already the fleets of the major tuna fishing nations are ranging the world's oceans in search of these valuable fishes. If the maximum catch is to be achieved and sustained in the face of increasing fishing pressure, scientific estimates of this maximum sustainable harvest must be made as quickly as possible. The World Tuna Meeting will review the status of knowledge and recommend programs of research, development, and management.

The meeting has attracted wide attention among fishery scientists and tuna industry people. Wide attendance from the United States and foreign countries is expected.

Scientists desiring to attend should notify Dr. J. L. McHugh, U. S. Bureau of Commercial Fisheries, Washington 25, D. C., so that accreditation can be arranged. Hotel reservations are being handled by Mr. Gerald V. Howard, U. S. Bureau of Commercial Fisheries, P. O. Box 6121, Point Loma Station, San Diego 6, California.

Manuscript Form. Manuscripts should be typed on one side of standard-size, white bond paper and double-spaced throughout. Pages should be consecutively numbered in upper right-hand corner. Sheets should not be fastened together in any way, and should be mailed flat. Inserts should be either typed on separate sheets or pasted on proper page, and point of insertion should be clearly indicated.

Original copy and one carbon copy of manuscript should be submitted. The author should retain a carbon copy. Although due care will be taken, the editors cannot be responsible for loss of manuscripts.

Introduction and Summary. It is desirable to state the purpose and scope of the paper in an introductory paragraph and to give a summary of results at the end of the paper.

Dictionary Style. It is recommended that authors follow capitalization, spelling, compounding, abbreviations, etc., given in *Webster's New International Dictionary* (unabridged), second edition; or, if desired, the *Oxford Dictionary.* Abbreviations of titles of publications should, if possible, follow those given in *World List of Scientific Periodicals.*

Footnotes. Footnotes should be used sparingly and never for citing references (see later). When used, footnotes should be consecutively numbered by superior figures throughout the body of the paper. Footnotes should be typed in the body of the manuscript on a line immediately below the citation, and separated from the text by lines running across the page.

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BATZO, RODERICK L., and J. K. RIPKIN. 1849. A Treatise on Pacific Gastropods. Rice and Shipley, Boston. vii + 326 pp., 8 figs., 1 map.

CRAWFORD, DAVID L. 1920*a*. New or interesting Psyllidae of the Pacific Coast (Homop.). Proc. Hawaii. Ent. Soc. 4(1): 12–14.

——— 1920*b*. The sandalwoods of Hawaii. Proc. Hawaii. Ent. Soc. 4(2): 374–375, 13 pls.

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VOL. XVI JULY 1962 No. 3

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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Shore Organisms at Macquarie Island

RITA R. COLWELL and JOHN LISTON
Bacterial Flora of Fish Collected at Rongelap and Eniwetok

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Red-Water Blooms off Northern Chile

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HAROLD ST. JOHN
Revision of the Genus Pandanus
Part 12. Queensland Pandanus

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(Continued on inside back cover)

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Ecology of Rocky Shore Organisms at Macquarie Island

RON KENNY[1] and NOEL HAYSOM[2]

IN 1948 the Antarctic Division, Australian Department of External Affairs, established a research station at Macquarie Island. As part of the biological work a study of the rocky shore ecology of the island was made (by R. K. during 1948–49 and N. H. in 1949–50).

Although large general collections have been made at Macquarie and other subantarctic islands by various expeditions (notably the Australian Antarctic Expedition, 1911–13, and the British, Australian, and New Zealand Antarctic Expedition, 1929–31) comparable ecological programmes in southern latitudes have been few. Of the papers on similar topics from temperate southern latitudes those of Isaac (1937) on South Africa, Guiler (1952) on Tasmania, Knox (1953) and Batham (1958) on South Island of New Zealand, and Guiler (1959) on Chile are relevant to this study.

MACQUARIE ISLAND

Macquarie Island (54° 29′ S, 158° 58′ E) is situated midway between Tasmania and the Antarctic mainland. The island, with associated rock outcrops to the north and south, is the exposed cap of an extensive submarine ridge running in a general north-south direction. The nearest neighbouring islands are the Auckland Is. and Campbell I., some 400 miles to the northeast (Fig. 1) and separated from the Macquarie Ridge by depths of more than 2,000 fathoms.

The upper levels of this ridge are narrow, a sounding of 1,548 fathoms having been recorded 5 miles east of Macquarie I. (Mawson, 1943).

A complete account of the geography and geology of Macquarie can be found in Mawson (1943). The island, 21 miles long and up to 3 miles wide, is largely composed of volcanic rock. Most of the eastern coastline is formed of a series of sand and shingle beaches separated by rocky headlands or reefs (Figs. 2, 3, 4) but in many places steep cliffs descend almost vertically to the sea (Fig. 5). Much of the west coast has extensive flat reefs and gradually sloping beaches often strewn with large boulders.

The sites investigated in detail (Fig. 6) were all at the north end of the island and were selected to give a variety of habitats and exposures to wave action. General observations were made at other locations.

The climate is typically subantarctic. Meteorological details made available by the Commonwealth Meteorological Bureau, Melbourne, are given in Table 1. The air temperature range is small, the maximum recorded during the period of this survey being 10.7 C (Jan 1950) and the minimum –8.3 C (Aug 1950). Although the total rainfall is not excessive, precipitation—rain, hail, sleet, or snow—occurs almost daily. Strong winds, including gusts of more than 100 knots, are a striking feature of the climate and are predominantly (more than 70%) from the north and northwest. However, climatically the island is milder than other subantarctic islands of similar latitude and there is no permanent ice sheet.

Heavy seas occur at all seasons of the year, and the coastline would be considered an exposed one by any standard (Fig. 7).

Macquarie I. lies within the area of Antarctic surface waters during part of the year, at least. The R.R.S. "Discovery II" plotted the Antarctic convergence in latitudes 53° and 54° S in this region during the winter months of 1932 (Mackintosh, 1946). In the 1948–50 period the monthly mean sea temperatures ranged from 7.2 C (Jan) to 2.8 C (July). Surface salinities to the west and east of the island were recorded by R.R.S. "Discovery II" during the 1932 winter and varied from 33.8‰ to 34.4‰ (Deacon, 1937).

A tide gauge was set up in Buckles Bay (see Fig. 6) but was wrecked by storms after a short

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[1] Zoology Department, University of Queensland, Brisbane, Australia. Manuscript received June 1, 1961.

[2] Fisheries Section, Department of Harbours and Marine, Brisbane, Australia.

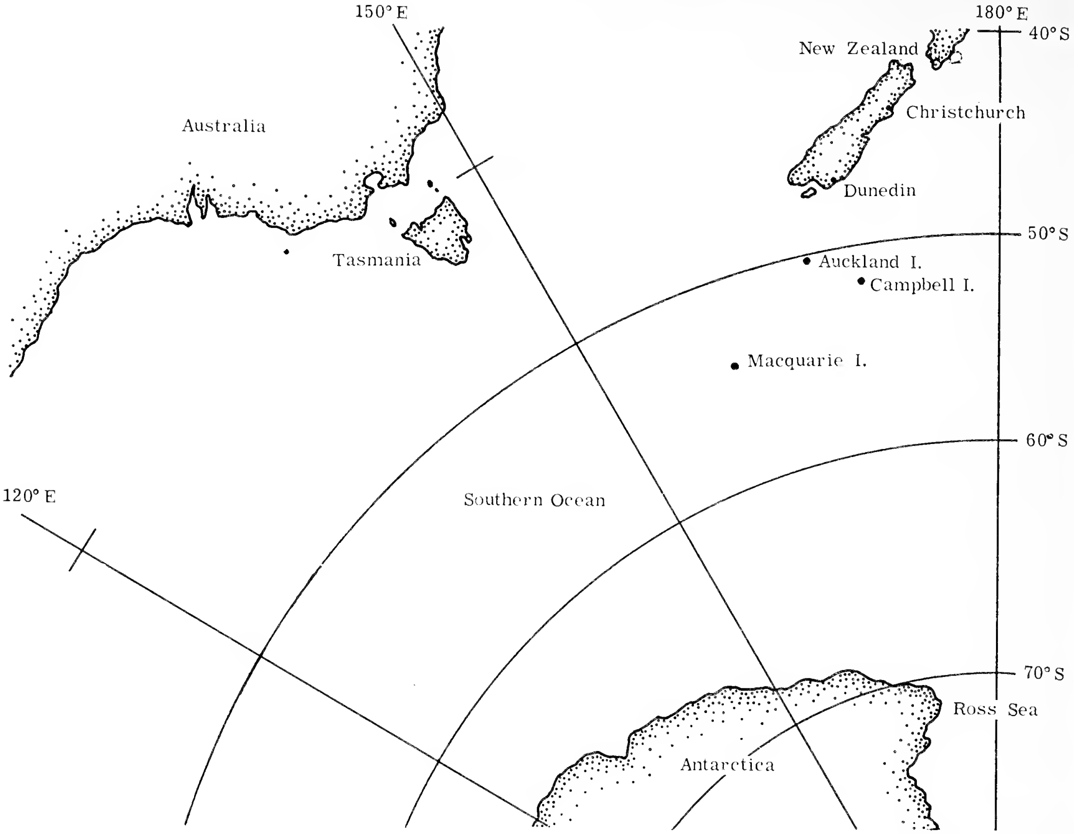

FIG. 1. Macquarie Island and its relationship to surrounding land masses.

period of operation. From the records available the spring range is 4 feet 6 inches and the neap range a little more than 2 feet.

General Features of Zonation

Six zones can be recognized on the rocky shore extending from above high-water springs to below low-water springs. The zones have been described in terms of "effective tidal heights" by Endean, Kenny, and Stephenson (1956) and other authors. These effective tidal heights are based on the correlation of data from the tide gauge at station 2 (see Fig. 6) and from general observations at this and other stations.

The sequence of dominant organisms forming the zonation pattern is:

(i) LICHEN ZONE: Extending from the area dominated by maritime terrestrial flora (Taylor, 1955), down the beach into the region of splash. The common organisms are lichens interspersed with some mosses.

(ii) *Porphyra* ZONE: *Porphyra umbilicalis* dominant from HWS[3] to below HWN.

(iii) "BARE" ZONE: Extending from just below HWN to approximately MSL in which the most obvious species was *Siphonaria lateralis.*

---

[3] In this paper the following abbreviations have been used:

high water spring tide, HWS
high water neap tide, HWN
mean sea level, MSL
low water neap tide, LWN
low water spring tide, LWS

TABLE 1

METEOROLOGICAL DATA FOR MACQUARIE I., 1948–50

	1948 Apr.–Dec.	1949	1950
Air temp. °C			
maximum	8.75	9.65	10.7
minimum	−3.65	−5.9	−8.3
mean	–	4.25	4.35
Total precip. (inches)	–	37.06	42.55
No. of days precip.	–	336	333
Mean wind vel. (knots)	–	18.2	19.3

(iv) UPPER RED ZONE: In which *Rhodymenia* sp. is dominant from MSL to LWN.

(v) KELP ZONE: *Durvillea antarctica* stipes cover almost the whole area of rock between LWN and LWS, overlying a layer of encrusting red coralline algae.

(vi) LOWER RED ZONE: The red corallines extend below LWS and support a variety of red algae (*Dellesseria* spp., and *Iridea* sp.) and brown algae (*Desmarestia* sp.).

The most striking features of this zonation pattern are the absence of an upper "littorinid" and a "barnacle" zone, and the plant domination of the shore. In five of the zones the obvious and dominant organisms are botanical, and although animals are common they are, generally, small and secondary to the algae and lichens in biomass. It is only in the "bare" zone, where *Siphonaria lateralis* is the commonest organism, that there is a faunal dominant.

Details of Particular Zones

LICHEN ZONE: This area is characterised by several species of lichen, the most obvious being *Verrucaria* sp. and an unidentified bright yellow form, and the red alga, *Hildenbrantia* sp.

Many plants, common in the terrestrial maritime association (Taylor, 1955) extend seawards into this zone in varying densities. The moss *Muelleriella crassifolia,* and the grass *Puccinellia macquariensis,* are more noticeable in relatively exposed locations. The vascular plants *Colobanthus muscoides* and *Cotula plumosa,* and the moss *Ceratodon purpureus* occur commonly in more sheltered areas. Isolated plants of tussock grass, *Poa foliosa,* are scattered through the upper section of this zone.

The faunal element of this zone is restricted to small species of cryptic habit living among the plants. The variable densities of these species at different localities appear to be controlled by the amount of detritus, forming a suitable habitat, in the rock crevices and around the plants.

The most frequently recorded animals are the mite *Halozates* sp., the beetles *Antarctotachinus crozetensis* and *Antarctophytosus macquariensis,* larvae of dipterans, *Coleopa macquariensis* and others, and various collembolans.

Porphyra ZONE: *Porphyra umbilicalis* forms a thick mat, the upper limit of which is reached by the sea only at high water of spring tides. In calm weather the dry weed forms a conspicuous band around the island's coastline.

The upper part of the zone is formed frequently of an association in which as well as the dominant *Porphyra* there are many plants of *Rhizoclonium* sp. and *Iridea boryana* and, less commonly, *Prasiola* sp. In some situations *Acrosiphonia pacifica* is found in patches, and this alga and *Chaetangium fastigium* are common in the lower part of the *Porphyra* complex.

Where pools or similar suitable habitats are available *Ulva lactuca, Enteromorpha intestinalis,* and *Cladophora* sp. extend throughout the *Porphyra* mat.

The animal species common at this level are those noted in the lichen zone, with fewer Collembola, and the addition of the oligochaetes *Lumbricillus macquariensis* and *Marionina antipodum.* The gastropod *Macquariella hamiltoni* has been observed in the *Porphyra* zone but typically is found at lower levels of the beach.

"BARE" ZONE: Considerable variation in the horizontal and vertical extent of this zone was observed (see below) and at some stations the "bare" zone was not noted. However, when well developed, it is marked by the close-cropped nature of the algal constituents, the common forms being *Chaetangium fastigium* and *Acrosiphonia pacifica.*

The dominant organism is *Siphonaria lateralis* which, though common throughout this level of the beach, appears to favour dissected and creviced rock surfaces. The species attains its maximum density at the lower limit of this zone (approximately MSL) and in suitable locations numbers up to 1,500 individuals per square metre.

Other common animals include *Macquariella hamiltoni,* the limpet, *Nacella delesserti, Lumbricillus macquariensis, Marionina antipodum,* numerous amphipods, *Hyale novae-zealandiae* being the most frequently recorded, and many small nematodes.

Some specimens of *Halozates* sp. and *Coleopa macquariensis* range down to this level but they are essentially fauna of the upper zones. Similarly a few nemerteans and turbellarians have been recorded from the "bare" zone but they are more common below MSL.

UPPER RED ZONE: This is a narrow zone in which the red alga *Rhodomenia* sp. is the dominant organism. In general, the boundaries of the zone are sharply defined. On certain reefs, however, the lower limit was ill marked and many plants of the dominant alga were observed among the stipes of the kelp and extending below LWS. The dense growth of *Rhodomenia* forms a thick covering, protecting a wide range of small animals.

The fauna shows elements from the higher zones and also many species which are usually found at lower levels.

Hyale novae-zealandiae is, numerically, the dominant animal and *Siphonaria lateralis, Nacella delesserti,* and *Macquariella hamiltoni* are the common secondary animals. *Lumbricillus macquariensis* and *Marionina antipodum* were recorded in small numbers.

Other animals noted are representatives of the fauna of lower tidal levels and are not as common as those mentioned in the preceding paragraph. They include the lamellibranchs *Kidderia pusilla* and *Gaimardia trapesina,* the

FIG. 2. View from Wireless Hill looking south along the isthmus with Hasselborough Bay on the right. Station 4 in the right middle distance. (Australian Department of Information photo.)

FIG. 3. Garden Cove, at low water. Traverses A and B (Fig. 9) were on rock faces in right middle distance.

gastropod *Laevilittorina caliginosa,* the isopod *Exosphaeroma gigas,* and small numbers of the polychaetes, *Boccardia polybranchia, Cirratulus cirratus, Platynereis magalhaensis,* and *Spirorbis aggregatus.* Small colonies of the bryozoan *Barentsia aggregata* are present.

KELP ZONE: In this zone the rock surfaces are dominated by the massive stipes of *Durvillea antarctica* (Fig. 8), many of the plants having holdfasts 40 cm in diameter. Among the *Durvillea* stipes the rock is covered by a layer of encrusting red coralline, alga, the upper limit of which is usually a little below that of the kelp. In the few situations (usually protected from wave action) where the kelp is poorly developed the coralline alga is the dominant organism.

The laminae of *Durvillea* are singularly devoid of life. However, the goose barnacle, *Lepas australis,* was recorded from pieces of kelp found on the beach after gales.

The recesses of the holdfasts support a dense and varied population which is listed in Table 2.

In contrast there is a marked paucity of species associated with the encrusting coralline where the kelp is absent. Small groups of *Spirorbis aggregata* and a few specimens of the echinoderms *Pseudopsolus macquariensis* and *Stichaster suteri* were noted.

LOWER RED ZONE: Below the *Durvillea* zone in the truly infralittoral is a community comprised of several species of red algae: *Ballia callitricha, Ceramium rubrum, Delessaria* sp., *Iridea* sp., *Plocamium coccineum,* and *Schizoseris* sp. The brown alga *Desmarestia rossi* is common and (as mentioned above) *Rhodymenia* frequently extends below the kelp zone. The coralline covering the rocks continues below LWS except in certain silted areas.

The fauna of this zone is a large and varied one with some animals dependent on a particular type of habitat and others distributed widely. In Table 3 the common species are listed with their representative habitats.

Comparison of Traverses

As would be expected, the vertical dimension of each of the dominant zones is influenced by the combined effects of the slope of the rock surface and the exposure to wave action.

Comparable measurements were made at particular localities and the zonation picture for each is shown in Figure 9.

> Garden Cove, traverse A; slope 80°, on the north shore of the cove, near the entrance to the cove and exposed to all weather from the east or southeast (Figs. 3, 10).
>
> Garden Cove, traverse B; slope 60°, on the north shore of the cove, partially protected from surf but covered by the wash from swell.
>
> Fish Trap, vertical; facing southeast, partially protected by offshore rocks and kelp (Fig. 5).

The obvious differences at these three localities are:

1) On traverse B the extension upwards of the zones above MSL, their greater width and greater density. The raising of effective tidal heights at the upper levels of sloping shores has been discussed by Endean, Kenny, and Stephenson (1956).

2) The wider "bare" zone and its sparser flora and fauna on the vertical slope.

3) The deeper extension, below LWS, of the kelp on traverse A due, presumably, to the heavier surf in this area.

The species composition was essentially the same in each case and only minor variations in density were noted. *Chaetangium fastigiatum* was less dense at A than at B and absent on the vertical face. *Rhodymenia* sp. was observed on the exposed rock face at A but not at either of the other localities.

Two "flat" reefs were surveyed in detail, station 1 in Buckles Bay being considered as typical of this type of rock formation, and a gently sloping platform near the fishtrap (Fig. 11) as a contrast to the nearby vertical face (see above).

Station 1 was reasonably protected by offshore rocks and a wide belt of *Durvillea.* The true tidal levels given in Figure 11 are those recorded from the tide gauge (which was installed on this reef) during its functional period in 1950. Although spread horizontally and modified by the intrusion of pools and gutters the vertical range of the major zones is comparable with that of the steeper reefs (Fig. 9).

The more protected and gently sloping (10°) reef near the fishtrap showed a simplified version of the typical zonation pattern with only the dominant organisms present in any density, and an expanded "bare" zone (Figs. 9, 11), which supported more gastropods, *Macquariella hamiltoni,* than usual as well as the typical *Siphonaria lateralis.*

The gullies crossing this reef were awash and many small *Durvillea* plants grew there.

The *Porphyra* and *Rhizoclonium* zone was protected from all but the heaviest weather and normally was dampened by fine spray only.

Station 2 (Fig. 9) was a vertical rock face on the shoreward side of a reef near station 1 and

TABLE 2

FAUNA OF *Durvillea* HOLDFASTS
(Arranged alphabetically)

VERY COMMON	COMMON	PRESENT
		Aphroceros sp.
Hyale novae-zealandiae	*Barentsia aggregata*	*Exosphaeroma gigas*
	Laevilittorina caliginosa	*Hyale hirtipalma*
	Macquariella hamiltoni	*Ias pubescens*
	Nemertopsella marri	*Jassa falcata*
	Spirorbis aggregata	*Munna maculata*
		Paramoera schellenbergi
		Procerodes ohlini
		Pseudopsolus macquariensis

FIG. 4. Buckles Bay with Station 1 reef in the middle distance.

sheltered from surf but washed by spent waves. The main variation from the typical pattern was the obliteration of the "bare" zone by the overlapping of the *Porphyra* and Red belts.

Role of Kelp

The large brown algae are the most conspicuous feature of the Macquarie I. marine flora. Extensive beds of *Macrocystis pyrifera* occur offshore in several fathoms of water, and the island is fringed by *Durvillea antarctica* attached to reef edges and offshore rocks (Figs. 8, 12).

Macrocystis, growing in deeper water, escapes much of the force of wave action and is characterised by a more slender and longer form than *Durvillea.* The only conspicuous organisms on the fronds of *Macrocystis* were extensive colonies of the hydroid *Orthopyxis platycarpa,* but the tangled holdfasts showed evidence of a rich infralittoral fauna. The fauna of *Durvillea* holdfasts has been listed above (Table 2).

Durvillea antarctica plays an important part in protecting the reefs from the full force of the surf, the floating fronds damping the breaking of the swell. However, during storms the laminae of the kelp are whipped against the rock surfaces and at some localities this appears to be a factor contributing to the sparseness of the "bare" zone fauna.

Rock Pools

Many rock pools were examined and in general revealed a group of organisms similar to that of the surrounding rocks, with the addition of species from lower tidal levels.

The pools maintained by splash or the high seas of storms present a habitat of extreme conditions. During the winter months they freeze on some occasions. At any time of the year the decomposition of broken kelp, hurled onto the reefs by storms, must cause considerable variation in chemical composition of the pools. During the summer period they are fouled by elephant seals, *Mirounga leonina.*

A pool, 5 m wide and 25 cm deep at approximately HWS near station 1, was examined on several occasions. At the end of the 1948–49 summer (17.ii.49) there was present a rich population including *Ulva, Enteromorpha, Rhodymenia,* small patches of encrusting red coralline alga, *Macquariella hamiltoni, Siphonaria lateralis, Exosphaeroma gigas, Hyale novaezealandiae, Marionina antipodum,* turbellarians, and copepods.

The same pool at the end of the 1949–50 summer (9.iii.50) was full of rotting kelp and sea elephant faeces with no trace of the former population.

Biotic Factors

As mentioned above, the movement of the kelp fronds is a probable factor in delineating the "bare" zone, but grazing of this area by molluscs, especially *Siphonaria,* could also contribute.

Predators may play an important part in limiting the population density of some species.

The introduced, flightless "woodhen," *Gallirallus australis,* and the Dominican gull, *Larus dominicanus,* forage in the upper algal zones for food. Examination of stomach contents of Dominican gulls shows that the gastropod *Cantharidus coruscans* forms a major part of the diet of these birds. The denser populations of these molluscs occurred where there was a heavy algal cover, presumably protecting them.

Stomach contents of the kelp-inhabiting fish *Notothenia macrocephala* included a wide variety of crustacean and polychaete fragments.

DISCUSSION

In contrast to Australian coastlines the Macquarie I. rocky shore is dominated by algae;

TABLE 3

FAUNA OF THE LOWER RED ZONE*

ORGANISM	HABITAT	ABUN-DANCE	ORGANISM	HABITAT	ABUN-DANCE
Aphroceras sp.	A,B	4	*Munna maculata*	E	2
Myriothela meridiana	B	4	*Tanais litoralis*	E	2
Halianthella kerguelensis	C	3	*Hyale novae-zealandiae*	B,C,D,E	2
Parantheopsis cruentata	C	3	*Jassa falcata*	B,C,D,E	2
Procerodes ohlini	D,E	3	*Paramoera schellenbergi*	B,C,D,E	2
Nemertopsella marri	B,D	4	*Halicarcinus planatus*	B	4
Lineus scotti	B,D	4	*Pycnogonum platylophum*	D	4
Nematoda (unidentified)	C	2	*Tanystylum neorhetum*	D	4
Arenicola assimilis	D	4	*Tanystylum styligerum*	D	4
Boccardia polybranchia	C	3	*Cantharidus coruscans*	A,B	3
Cirratulus cirratus	C	3	*Laevilittorina caliginosa*	A,D,E	2
Fabricia alata	C	3	*Macquariella hamiltoni*	A,D,E	2
Nereis kerguelensis	C	3	*Nacella delesserti*	A,B	3
Platynereis magalhaensis	C,D	2	*Gaimardia trapesina*	E	2
Spirorbis aggregatus	A,B	3	*Kidderia pusilla*	C	2
Marionina werthi	C	3	*Barentsia aggregata*	B	4
Copepoda (unidentified)	C,D,E	2	*Stichaster suteri*	A,B	4
Cassidinopsis emarginata	E	2	*Pseudopsolus macquariensis*	A,B,C	2
Exosphaeroma gigas	D,E	1	*Molgula novae-zealandiae*	C	2
Ias pubescens	D,E	3			

* Letter symbols refer to type of habitat; numerical symbols to relative density of species; organisms are listed alphabetically within taxonomic groups.

A, upper surface of rocks
B, crevices
C, sand and mud
D, under embedded stones
E, algal fronds

1, very common
2, common
3, present
4, occasional specimens

FIG. 5. Fish trap station, showing dense masses of *Durvillea.*

Porphyra, Durvillea, and various red algae being the most obvious organisms. The greater role played by the algal elements of the biota in higher southern latitudes has been noted by other writers, like Bennett and Pope (1952), Guiler (1960), and Knox (1960). The observations in this report suggest that Macquarie approaches the extreme condition of this latitudinal progression in the Australian sector of the Southern Ocean. Other islands in comparable southern latitudes, Kerguelen I. and Heard I., show a similar algal predominance (personal observation, R. K.).

Stephenson and Stephenson (1949) have suggested that a "littorinid-balanoid-laminarian" zonation is of almost universal occurrence on cool temperate exposed rocky shores although the species present may vary. The kelp zone at Macquarie can be considered as the "laminaria" of the typical plan. Nothing equivalent to the "littorinid" or "balanoid" zones was observed. With the absence of these zones and the climatic conditions of frequent storms, high winds, and large spray areas, it is difficult to correlate the Macquarie pattern with the generalised plan of either Stephenson and Stephenson (1949) or Womersley and Edmonds (1952).

Doty (1957), in his review, comments on the intermingling of the terrestrial and truly littoral flora in areas of heavy spray, and equates the laminarian and Delesseriaceae zone of the North Pacific with the infralittoral zone of Stephenson and Stephenson (1949). A similar situation prevails at Macquarie I.

A littorinid and a balanoid zone are recorded from Tasmania (Guiler, 1952) and southern New Zealand (Batham, 1960), although in the former area the barnacles were considered to be of reduced importance, compared with lower latitudes. Powell (1955) reports littorinids from Auckland I.

Mussels, common on coasts of southern Australia (Bennett and Pope, 1952), New Zealand (Batham, 1960), and Chile (Guiler, 1959), and recorded by Powell (1955) at Auckland I., were not collected in this survey.

The tube worm, *Spirorbis aggregatus,* occurs in patches and cannot be considered ecologically equivalent to the zones of tube-building polychaetes in warmer latitudes (Dakin, Bennett, and Pope, 1948; Bennett and Pope, 1952). In New Zealand the tube-building polychaete, *Pomatoceras coeruleus,* is less common in the south, near Dunedin (Batham, 1956), than near Christchurch (Knox, 1953).

The *Pyura* zone, so prominent on Australian shores (Dakin, Bennett, and Pope, 1948), New Zealand (Batham, 1956), and South American shores (Guiler, 1959) is not represented at Macquarie, although small ascidian (*Molgula*) communities were noted at the lower levels of the shore.

On the Pacific coast of South America species of *Siphonaria, Nacella,* and *Lessonia* are important organisms (Guiler, 1959) and these genera are represented in the collections from Macquarie.

Of southern hemisphere localities at which comparable investigations have been made, the west coast of South Africa (Isaac, 1937) shows a general format similar to Macquarie I. There, the shore is alga-dominated and shows zones

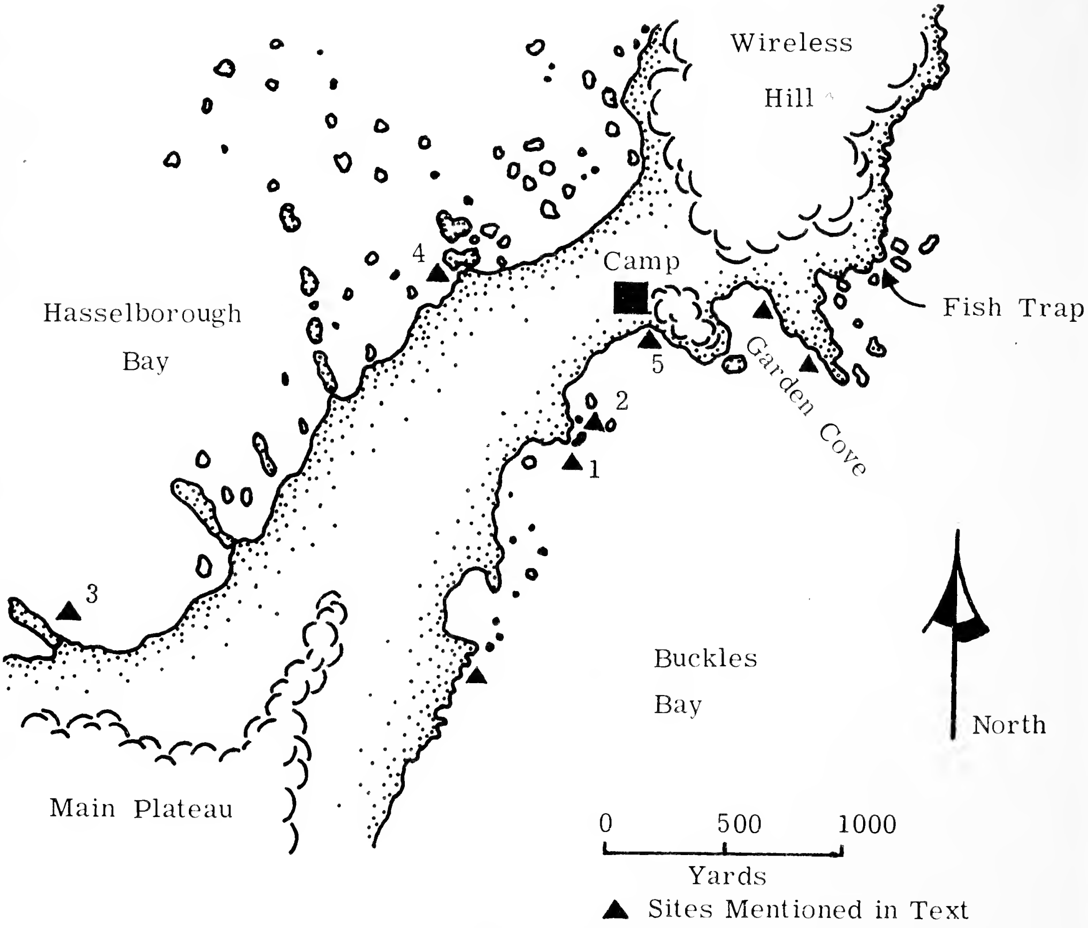

FIG. 6. Isthmus area, Macquarie Island, showing localities mentioned in text.

FIG. 7. Surf conditions at Station 1 during heavy weather.

of *Porphyra, Chaetangium,* a "bare" area with limpets, *Iridaea,* a *Champia*-Corallinaceae complex, and an *Ecklonia-Laminaria-Macrocystis* belt. This coast is affected by the Benguela current and, although in latitude 31° S, is essentially a cold water environment.

In the northern hemisphere there have been many reports of rocky shore zonation in latitudes similar to Macquarie I. For example, Kitching (1935) noted the typical littorinid-balanoid-laminaria pattern on the coast of Argyll, in latitude 56° N, but this area is not isolated by a sea barrier (Crisp and Southward, 1953) and apparently is subjected to less rigorous climatic conditions.

Madsen (1936), discussing the shore fauna of East Greenland, recorded no barnacles or molluscs, presumably due to the short duration of ice-free conditions. He considered that the northern limit of *Balanus balanoides* and littoral molluscs formed the zoological boundary of the Arctic. If the Macquarie fauna is examined on a similar basis, the absence of barnacles and the concentration of molluscs at the lower tidal levels suggest that this locality is near the zoological limit of the Antarctic, with respect to the littoral fauna.

This suggestion is borne out by the seasonal movements of the Antarctic Convergence from north to south of the island and the recorded inshore sea temperatures (see above). Vaughan (1940) delineates the "subpolar" water mass as varying from 5 to 10 C, which is a higher range than that recorded at Macquarie I.

However, Southward (1958) remarks that the differences between the Antarctic and Subantarctic littoral fauna result from varying degrees of tolerance of cold and ice action rather than from particular differences in the species composition of the zonation plan.

Table 4 lists 58 species of plants and animals collected in this survey for which definite distribution records have been traced. Of this number, 8 species appear to be endemic to Macquarie, 14 have been noted in the New Zealand area, 12 have been recorded from Kerguelen, 18 have wide Subantarctic distribution, and 6 have been recorded from Antarctica. It is possible that species listed from the Kerguelen and Magellan areas may in fact have a wider Subantarctic distribution and further collections may increase the listing of Antarctic littoral forms.

From these collections it would appear that the littoral biota of Macquarie I. is of a generalised Subantarctic type (*Adenocystis, Durvillea,*

TABLE 4

BIOGEOGRAPHIC DISTRIBUTION OF SOME RECORDED SPECIES

SPECIES	ENDEMIC	N.Z. SUBANTARCTIC REG.	KERGUELEN REG.	MAGELLAN-FALKLAND-STH. GEORGIA REG.	CIRCUMPOLAR SUBANTARCTIC	ANTARCTIC MAINLAND
Enteromorpha intestinalis					×	
Adenocystis utricularis					×	
Desmarestia willi					×	
Durvillea antarctica					×	
Lessonia variegata					×	
Macrocystis pyrifera					×	
Ploccameum coccineum						×
Halcampoides kerguelensis			×			
Procerodes ohlini			×			
Lineus scotti		×				
Barentsia aggregata			×			
Hemiarthrum hamiltonorum	×					
H. setulosum					×	×
Plaxiphora aurea					×	
Terenochiton fairchildi	×					
Cantharidus coruscans		×				
Laevilittorina caliginosa				×		
Macquariella hamiltoni		×				
Margarella macquariensis		×				
Nacella delesserti			×			
Siphonaria lateralis					×	
Gaimardia smithi		×				
G. trapesina					×	
Kidderia macquariensis	×					
K. pusilla		×				
Tawera mawsoni	×					
Arenicola assimilis		×		×		
Cirratulus cirratus					×	
Nereis kerguelensis					×	
Notomastus latericeus				×		×
Platynereis magalhaensis				×		
Polycirrus kerguelensis			×	×		×
Potamilla antarctica						×
Scolelepsis cornifera			×			
Lumbricillus macquariensis		×				
Marionina antipodum		×				
M. werthi			×			
Exosphaeroma calcareous				×		
E. gigas					×	
Ias pubescens			×			
Janira neglecta		×				
Tanais litoralis			×			
Acontiostoma marionis					×	
Hyale hirtipalma					×	
H. novae-zealandiae		×				
Jassa falcata					×	
Nannonyx kidderi		×				
Parajassa tristanensis				×		
Paramoera macquariae			×			
P. schellenbergi			×			
Pycnogonum platylophum				×		
Tanystylum styligerum			×	×		
Asterina hamiltoni	×					
Sporasterias directa	×					
S. mawsoni	×					
S. sphoerulata	×					
Stichaster suteri		×				
Pseudopsolus macquariensis		×				
Harpagifer bispinis					×	
Notothenia macrocephala					×	

FIG. 8. *Durvillea* zone, at low water.

Exosphaeroma, Jassa, Lessonia, Macrocystis, Notothenia, Siphonaria, etc.). There is a definite relationship between Macquarie I. and the Kerguelen region, nearly 20% of the species listed being present in these two localities. This similarity has been noted previously, by Dell (1952) discussing the fauna in general and by Powell (1951) with reference to the molluscs.

The affinities with the New Zealand area (see also Chilton, 1909) are equally strong; and Powell (1955) lists *Cantharidus coruscans* and *Margarella macquariensis,* both previously considered endemic to Macquarie I., from the Auckland Is.

The endemic species (15% of those listed) are molluscs and echinoderms. Ekman (1953) has commented on the endemic nature of the echinoderm fauna, and to a lesser extent the molluscan fauna, and uses this distribution to suggest that Macquarie I., occupies a position quite distinct from the New Zealand Subantarctic islands.

With one exception, *Ploccameum coccineum,* the species reported from Antarctica are also known from Subantarctic localities other than Macquarie I.

Species Recorded

The species collected in this survey are listed below. In some groups the list is incomplete due to identification problems. Many species previously recorded from Macquarie I. were not represented in these collections.

Chlorophyceae
  Cladophora spp.
  Enteromorpha bulbosa (Suhr) Kuetz
  Enteromorpha intestinalis (L)
  Monostroma sp.
  Prasiola sp.
  Rhizoclonium sp.
  Ulva lactuca (L)
Phaeophyceae
  Adenocystis utricularis (Bory) Skottsberg

- *Chordaria dictyosiphon* (Harvey) Kuetz
- *Desmarestia willi* Riensch
- *Durvillea antarctica* (Chamisso) Hariot.
- *Ectocarpus confervoides* (Roth) Le Jolis
- *Geminocarpus geminatus* (Hooker and Harvey) Skottsberg
- *Lessonia variegata* Agardh
- *Macrocystis pyrifera* (L) Agardh
- *Scytosiphon lomentaria* (Lyngbye) Agardh

Rhodophyceae
- *Acrosiphonia pacifica* Kütz
- *Ballia callitricha* (Agardh) Montagne
- *Bostrychia vaga* Hooker and Harvey
- *Ceramium rubrum* (Hudson) Agardh
- *Chaetangium fastigium* (Bory) Agardh
- *Corallina officinalis* (L)
- *Delessaria* spp.
- *Hildenbrantia* sp.
- *Iridea oborata* (Kütz) Setchell and Gardner
- *Melobesia* sp.
- *Porphyra columbina* Montagne
- *P. umbilicalis* (L) Agardh
- *Plocamium coccineum* Lyngbye
- *Polysiphonia anisogona* Hooker and Harvey
- *Rhodymenia* spp.
- *Schizoseris* sp.

Lichens
- *Verrucaria* sp.

Mosses
- *Ceratodon purpureus* (Hedwig)
- *Muelleriella crassifolia* (Hooker)

Angiosperms
- *Colobanthus muscoides* Hooker
- *Cotula plumosa* Hooker
- *Poa foliosa* Hooker
- *Puccinellia macquariensis* (Cheeseman)

Porifera
- *Aphroceras* sp.

Coelenterata
- Hydroidea
  - *Myriothela meridiana* Briggs
  - *Orthopyxis platycarpa* Bale
- Actiniaria
  - *Halcampoides kerguelensis* Kwietniewski
  - *Parantheopsis cruentata* Couth

Platyhelminthes
- *Procerodes ohlini* (Bergendal)

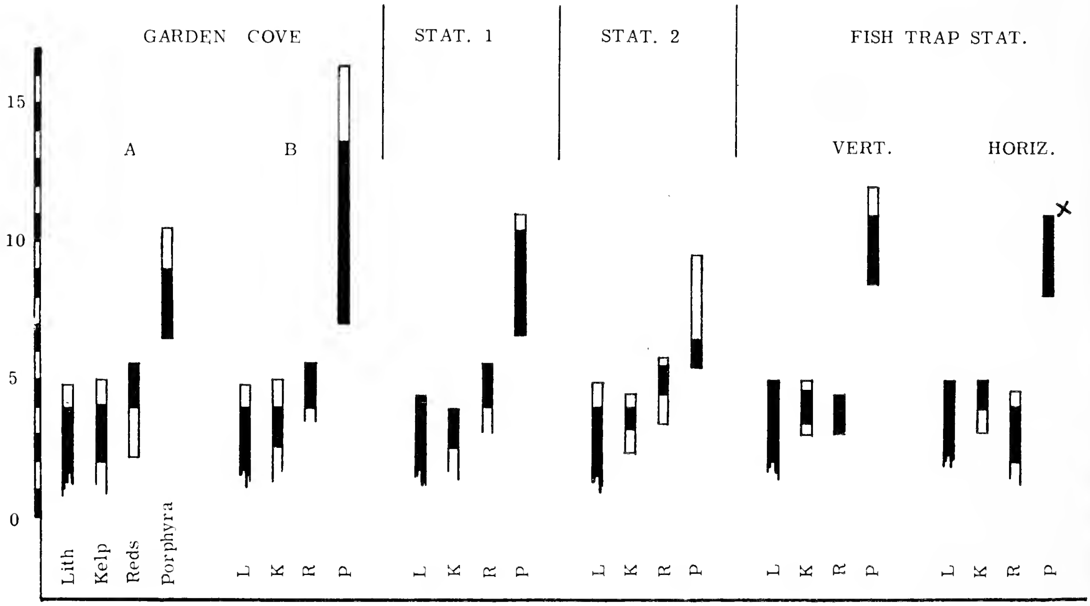

FIG. 9. Comparison of zonation at various localities:
x—see Fig. 11
solid bar—dense growth
open bar—sparse growth

FIG. 10. Garden Cove, at low water. Main traverse area showing *Durvillea,* "bare" zone, and *Porphyra.*

- Nemertea
  - *Nemertopsella marri* Wheeler
  - *Lineus scotti* Baylis
- Bryozoa
  - *Barentsia aggregata* Johnston and Angel
- Mollusca
  - Amphineura
    - *Hemiarthrum hamiltonorum* Iredale and Hull
    - *H. setulosum* Dall
    - *Plaxiphora aurea* Spalowsky
    - *Terenochiton fairchildi* Iredale and Hull
  - Gastropoda
    - *Cantharidus coruscans* (Hedley)
    - *Laevilittorina caliginosa* Gould
    - *Macquariella hamiltoni* (Smith)
    - *Margarella macquariensis* Hedley
    - *Nacella delesserti* Phillipi
    - *Siphonaria lateralis* Gould
  - Lamellibranchiata
    - *Gaimardia smithi* Suter
    - *G. trapesina* Lamark
    - *Kidderia macquariensis* Hedley
    - *K. pusilla* Gould
    - *Tawera mawsoni* Hedley
- Annelida
  - Polychaeta
    - *Arenicola assimilis affinis* Ashworth
    - *Boccardia polybranchia* (Haswell)
    - *Cirratulus cirratus* (Muller)
    - *Exogene* sp.
    - *Fabricia alata* Ehlers
    - *Lumbrinereis cingulata* (Ehlers)
    - *Nereis kerguelensis* McIntosh
    - *Notomastus latericeus* Sars
    - *Platynereis magalhaensis* Kinberg
    - *Polycirrus kerguelensis* (McIntosh)
    - *Potamilla antarctica* (Kinberg)
    - *Scolelepsis cornifera* Ehlers
    - *Spirorbis aggregatus* Caullery and Mesnil
    - *Syllis* sp.
    - *Thelepus plagiostoma* (Schmarda)
    - *Typosyllis* sp.

- Oligochaeta
  - *Lumbricillus macquariensis* Benham
  - *Marionina antipodum* Benham
  - *M. werthi* Michaelsen
- Arthropoda
  - Cirripedia
    - *Lepas australis* Darwin
  - Isopoda
    - *Cassidinopsis emarginata* (Guerin)
    - *Exosphaeroma calcareous* (Dana)
    - *E. gigas* (Leach)
    - *Ias pubescens* (Dana)
    - *Janira neglecta* Chilton
    - *Limnoria antarctica* Pfeffer
    - *Munna maculata* Beddard
    - *Tanais litoralis* Vanhoffen
  - Amphipoda
    - *Acontiostoma marionis* Stebbing
    - *Hyale hirtipalma* (Dana)
    - *H. novae-zealandiae* (Thomson)
    - *Jassa falcata* (Montagne)
    - *Nannonyx kidderi* (Thomson)
    - *Parajassa tristanensis* (Stebbing)
    - *Paramoera macquariae* Nicholls
    - *P. schellenbergi* Nicholls
  - Brachyura
    - *Halicarcinus planatus* (Fabricius)
  - Pycnogonida
    - *Pycnogonum platylophum* Loman
    - *Tanystylum neorhetum* Marcus
    - *T. styligerum* Miers

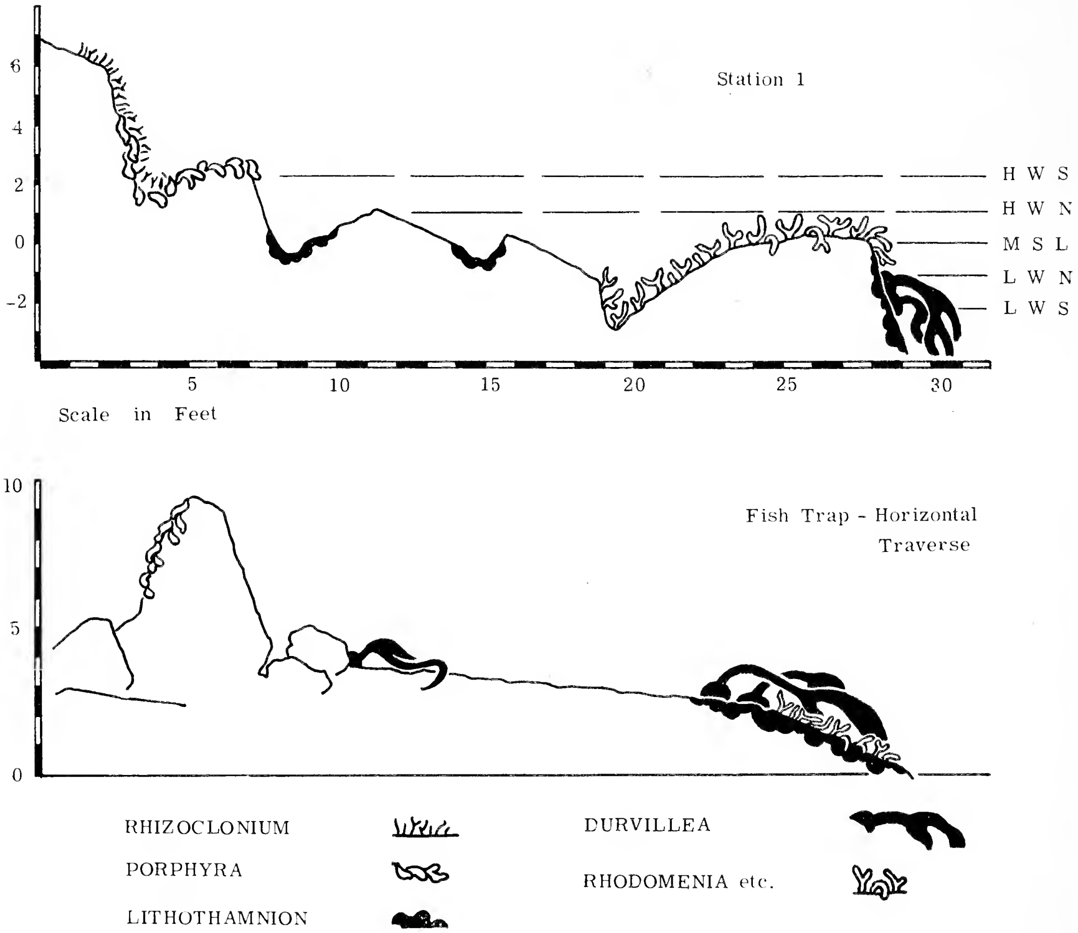

FIG. 11. Horizontal zonation.

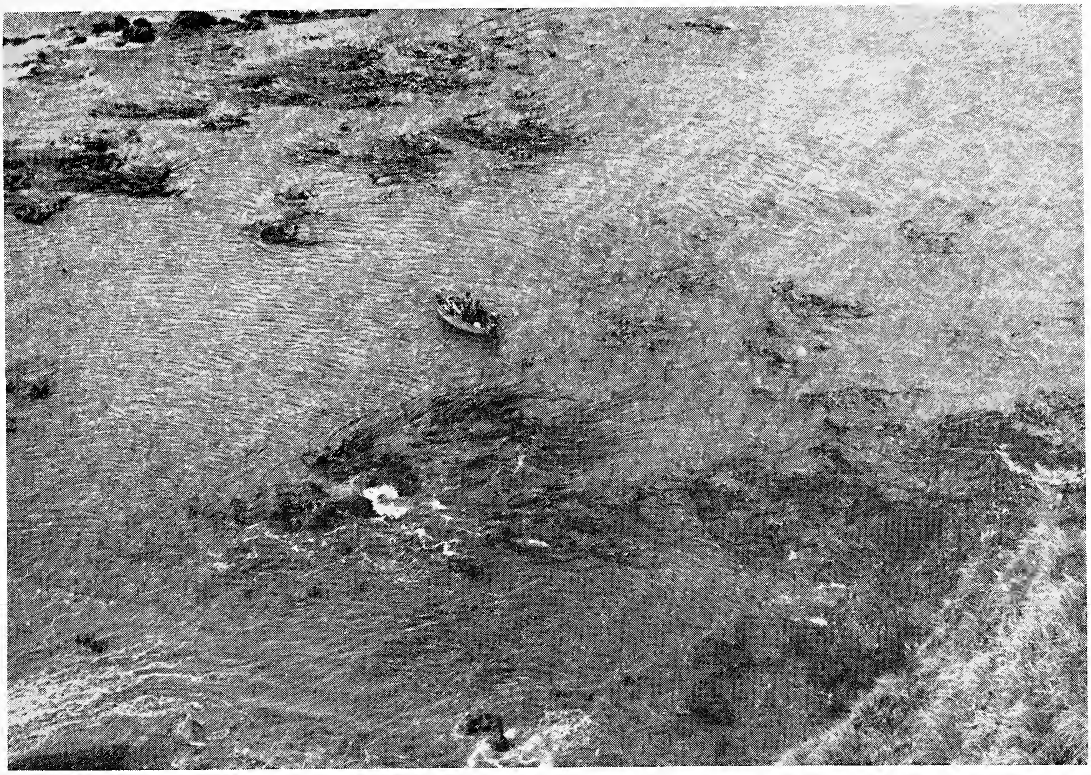

FIG. 12. Entrance to Garden Cove, viewed from Camp Hill, showing kelp growth.

- Acarina
  - *Halozates* sp.
- Insecta
  - *Antarctophytosus macquariensis* Womersley
  - *Antarctopria latigaster* Brues
  - *Antarctotachinus crozetensis* Enderlein
  - *Coelopa macquariensis* Womersley
  - *Ephydra macquariensis* Womersley
  - *Procanace macquariensis* Womersley

Echinodermata
- Asteroidea
  - *Asterina hamiltoni* Koehler
  - *Sporasterias directa* (Koehler)
  - *S. mawsoni* (Koehler)
  - *S. sphoerulata* (Koehler)
  - *Stichaster suteri* (Loriol)
- Holothuroidea
  - *Pseudopsolus macquariensis* (Dendy)

Chordata
- Urochordata
  - *Molgula novaezelandiae* (Michaelsen)
- Pisces
  - *Harpagifer bispinis* (Schneider)
  - *Notothenia macrocephala* Gunther
- Aves
  - *Gallirallus australis scotti* (Grant)
  - *Larus dominicanus* Lichtenstein
- Mammalia
  - *Mirounga leonina* (L)

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Professor W. Stephenson (Zoology Department, University of Queensland, Australia) kindly read and criticised the manuscript.

SUMMARY

The major features of the rocky shore zonation pattern at Macquarie I., are described as comprising a lichen zone; a *Porphyra* zone; a "bare" zone dominated by *Siphonaria;* an upper red algal zone, predominantly *Rhodymenia;* a *Durvillea* zone; and a lower red algal zone of *Dellessaria, Iridea,* and *Desmarestia.*

The secondary organisms associated with the above zones are listed.

The zonation pattern is compared with similar ecological situations in southern Australia, New Zealand, South Africa, and South America. The algal domination of the shore shows much in common with the west coast of South Africa.

The absence of barnacles and littorinids suggests that the Macquarie shore is more typically Antarctic than Subantarctic. The geographic distribution of species shows the island to have a closer biogeographic relationship to other Subantarctic islands than to the New Zealand area.

REFERENCES

BATHAM, E. J. 1958. Ecology of a southern New Zealand exposed rocky shore at Little Papanui, Otago Peninsula. Trans. Roy. Soc. N. Z. 85: 647.

BENNETT, I., and E. C. POPE. 1953. Intertidal zonation of the exposed rocky shores of Victoria, together with a rearrangement of the biogeographical provinces of temperate Australian shores. Aust. Jour. Mar. Freshw. Res. 4: 105.

CHILTON, C. 1909. The Sub Antarctic Islands of New Zealand. Canterbury, N. Z.

CRISP, D. J., and A. J. SOUTHWARD. 1953. Isolation of intertidal animals by sea barriers. Nature 172: 208. No. 4370.

DAKIN, W. J., I. BENNETT, and E. C. POPE. 1948. A study of certain aspects of the ecology of the intertidal zone of the New South Wales coast. Aust. Jour. Sci. Res. ser. B, 1: 176.

DEACON, G. E. R. 1937. The hydrology of the Southern Ocean. Discovery Reps. 15: 1.

DELL, R. K. 1952. In: The Antarctic Today, Wellington, N. Z.

DOTY, M. S. 1957. Rocky intertidal surfaces. Geol. Soc. Am., Mem. 67: 535.

ENDEAN, R., R. KENNY, and W. STEPHENSON. 1956. The ecology and distribution of intertidal organisms on the rocky shores of the Queensland mainland. Aust. Jour. Mar. Freshw. Res. 7: 88.

EKMAN, S. 1953. Zoogeography of the Sea. London.

GUILER, E. R. 1952. The nature of intertidal zonation in Tasmania. Pap. Proc. Roy. Soc. Tas. 86: 31.

——— 1959. The intertidal ecology of the Montemar area, Chile. Pap. Proc. Roy. Soc. Tas. 93: 165.

——— 1960. The intertidal zone forming species on rocky shores of the East Australian Coast. J. Ecology 48: 1.

ISAAC, W. E. 1937. Studies of South African seaweed vegetation, I. West coast from Lamberts Bay to the Cape of Good Hope. Trans. Roy. Soc. S. Afr. 25: 115.

KITCHING, J. A. 1935. An introduction to the ecology of intertidal rock surfaces on the coast of Argyll. Trans. Roy. Soc. Edinb. 58: 351.

KNOX, G. A. 1953. The intertidal ecology of Taylor's mistake, Banks Peninsula. Trans. Roy. Soc. N. Z. 81: 189.

——— 1960. In: Biology of the Southern Cold Temperate Zone, ed. Holdgate, Nature 185: 203. No. 4708.

MACKINTOSH, N. A. 1946. The Antarctic Convergence and the distribution of surface temperature in Antarctic waters. Discovery Reps. 23: 177.

MADSEN, H. 1936. Investigations on the shore fauna of East Greenland with a survey of the shores of other Arctic regions. Medd. om Grønland 100(8): 1.

MAWSON, SIR D. 1943. Macquarie Island, its geography and geology. Aust. Antarctic Exp. Reps. ser. A, 5: 1.

POWELL, A. W. B. 1951. Antarctic and Subantarctic Mollusca. Discovery Reps. 26: 47.

——— 1955. Mollusca of the southern islands of New Zealand. Cape Exp. Series, Bull. 15.

SOUTHWARD, A. J. 1958. Zonation of plants and animals on rocky sea shores. Biol. Rev. 33: 137.

STEPHENSON, T. A., and A. 1949. Universal features of zonation between tide-marks on rocky shores. J. Ecology 37: 289.

TAYLOR, B. W. 1955. The flora, vegetation, and soils of Macquarie Island. Aust. Nat. Antarct. Res. Exp. Reps. Ser. B, 2: 1.

VAUGHAN, T. W. 1940. Ecology of modern marine organisms with reference to paleogeography. Bull. Geol. Soc. America 51: 433.

WOMERSLEY, H. B. S., and S. J. EDMONDS. 1952. Marine coastal zonation in southern Australia in relation to a general scheme of classification. J. Ecology 40: 84.

Bacterial Flora of Seven Species of Fish Collected at Rongelap and Eniwetok Atolls[1]

RITA R. COLWELL[2] and JOHN LISTON[3]

A VERY EXTENSIVE LITERATURE exists concerning the normal bacterial flora of marine fish species common to the northern ocean areas, i.e., the North Sea (Stewart, 1932; Aschehoug and Vesterhus, 1943; Reay and Shewan, 1949; Liston, 1956, 1957; Georgala, 1958), the North Atlantic (Reed and Spence, 1929; Gibbons, 1934*a*, 1934*b*; Dyer, 1947), and the North Pacific (Hunter, 1920; Fellers, 1926; Snow and Beard, 1939; Kiser, 1944; Kiser and Beckwith, 1942, 1944; Liston, 1959). These studies of the aerobic heterotrophic bacterial flora found on a number of different species of northern ocean fishes have shown that, while the generic distribution of the bacteria associated with freshly caught marine fish may vary quantitatively, the following genera predominate fairly consistently: *Pseudomonas, Achromobacter, Flavobacterium,* and *Micrococcus.* The genera *Proteus, Sarcina, Bacillus, Corynebacterium,* and *Serratia* are encountered less often. Some investigators have discussed the biochemistry of the organisms isolated from marine fish (viz., Thjøtte and Sømme, 1943) but most of the physiology and biochemistry is limited to only a few properties studied for classifying the microorganisms. A somewhat more extensive discussion of the anabolic and catabolic aspects of the bacterial groups found on North Pacific fish has been given by Colwell (1961) and Liston and Colwell (1962).

There is relatively little information available on the bacteriology of fishes common in warm water areas. Wood (1940, 1950, 1952, 1953) studied marine fish caught off the coast of Australia and reported on the numbers and the types of bacteria found on these animals. Some of his results are at variance with those reported by workers in the northern areas. Thus, he reported large numbers of *Corynebacterium* and *Mycoplana* species from some of the fish sampled. This might indicate that there are differences existing with respect to geographical location of the fish species.

Venkataraman and Sreenivasan (1952, 1954), Velankar (1955, 1956), and Velankar and Kamasastri (1956) carried out bacteriological studies of fish caught in the waters off the coast of India. The results of these workers are at variance with those of Wood, but also indicate peculiar distributions of bacterial genera which suggest that factors related to the physical environment may affect the commensal flora of the fish species.

Periodic studies of the effects of the atomic testing program on the biota of the Marshall Islands have been made since 1946 by the staff of the Applied Fisheries Laboratory, University of Washington (Biddulph and Cory, 1952; Donaldson et al., 1948, 1949, 1956; Palumbo, 1955; Seymour et al., 1957). Since it was relatively simple to arrange for animals collected during these surveys to be sampled bacteriologically, the bacterial flora of the marine fish in southern and northern Pacific Ocean areas could then be compared directly. The bacterial flora of invertebrate animals collected during certain of the atomic testing program studies (Bonham, 1958; Held, 1960) have been analyzed and are reported elsewhere (Colwell and Liston, 1961*a*). The investigations reported in this paper were designed (1) to study the bacterial flora of marine fish of the central Pacific Ocean, i.e., the Rongelap and Eniwetok atolls of the Marshall Islands; (2) to investigate the possibility of geographically

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imposed variation of a natural flora; and (3) to study the question of host specificity in terms of the commensal bacterial flora and the animal host.

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MATERIALS AND METHODS

The animals sampled were the surgeon fish, *Acanthurus triostegus triostegus* (Linnaeus), the snapper, *Aprion virescens* Valenciennes, the jack, *Caranx ferdau* Forskål, the grouper, *Epinephelus merra* Bloch, the goatfish, *Mulloidichthys samoensis* (Gunther), the siganid, *Siganus rostratus* (Valenciennes), and the barracuda, *Sphyraena helleri* Jenkins.

The sampling procedure followed was the sterile-swab technique whereby cotton swabs, sterilized in separate 16 × 150 mm screw-capped culture tubes containing 1–2 cc aged sea water plus 0.5% peptone, were used to sample gill, gut, mouth, and skin areas of the animals. Streaks were then made, in the field, onto the surface of slanted agar in small (1½ oz) prescription bottles. The bottles were transported by air to the College of Fisheries Laboratories at the University of Washington, Seattle, where streakings from the prescription bottles were made onto a medium consisting of 0.5% yeast extract and 0.8% nutrient agar in 1 liter of aged sea water (MacLeod et al., 1954). The colonies appearing after 5 days at 25 C (RT) were picked from the agar into tubes of sea water broth, a Nutrient Broth (Difco) made up with aged sea water in place of distilled water. Each isolate was restreaked three times in order to ensure purity, before the testing program was carried out.

Pure cultures in a medium of 1.0% peptone in sea water were used as the source of organisms for carrying out the descriptive procedures, which tested morphological, physiological, and biochemical characteristics of the bacteria.

Morphology was determined by observation of 24–48 hr cultures, using an American Optical Company "Phasestar" phase-contrast microscope. The Gram stain and the Casares-Gil flagella stain (Manual of Microbiological Methods, 1957) were routinely made. Growth characteristics on agar and in liquid media at 0 C, 25 C (RT) and 37 C were recorded.

Sea water requirement was tested by streak plating on agar containing sea water and on a duplicate distilled water–Nutrient Agar plate. Sensitivity to the antibacterial agents was determined by disc tests (Difco "Uni-discs" and "antibiotic discs") or by ditch tests in the case of the 0/129 compound (Collier, Campbell, and Fitzgerald, 1950; Shewan, Hodgkiss, and Liston, 1954).

Except for the following, all biochemical tests were carried out as described in the Manual of Microbiological Methods (1957): the Hugh and Leifson (1953) test for anaerobic fermentation of sugar was performed; and the trimethylamine oxide (TMO) reduction test as described by Wood and Baird (1943).

For a discussion of the tabulating and handling of the taxonomic data, see Colwell and Liston (1961*b*).

RESULTS AND DISCUSSION

The distribution of bacterial genera within the commensal floras of the seven species of fish sampled in this study is given in Table 1. *Pseudomonas* and *Achromobacter* species were predominant in the floras of *Acanthurus triostegus, Caranx ferdau, Epinephalus merra, Siganus rostrata, and Sphraena helleri. Aprion virescens* yielded more nonfecal enterobacterial species, and *Mulloidichthys samoensis* more of the Gram positive bacterial types. However, the bulk of the flora in six of the seven species of fish studied consisted of the Gram negative, asporogenous, rodlike bacilli of the *Pseudomonas, Vibrio,*

TABLE 1

GENERIC DISTRIBUTION OF AEROBIC HETEROTROPHIC BACTERIA ASSOCIATED WITH SEVEN SPECIES OF MARINE VERTEBRATES

(Expressed as per cent)

ANIMAL SPECIES	*Pseudomonas*	GUT GROUP *Vibrio*	*Achromobacter*	*Flavobacterium*	*Corynebacterium*	*Bacillus*	*Micrococcus*	ENTEROBACTERIA*	OTHER†	TOTAL NUMBER IN SAMPLE
Acanthurus triostegus	36.7	5.3	26.2	10.6	0.0	10.6	0.0	0.0	10.6	19
Aprion virescens	11.1	11.1	22.2	11.1	0.0	0.0	0.0	44.5	0.0	9
Caranx ferdau	44.5	11.1	22.2	0.0	0.0	0.0	11.1	11.1	0.0	9
Epinephalus merra	70.0	10.0	0.0	0.0	0.0	0.0	0.0	20.0	0.0	10
Mulloidichthys samoensis	8.3	4.2	25.0	12.5	12.5	8.3	12.5	0.0	16.7	24
Siganus rostrata	60.0	0.0	0.0	0.0	0.0	20.0	0.0	20.0	0.0	5
Sphraena helleri	0.0	0.0	60.0	20.0	0.0	0.0	20.0	0.0	0.0	5

* *Aerobacter, Aeromonas, Proteus.*
† *Alcaligenes, Brevibacterium, Arthrobacter, Photobacterium,* yeasts.

Achromobacter, and *Flavobacterium* groups. Only one species, the goatfish (*Mulloidichthys samoensis*), showed a balanced flora of Gram positive versus Gram negative types of bacteria. Of the Gram negative types of bacteria forming the commensal floras, *Pseudomonas* and *Achromobacter* species predominated. The Gram positive groups found on the fish varied, i.e., higher numbers of *Bacillus* species were found on *Acanthurus triostegus* and *Siganus rostrata,* and higher numbers of *Micrococcus* species on *Caranx ferdau* and *Sphraena helleri.*

In Table 2, a comparison of the two areas studied is given. *Pseudomonas* species predominated in the Eniwetok samples and *Achromobacter* species in the Rongelap samples.

Studies of bacteria found on animals taken in the waters off the west coast of India and off the coast of Australia (Venkataraman and Sreenivasan, 1952; Wood, 1940) indicated that Gram positive types of bacteria, such as *Micrococcus, Bacillus,* and *Corynebacterium,* tend to predominate significantly in the floras of sea fish from these warm water areas. The results of this study,

TABLE 2

GENERIC DISTRIBUTION OF BACTERIA FOUND ON MARINE ANIMALS

(Expressed as per cent)

AREA OF CAPTURE	*Pseudomonas*	GUT GROUP *Vibrio*	*Achromobacter*	*Flavobacterium*	*Corynebacterium*	*Bacillus*	*Micrococcus*	ENTEROBACTERIA*	OTHER†	TOTAL NUMBER IN SAMPLE
Eniwetok Atoll	52.7	10.6	7.9	2.6	0.0	2.6	2.6	21.0	0.0	38
Rongelap Lagoon	11.1	2.8	27.9	16.7	8.3	11.1	8.3	0.0	13.8	36

* *Aerobacter, Aeromonas, Proteus.*
† *Alcaligenes, Brevibacterium, Arthrobacter, Photobacterium,* yeasts.

as seen from Tables 1 and 2, do not corroborate those findings. Indeed, it would appear that, except for the slightly higher incidence of Gram positive and nonfecal, enterobacterial types, the bacterial flora of the fish of Rongelap and Eniwetok is very similar to that reported for fish in northern waters (Reay and Shewan, 1949; Liston, 1957, 1959; Colwell, 1961).

The great number of *Micrococcus* and *Mycoplana* species reported by Wood (1940, 1953) and of *Bacillus* species reported by Venkataraman and Sreenivasan (1952, 1954) have not been encountered in this study. Since Velankar (1956) and Velankar and Kamasastri (1956) also isolated very high numbers of *Bacillus* species in their studies of fish, it may well be that such factors as fresh water run-off or low sea water-fresh water interchange in the inshore areas where the fish were captured alter the composition of the bacterial commensal floras. Under these circumstances it is not unlikely that *Bacillus* species form a significant part of the commensal bacterial flora of fish of Mandapam and Telicherry, off the west coast of India, as reported by these workers. However, in view of the results obtained in our studies it would be unwise to assume that the associated bacterial flora of fish species inhabiting waters on or near the equator differs significantly from the flora of fish in the northern waters.

In Table 3, the characteristics of bacteria isolated from the seven species of fish are given. Nearly all the cultures tested (76–100%) were capable of growth at 37 C. Thirty to 60% of the cultures peptonized milk, and more than 50% of the cultures liquefied gelatin. However, bacteria isolated from *Aprion virescens* and *Caranx ferdau* were generally less proteolytic, on the basis of the milk peptonization and gelatin liquefaction tests. High urease and nitratase activity was noted in most of the cultures tested. Trimethylamine oxide reducers were isolated from *Acanthurus triostegus, Caranx ferdau,* and *Epinephalus merra.*

Table 4 shows a comparison of carbohydrate degradation tests for bacteria from the seven animal species. As evidenced by the Hugh and Leifson test (1953), 40–78% of all the cultures tested attacked glucose oxidatively and, roughly speaking, 20–67% were glucose fermenting. Cultures taken from *Acanthurus triostegus* were predominantly oxidative in attack on glucose in comparison with the other species tested. Significantly high fermentative attack on carbohydrates, in general, was noted for cultures taken from *Aprion virescens* and *Mulloidichthys samo-*

TABLE 3

BIOCHEMICAL AND PHYSIOLOGICAL CHARACTERISTICS OF BACTERIA ASSOCIATED WITH SEVEN SPECIES OF MARINE VERTEBRATES

(Expressed as per cent positive)

ANIMAL SPECIES	MOTILE	GROWTH AT 0 C	GROWTH AT 37 C	PENICILLIN SENSITIVE	LITMUS MILK PEPTONIZED	GELATIN LIQUEFIED	UREASE POSITIVE	NITRATE REDUCED	TRIMETHYLAMINE OXIDE REDUCED	INDOLE PRODUCED	HYDROGEN SULFIDE PRODUCED	GROWTH IN KOSER'S CITRATE
Acanthurus triostegus	83.4	7.1	76.4	58.9	38.8	83.4	31.2	53.1	25.0	0.0	11.8	35.4
Aprion virescens	55.5	14.3	85.8	22.2	11.1	11.1	28.6	100.0	0.0	0.0	14.3	42.9
Caranx ferdau	88.8	33.3	77.7	33.3	11.1	44.4	25.0	33.3	16.7	0.0	0.0	0.0
Epinephalus merra	100.0	44.4	100.0	0.0	50.0	50.0	44.4	30.0	16.7	0.0	22.2	88.8
Mulloidichthys samoensis	58.3	25.0	100.0	90.0	33.3	70.8	28.2	25.0	0.0	4.2	8.3	12.5
Siganus rostrata	80.0	0.0	100.0	0.0	60.0	100.0	0.0	60.0	0.0	0.0	66.6	0.0
Sphraena helleri	20.0	40.0	100.0	75.0	0.0	60.0	60.0	60.0	*	0.0	0.0	0.0

* Not tested.

TABLE 4

SOME BIOCHEMICAL CHARACTERISTICS, TESTING CARBOHYDRATE UTILIZATION AND DEGRADATION, OF AEROBIC HETEROTROPHIC BACTERIA FROM MARINE FISH

(Expressed as per cent positive)

ANIMAL SPECIES	HUGH AND LEIFSON (Aerobic)	HUGH AND LEIFSON (Anaerobic)	LACTOSE	MALTOSE	MANNITOL	SUCROSE	GALACTOSE	VOGES-PROSKAUER REACTION	METHYL RED REACTION	STARCH HYDROLYZED
Acanthurus triostegus	53.1	5.9	11.8	41.3	29.5	35.4	23.1	0.0	11.8	31.2
Aprion virescens	77.7	66.6	55.5	77.7	71.5	57.2	66.6	28.6	28.6	0.0
Caranx ferdau	44.4	22.2	0.0	11.1	50.0	25.0	16.7	12.5	12.5	16.7
Epinephalus merra	60.0	30.0	33.3	33.3	28.6	22.2	16.7	22.2	0.0	0.0
Mulloidichthys samoensis	54.2	12.5	37.5	58.3	50.0	37.5	45.8	0.0	37.5	8.3
Siganus rostrata	40.0	20.0	33.3	33.3	33.3	33.3	0.0	33.3	66.6	0.0
Sphraena helleri	60.0	20.0	20.0	20.0	20.0	20.0	40.0	0.0	0 0	20.0

ensis. In the overall pattern, for all seven species, relatively high numbers of carbohydrate-utilizing bacteria were isolated from the fish taken in both Rongelap Lagoon and on Eniwetok Atoll.

In their general physiology, therefore, the bacteria from the warm water fish do show differences from the bacteria from cold water fish. The latter have been described as predominantly psychrophilic organisms with a characteristically oxidative metabolism in most cases. This difference may well be related to the higher ambient temperatures of the tropical areas.

SUMMARY

Eighty-one cultures were isolated from seven species of fish captured in Rongelap Lagoon and near Eniwetok Atoll. The composition of the commensal floras, as measured by generic distribution of the bacterial cultures isolated in the samples, showed that the *Pseudomonas/Vibrio, Achromobacter,* and *Flavobacterium* groups predominated. The generic distribution within the floras of the fish captured in the southern areas of the North Pacific Ocean did not indicate that geographical factors effect changes in the commensal floras, insomuch as the data obtained showed good agreement with results obtained by other investigators. Some variations were observed within the bacterial floras of the seven species of fish studied. No species-specific commensal flora was noted.

Biochemical and physiological characteristics studied suggest that the aerobic heterotrophic bacteria commensal to fish inhabiting the waters of Rongelap Lagoon and Eniwetok Atoll are active in proteolysis and in carbohydrate degradation and, in contrast to the psychrophilic bacteria of northern fish, tend to be mesophilic.

REFERENCES

ASCHEHOUG, V., and R. VESTERHUS. 1943. Investigations of the bacterial flora of fresh herring. Z. fur Bakt. Parasit. Infect., Abt. III, 106: 5–27.

BIDDULPH, O., and R. CORY. 1952. The relationship between Ca^{45}, total calcium and fission product radioactivity in plants of *Portulaca oleracea* growing in the vicinity of the atom bomb test sites on Eniwetok Atoll. Washington State Coll. U. S. Atomic Energ. Comm. Rep. UWFL-31.

BONHAM, KELSHAW. 1958. Radioactivity of invertebrates and other organisms at Eniwetok Atoll during 1954–55. Applied Fisheries Lab., Univ. of Washington, MS.

COLLIER, H. O. J., N. R. CAMPBELL, and M. E. H. FITZGERALD. 1950. Vibriostatic activity in certain series of pteridines. Nature 165: 1004–1005.

COLWELL, R. R. 1961. Commensal bacteria of marine animals. A study of their distribution, physiology and taxonomy. Ph. D. Thesis, Univ. of Washington. 198 pp.

COLWELL, R. R., and J. LISTON. 1961*a*. The bacterial flora of certain marine invertebrates. J. Insect. Pathol.: In press.

——— ——— 1961*b*. Taxonomic relationships among the pseudomonads. J. Bacteriol. 82: 1–14.

DYER, F. E. 1947. The microorganisms from Atlantic cod. J. Fish. Res. Bd. Can. 7: 128–136.

DONALDSON, L. R., et al. 1948. Concentration of active materials by hydroids in the Bikini lagoon during the summer of 1947. Applied Fisheries Lab., Univ. of Washington. U. S. Atomic Energ. Comm. Rep. UWFL-11.

——— A. H. SEYMOUR, and J. R. DONALDSON. 1949. Radiological analysis of biological samples collected at Eniwetok May 16, 1948. Applied Fisheries Lab., Univ. of Washington. U. S. Atomic Energ. Comm. Rep. UWFL-18.

——— et al. 1956. Survey of radioactivity in the sea near Bikini and Eniwetok atolls, June 11–21, 1956. Applied Fisheries Lab., Univ. of Washington. U. S. Atomic Energ. Comm. Rep. UWFL-46.

FELLERS, C. R. 1926. Bacteriological investigations on raw salmon spoilage. Univ. of Washington Publ. Fish. 1: 157–188.

GEORGALA, D. L. 1958. The bacterial flora of the skin of North Sea cod. J. Gen. Microbiol. 18: 84–91.

GIBBONS, N. E. 1934*a*. The slime and intestinal flora of some marine fishes. Contrib. Canad. Biol. Fish., Biol. Bd. Can. 8: 275–290.

——— 1934*b*. Lactose-fermenting bacteria from the intestinal contents of marine fish. Contrib. Canad. Biol., Biol. Bd. Can. 8: 291–300.

HELD, E. E. 1960. Land crabs and fission products at Eniwetok Atoll. Pacific Sci. 14(1): 18–27.

HUGH, R., and E. LEIFSON. 1953. The taxonomic significance of fermentative versus oxidative metabolism of carbohydrates by various gram negative bacteria. J. Bacteriol. 66: 24–26.

HUNTER, A. C. 1920. Bacterial groups in decomposing salmon. J. Bacteriol. 5: 543–552.

KISER, J. S. 1944. Effects of temperatures approximating 0°C upon growth and biochemical activities of bacteria isolated from mackerel. Food Res. 9: 257–267.

——— T. D. BECKWITH. 1942. Effect of fast-freezing upon the bacterial flora of mackerel. Food Res. 7: 255–259.

——— T. D. BECKWITH. 1944. A study of the bacterial flora of mackerel. Food Res. 9: 250–256.

LISTON, J. 1956. Quantitative variations in the bacterial flora of flatfish. J. Gen. Microbiol. 15: 305–314.

——— 1957. The occurrence and distribution of bacterial types on flatfish. J. Gen. Microbiol. 16: 205–216.

——— 1959. The bacterial flora of Pacific fish. Bacteriol. Proc., p. 12.

——— R. R. COLWELL. 1962. Host and habitat relationships of marine commensal bacteria. Bacteriol. Rev., in press.

MACLEOD, R. A., E. ONOFREY, and M. E. NORRIS. 1954. Nutrition and metabolism of marine bacteria, I. Survey of nutritional requirements. J. Bacteriol. 68: 680–686.

Manual of Microbiological Methods. 1957. Society of American Bacteriologists. McGraw-Hill, Inc., New York. 315 pp.

PALUMBO, R. F. 1955. Uptake of iodine-131 by the red alga *Asparagopsis taxiformis*. Applied Fisheries Lab., Univ. of Washington. U. S. Atomic Energ. Comm. Rep. UWFL-44.

REAY, G. A., and J. M. SHEWAN. 1949. The spoilage of fish and its preservation by chilling. Adv. Food Res. 2: 344–393.

REED, G. M., and C. M. SPENCE. 1929. The intestinal and slime flora of the haddock: A preliminary note. Contrib. Canad. Biol. Fish., N.S. 4: 257–264.

SEYMOUR, A. H., et al. 1957. Survey of radioactivity in the sea and pelagic marine life west of the Marshall Islands, September 1–20, 1956. Applied Fisheries Lab., Univ. of Washington. U. S. Atomic Energ. Comm. Rep. UWFL-47.

SHEWAN, J. M., W. HODGKISS, and J. LISTON. 1954. A method for the rapid differentiation of certain non-pathogenic asporogenous bacilli. Nature 173: 208.

SNOW, J. E., and P. J. BEARD. 1939. Studies on the bacterial flora of North Pacific salmon. Food Res. 4: 563–585.

STEWART, M. M. 1932. The bacterial flora of the slime and intestinal contents of the haddock (*Gadus aeglefinus*). J. Mar. Biol. Assn. 18: 35–50.

THJØTTE, TH., and O. M. SØMME. 1943. The bacterial flora of normal fish. Skrift. Norsk. Videnskap.-Akad., Oslo, 1. Mat.-Naturv. Klasse. 4: 1–93.

VELANKAR, N. K. 1955. Bacteria in the inshore environment at Mandapam. Ind. J. Fish. 2: 96–112.

——— 1956. The bacterial flora, trimethylamine and total volatile nitrogen of fish muscle at 3°C. Ind. J. Fish. 3: 261–268.

——— P. V. KAMASASTRI. 1956. The bacterial flora, trimethylamine and total volatile nitrogen of fish muscle at 0°C (in ice). Ind. J. Fish. 3: 269–289.

VENKATARAMAN, R., and A. SREENIVASAN. 1952. A preliminary investigation of the bacterial flora of the mackerels off the West Coast. Ind. J. Med. Res. 40: 529.

——— ——— 1954. Bacteriology of inshore seawater and of mackerels off Tellicherry (Malabar). Proc. Nat. Inst. Sci. India 20: 651.

WOOD, A. J., and E. A. BAIRD. 1943. Reduction of trimethylamine oxide by bacteria. J. Fish. Res. Bd. Canad. 6: 194–201.

WOOD, E. J. F. 1940. Studies on the marketing of fresh fish in eastern Australia. Part III. The bacteriology of spoilage of marine fish. Coun. Sci. Industr. Res. Austr. Rept. No. 3, Pamph. 100: 1–92.

——— 1950. The bacteriology of shark spoilage. Austr. J. Mar. Freshw. Res. 1: 129–138.

——— 1952. The micrococci in a marine environment. J. Gen. Microbiol. 6: 205–210.

——— 1953. Heterotrophic bacteria in a marine environment of Eastern Australia. Austr. J. Mar. Freshw. Res. 4: 160-200.

Red-Water Blooms off Northern Chile, April–May 1956, with Reference to the Ecology of the Swordfish and the Striped Marlin[1]

DONALD P. DE SYLVA[2]

FROM MID-APRIL to early May 1956 the writer participated in the University of Miami–Lou Marron Pacific Billfish Expedition off northern Chile in the Peru Coastal Current (Sverdrup et al., 1942: 701–702). During this period, water temperatures and plankton tows were taken, and observations were made on the biology and distribution of several planktonic and nektonic species.

The data accumulated suggest that certain hydrographic features of the region favor the establishment of a food web beginning with phytoplankton blooms and culminating with the concentration of broadbill swordfish, *Xiphias gladius* Linnaeus, and striped marlin, *Tetrapturus audax* Philippi.

METHODS AND MATERIALS

From Apr 18 to May 10, cruises were made from Iquique on several vessels. Although the primary purpose of these cruises was to capture swordfish and marlin, the cruises were planned to permit temperature transects to be made along the coast, and to deduce therefrom, in the absence of salinity data, a pattern of surface currents and their ecological effects upon marine organisms. A bucket thermometer was used to take a total of 182 surface temperatures over a 1-week period, and 22 bathythermograph casts up to 180 m were made on May 2.

Approximate locations at sea were determined on nautical charts by running time and by the use of landmarks. Because of the conspicuous peaks of the Andes foothills, it was usually possible to locate the positions reasonably well, but these are only approximate positions.

On several of the cruises, surface plankton tows were made with a 1-m, size 00 mesh, nylon plankton net, and collections were preserved in 5% formalin. These were deposited at the Institute of Marine Science, University of Miami.

A running log was kept on hydrographic, meteorological, and biological information. These data included water and air temperatures; wind, sea, and other pertinent data; occurrence of swordfish, striped marlin, squids, bonito, anchovies, and plankton concentrations. Original hydrographic data were deposited with the U. S. Navy Hydrographic Office as "Cruise 1366, R/V *Genie* II." The writer's data have been markedly supplemented by Mr. and Mrs. John A. Manning's logbook on the biological aspects. In addition, some information was available from local fishermen on the occurrence of swordfish and marlin, as well as on the stomach contents of swordfish.

HISTORICAL BACKGROUND

The sea off Chile and particularly off Peru has been studied for many years. Sears (1954) has summarized much of the pertinent literature on hydrography. Other papers on hydrography include Dall (1909), Bini (1952), de Buen (1957), and Posner (1957). Plankton blooms have been noted by Murphy (1926) and Gunther (1936*a*), and fish mortality by Cienfugos (1895), Coker (1910), Lavalle (1917*a,b,* 1924), Rahm (1937), Falke (1939, 1950), Brongersma-Sanders (1948, 1957), and Schwabe (1951). The distribution and mortality of squids is covered by d'Orbigny (1835–43), Hupe (in Gay, 1854), Pfeffer (1912), Schneider (1930); pelagic fishes are discussed by Bini (1952), Mann (1954), University of Miami (1955), de Buen (1957), and Manning (1957). A number of these authors have discussed the interesting phenomenon and consequences of the junction

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of the cold Peru Current (*sensu lato*) with that of the Equatorial Counter Current which occasionally results in the mass death of organisms. Hydrographic information indicates that the mortality off Peru may be due essentially to the junction of warm and cold waters resulting in traumatic death for many organisms due to the sudden temperature change (Posner, 1957). Sears (1954) pointed out that upwelling and surface warming off Peru may also result in phytoplankton blooms and death of organisms, the red water there being known as "aguaje." The causes of the two types of catastrophes are evidently distinct, although the results are similar. Red water also occurred in a transitional zone observed during the present study between southern Peru and northern Chile, at approximately 20° S. Here, tongues of warm water from the north are apparently restricted to the shallow surface layers (Bini, 1952). The result of this juncture is the production of red water, and the subsequent concentration of several organisms.

TEMPERATURE DATA

Only limited environmental information is available from a quasi-synoptic pattern of surface temperatures (Fig. 1). Since temperatures were taken over a period of 1 week, the data must be viewed with reservations. Sears (1954) doubted the reliability of surface temperatures for interpreting hydrographic conditions where solar heating is appreciable. However, the prevalence of a persistent cloud cover during the period of study would seem to preclude any extensive surface heating (U. S. Navy Hydrographic Office, 1938).

Tongues of warm water flowing from the north are juxtaposed with northward-flowing cooler waters from the Peru Coastal Current. Earlier studies (University of Miami, 1955) suggest that the front, a junction of the colder and warmer waters, moves north later in the year. Gunther (1936*a,b*), Bini (1952), and Posner (1957) showed that a warm lens off Peru may flow from the offshore anticyclonic eddy. As evidenced by the bathythermograph data taken in the present study, these lenses (Figs. 2–4) are thin and stratified, overlying the colder Peru Coastal Current water from the south, with little mixing probably occurring except by diffusion processes. There is some indication from vertical profiles and thermocline depth (University of Miami, 1955) that to the north some onshore movement of water occurs.

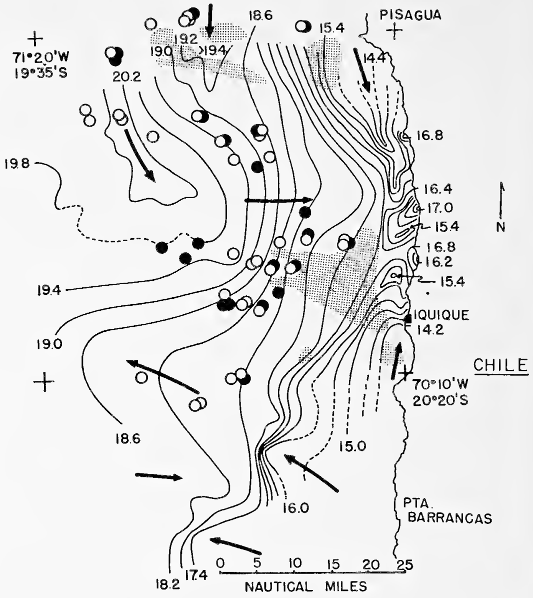

FIG. 1. Distribution of red-water patches (stippled area), swordfish (open circles), and striped marlin (closed circles) in relation to surface water temperatures (° C) off northern Chile, Apr–May 1956. Arrows represent probable surface currents. Isotherms are contoured every 0.4 C.

No bathythermograph casts were made close to shore, but upwelling of cool subsurface waters is evident in the surface temperatures (Fig. 1), and a cool southward-flowing tongue is advected coastwise from Pisagua. The prevailing southeast trade winds which are strongly developed during the winter are responsible for this upwelling (Wooster, 1959). Gunther (1936*b*) pointed out that in these waters upwelling occurs between 40 and 360 m, yet there is no indication that any of these nutrient-rich waters are carried into the relatively impoverished photic zone.

Close to and parallel with a weak divergence region, a relatively wide convergence region is seen between the cooler coastal water and the warm advected tongues from the north. Data taken by Mr. and Mrs. Manning in late May suggest that this convergence region may move northerly as winter approaches (see Wooster, 1959, for data on the Peru Current). Similarly, it would be expected to migrate southward with the advent of warmer temperatures from the north.

NUTRIENTS

Posner (1957) showed that during his study the surface waters of the Peru Current were rather nutrient-poor, at least in the latitudes from 3° to 14° 30′ S, and it is seen that surface waters from the north extend well into the Iquique area (Fig. 1). There is no information available to me on the amount, source, or distribution of nutrients in the Peru Current off Chile. Upwelling of nutrient-rich deep waters into the photic zone, leaching of nitrate and guano deposits from the coastal region, excreta from guano birds, and the decomposition of squids of the plankton blooms, may contribute to the production. Mortality of squids off Chile is a well-known annual event which was first noted by d'Orbigny (1835–43) and was subsequently described by Schneider (1930), Schwabe (1951), and Wilhelm (1930, 1932, 1954). The death of squids appears to be connected with the reproductive cycle and the termination of spawning (see McGowan, 1954). The possibility of a nutrient supply from decomposing animals for "red tides" off the Florida west coast has been discussed by Ingle and de Sylva (1955). Clearly, the nutrient cycle in Chilean waters needs intensive study, but for the purposes of the present discussion it must suffice to say that nutrients must have been plentiful during the period of red-water blooms.

RED-WATER BLOOMS

During the observations made in Apr and May, the dominant phytoplankton organism in red-water patches (Fig. 1) was identified by the writer as *Prorocentrum micans* Ehrenberg. This organism had reached bloom proportions by late Apr, coloring the water a deep rusty red. Interspersed with this dinoflagellate were unidentified globigerines and ciliates. The concentration of *Prorocentrum* in a red-water patch off Iquique on Apr 28, 1960 was esti-

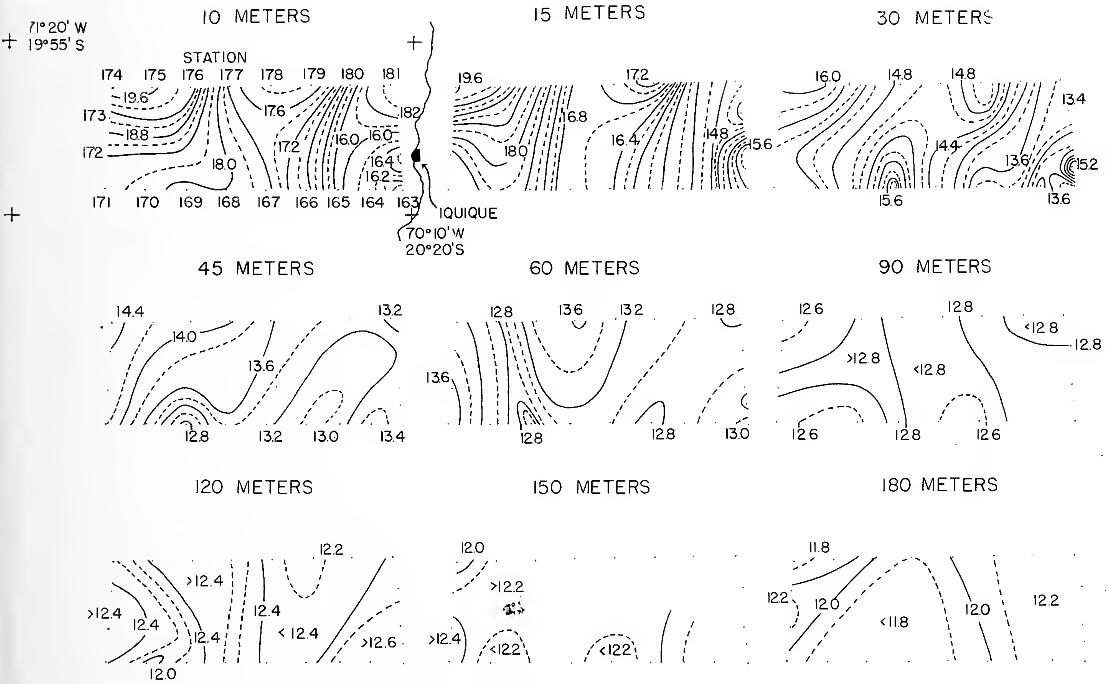

FIG. 2. Distribution of temperature (° C) off Iquique, Chile, on May 2, 1956, at various depths, based on bathythermograph readings. Isotherms are contoured every 0.4 C.

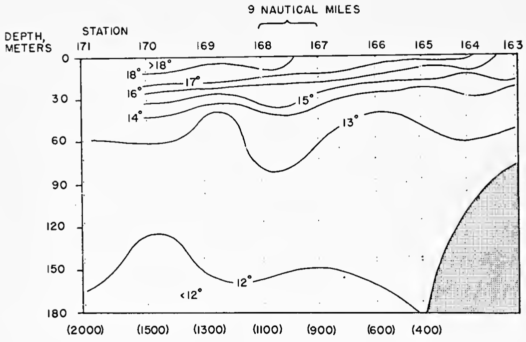

FIG. 3. Transect south of Iquique, Chile, at approximately 20° 18′ S, on May 2, 1956, based on bathythermograph readings. Isotherms are contoured every 1.0 C. Figures in parentheses are depths. (See Fig. 2 for station plan.)

mated to be 20,000 per 1. During late Apr and early May the phytoplankton patches were distributed relatively close to shore in the convergence areas, parallel to shore. These patches occurred along junctures of warm offshore waters and cooler coastal waters. The red water during early May was found only along this juncture. However, by mid and late May red water had extended to 60 miles offshore (Mrs. John A. Manning, *in litt.*). The red-water patches were found along convergence lines rather than in upwelled areas close to shore, and at the time the studies were made they were seldom found in blue, blue-green, or white water, but were found in the dirty green water characteristic of the inshore areas.

The occurrence of red-water conditions was associated in early May with the appearance of a few dying cormorants and an occasional dead or dying fish at the surface. However, by late May angling was reportedly poorer in the Iquique area, and many dead cormorants, shearwaters, and other birds were seen in the red-water patches close to shore and even offshore. On May 27, Mrs. Manning observed dead birds 45–50 miles offshore. Concurrent with the appearance of sick and dead birds in the area, it was noted that the birds which formerly fed actively on the schools of surface-swimming fish were reluctant to feed despite the presence of schools of anchovies in red water. Additional information on the extent of red water is given by Manning (1957).

It is not certain if the populations of *P. micans* were advected from the north into the nutrient-rich waters of the south, or whether the nutrient-laden (i.e., guano) waters from the north were inoculated by phytoplankton from the south. Since this is a coastal species which also causes red-water conditions off southern California (Brongersma-Sanders, 1957: 980), its zoogeographical affinities would be more nearly with those of the Eastern Tropical Pacific than with the waters of the cool Southeast Pacific. A chart given by Brongersma-Sanders (op. cit.: 952, fig. 4) shows that red-water blooms in the eastern part of the Pacific Ocean are limited essentially to tropical waters. Thus it seems more likely that the source of *P. micans* was from northern waters.

ZOOPLANKTON

Numerous tows were made with a 1-m plankton net in the surface waters off Iquique. The dominant organisms were euphausiids, zoea, copepods, and, at times, an unidentified scyphozoan, similar in appearance to *Linuche*. Cursory examination of the guts of the euphausiids and copepods in the field showed red pigmentation. Although subsequent microscopic examination in the laboratory did not reveal identifiable dinoflagellates, the red pigment was assumed to have originated from organisms in the surrounding water, since concentrations of the reddish dinoflagellates were observed at the same time the tows were made. The zooplankton concentrations were especially heavy early in the morning and toward dusk, although copepods tended to be somewhat more numerous in the twilight hours than at dusk. While much work is needed on this subject, it is suggested that zooplankton had grazed extensively on the populations of *Prorocentrum*.

ANCHOVIES

The distribution of the anchovy, *Engraulis ringens* Jenyns, coincided closely with that of the red-water patches (Fig. 1). A few anchovies were seen offshore, but they were most common in the red-water patches at the juncture of the cold and warmer waters. The anchovies apparently were not affected by the red water; at least no sick or dying specimens were observed.

Although no fresh anchovies were captured by us during this study, Rojas (1953) found that the stomachs of anchovies taken off Peru contained diatoms, dinoflagellates, and zooplankton. By far the greatest proportion was diatoms, while dinoflagellates and zooplankton were relatively less important in the stomach contents. Rojas postulated a preference by anchovies for diatoms, although this would seem to relate more to availability, particularly since in the accompanying data the relative abundance in plankton nets corresponded closely with the kinds found in the stomachs.

Anchovies are fed upon by pelicans, cormorants, shearwaters, and petrels, and subsequently these species were observed dead and dying along the coast.

SQUIDS

The giant squid or jibia, *Dosidicus gigas* (d'Orbigny), occurred throughout the region of study, that is, both in the inshore green water and in the offshore blue water, but it seemed more abundant close to shore. It also occurred farther north at the junction of the warm and cool waters. At night it could be taken on hook and line from 7 to 10 m in depth, where it seemed common. Giant squid were often observed by us while trolling our baits. A smaller squid, *Loligo gahi* d'Orbigny, is more of an inshore species than *Dosidicus gigas*. A number of these small forms were taken from bonito stomachs and they in turn contained unidentifiable fragments of fish flesh. Specimens of *D. gigas* were dissected; of eight freshly caught individuals examined two were empty; three stomachs contained fragments of anchovies; one stomach contained a saury, *Scomberesox equirostrum* LeSueur; and two stomachs contained squid flesh. Rahm (1937) obtained plankton and fish remains from squid off the southern Peruvian coast; Wilhelm (1954), in examining specimens of *Dosidicus gigas*, found numerous crustaceans, as well as hake, *Merluccius gayi* (Guichenot), and small individuals of *Dosidicus gigas*.

Dr. Gilbert L. Voss (*in litt.*) states that there is another genus and species of ommastrephid squid found commonly in these waters which is confused with *D. gigas*. Thus, definite identification of the smaller squids must await a thorough taxonomic study of the cephalopods of that area.

Kojima (1959) inferred that in Japanese waters squid, *Ommastrephes sloani pacificus* (= *Todarodes pacificus*), diurnally undergo a vertical migration, emerging from the depths in the early evening and descending at dawn. He further pointed out that following this migration a passive "migratory" drift resulted in concentration of squid. If such a drift does occur off Chile then one might expect to find concentrations of either species of squid in convergence areas, thus making them more available to predatory fishes.

BONITO

Bonito, *Sarda chilensis* (Cuvier), are very abundant in the coastal green waters off Iquique, where they are fished commercially with purse seines. Like the anchovy, they were usually found in the dirty or red-water patches. Thirty bonito were caught on hook and line and their stomachs examined. Of these, 7 appeared to have recently regurgitated their food; 13 contained squid flesh, eyeballs, or beaks; 2 contained fish flesh; 8 had fish vertebrae, probably from clupeoids. All bonito were taken close to shore amid schools of anchovies and plankton swarms. The small squid in the bonito stomachs could not be positively identified but they appeared to be *Loligo gahi*.

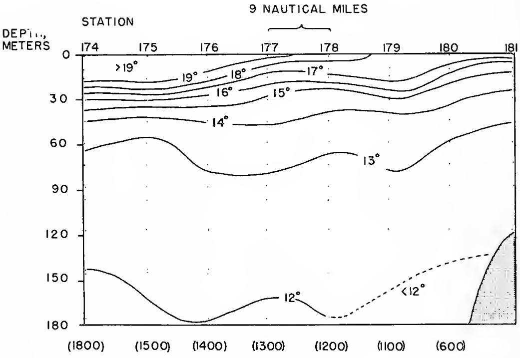

FIG. 4. Transect north of Iquique, Chile, at approximately 20° 05′ S, on May 2, 1956, based on bathythermograph readings. Isotherms are contoured every 1.0 C. Figures in parentheses are depths. (See Fig. 2 for station plan.)

TABLE 1

FREQUENCY DISTRIBUTION OF SURFACE WATER TEMPERATURES (° C) IN WHICH SWORDFISH AND STRIPED MARLIN WERE OBSERVED IN WATERS OFF NORTHERN CHILE FROM APR 8 TO MAY 28, 1956

TEMPERATURE (° C)	SWORDFISH					STRIPED MARLIN				
	Apr	Apr	May	May	Total	Apr	Apr	May	May	Total
	8–18	23–30	2–12	22–28		8–18	23–30	2–12	22–28	
17.4				1	1					
17.6							1			1
17.8				1	1					
18.0				2	2				1	1
18.2								1		1
18.4										
18.6		1		1	2					
18.8		2	2		4		1	4	1	6
19.0		4	7		11		1	5		6
19.2			8		8			3		3
19.4			3		3		3	4		7
19.6		2	2		4			1		1
19.8			1		1		3			3
20.0	2	2	2		6		1			1
20.2		1			1		2			2
20.4	2	2			4					
20.6	1	1			2	1				1
Mean temperature					19.3					19.2

SWORDFISH AND MARLIN

Swordfish were observed or caught where the warmer eddies from offshore and to the north were adjacent to the colder waters of the Peru Coastal Current from the south (Fig. 1). Generally they were taken in clear blue or white water above 18.8 C, with the greater numbers occurring in the warmer waters. There was a distinct tendency, over a 6-week period in Apr and May, for the swordfish to follow the retreating marine "warm front" to the north (see Manning, 1957), which also seemed to present a front for squids. This front left in its wake large patches of red water, at the edge of which the swordfish occurred. Swordfish occurred in only somewhat warmer water than did striped marlin (Table 1), which often were seen at the edge of but seldom in the red-water patches, as well as in the white or blue water.

Seven female swordfish were examined. In the five which contained food, 24 squid (*Dosidicus*) were found. Although no bonito were observed, the natives reported that bonito are eaten by swordfish, and occasionally by marlin. LaMonte (1955) noted that striped marlin off Chile and Peru contained only squid, and LaMonte and Marcy (1941) reported that they always found partially digested squid in the stomachs of marlin and swordfish. Stomach contents of marlin and swordfish examined during the present study suggest that most feeding occurs near the surface. Off southern California, however, Mr. Robert L. Wisner (*in litt.*) reports that the stomach contents of swordfish indicate that they feed on rather deepwater fishes.

During the present study, three striped marlin, all females, were examined; all contained food. One had eaten squid and anchovies; the second contained 42 anchovies and three scads, *Trachurus symmetricus murphyi* Nichols; and the third contained an undetermined number of anchovies and one saury. In southern California waters, Hubbs and Wisner (1953) found that the saury, *Cololabis saira* (Brevoort), was the most important item in the stomachs of striped marlin, with anchovy, *Engraulis mordax* (Girard), being of considerable importance. They attributed the apparent importance of sauries merely to their abundance in the offshore areas in which the marlin had been feeding.

CONCLUSIONS

It is suggested that hydrographic conditions during the present study off Iquique resulted in an influx of a thin warm-water layer from the north containing dinoflagellate populations; an admixture of nutrients, derived at least in part from upwelled coastal water from the south, caused growth of the dinoflagellate population, which resulted in a concentration of the zooplankton crop. Subsequently, anchovies concentrated and fed in these plankton patches and they in turn attracted squid and bonito. Swordfish and striped marlin moved into this region apparently attracted by the concentrations of squids as well as of anchovies. However, they were also probably affected by decreasing water temperatures, as this concentration seemed to be part of a northerly migration toward the onset of winter, following the northward-retreating warm front. It was reported that by late May, most swordfish were being taken well north of the Iquique area toward Arica. This exodus may have been further prompted by the growth in area (to 60 miles offshore) of reported red-water conditions unfavorable to swordfish.

ACKNOWLEDGMENTS

I wish to express my sincere appreciation to Mr. and Mrs. John A. Manning for furnishing data from their cruises off northern Chile, for the use of their boat and equipment, for their many worthwhile suggestions, and for constant encouragement during my stay in Chile. Thanks are due Mr. and Mrs. Lou Marron for the use of their boat and for financial support of the expedition which permitted the scientific aspects to be carried out. Appreciation is expressed to Captain Walter H. Gorman and Mr. James Lynch for field assistance, and to Mr. Albert van der Riet for observations on the distribution of swordfish and marlin. Field work would have been impossible without the able assistance and advice of the Chilean boat crews. Thanks are also due Mr. Syres Dawson of Grace y Cía for the use of shore-based facilities, and to Mr. Armando Huerta and his staff at the Hotel Prat, Iquique, for their kind cooperation in supplying the needed space and equipment. Drs. F. G. Walton Smith and Gilbert L. Voss of the Institute of Marine Science, University of Miami, supplied valuable information on the planning of the expedition, and their criticisms and suggestions toward the improvement of the manuscript were supplemented by those of Drs. F. F. Koczy, H. B. Moore, and C. R. Robins.

SUMMARY

1) Surface temperatures and bathythermograph readings were taken, and observations on the distribution of several marine organisms were made in Apr and May 1956 over a relatively small area north and south of Iquique, Chile, and seaward to about 60 nautical miles in the Peru Coastal Current.

2) The area is characterized by a narrow continental shelf with deep water close to shore and complex coastal currents, with a drift of warm water from the north superimposed upon upwelled cool water.

3) Admixture of these two bodies of water appeared to favor the growth of dinoflagellates ("aguaje"), which in turn supported a food web of copepods, zoea, euphausiid shrimp, anchovies, bonito, and squids.

4) The concentrations of squids, bonito, and anchovies, as foods of swordfish and marlin, are thought to be an indirect result of the productivity caused by the juncture of the two currents.

5) The distribution of the swordfish and marlin in northern Chile, based on personal sightings and records from fishermen, is discussed in relation to ecological conditions.

REFERENCES

BINI, G. 1952. Osservazioni sulla fauna marina della coste del Chile e del Perù con speciale riguardo alle specie ittiche in generale ed ai tonni in particolare. Boll. Pesca, Piscicolt. e Idrobiol., A, 7(1): 11–60, 27 figs.

BRONGERSMA, M. 1948. The importance of upwelling water to vertebrate paleontology and oil geology. Verhandl. K. Nederl. Akad. Wetensch., Afd. Natuurkunde, 2 ser., 45(4): 1–112, 7 figs.

BRONGERSMA-SANDERS, M. 1957. Mass mortality in the sea. In: J. W. Hedgpeth, ed., Treatise on marine ecology and paleoecology. Mem. Geol. Soc. Amer. 67(1): 941–1010, 7 figs.

CIENFUGOS, M. 1895. Fenómenos volcánicos submárinos observados en la bahía de Talcahuano. Actes Soc. Sci. Chili 5: 103–104.

COKER, R. E. 1910. The fisheries and the guano industry of Peru. Bull. U.S. Bur. Fish. 28(1): 333–365, pls. 12–17.

DALL, W. E. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine mollusca of the Peruvian zoological province. Proc. U.S. Natl. Mus. 37 (1704): 147–294, pls. 20–28.

DE BUEN, F. 1957. Pelagic fishes and oceanographic conditions along the northern and central coast of Chile. Proc. UNESCO Sympos. Phys. Oceanogr., Tokyo 1955: 153–155.

FALKE, H. 1939. Über rezente Sedimentbildung in der Bucht von Concepcion (Mittell-Chile). Petroleum 35(34): 640–644; (35): 658–662.

——— 1950. Das Fischsterben in der Bucht von Concepcion (Mittell-Chile). Senckenbergiana: 31(½): 57–77, 5 figs.

GUNTHER, E. R. 1936*a*. Variations in the behavior of the Peru Coastal Current with an historical discussion. J. Roy. Geogr. Soc. 88: 37–65, 6 figs.

——— 1936*b*. A report on oceanographical investigations in the Peru Coastal Current. Discovery Repts. 13: 107–276, 71 figs.

HUBBS, C. L., and R. L. WISNER. 1951. Food of marlin in 1951 off San Diego, California. Calif. Fish Game 39(1): 127–131, figs.

HUPÉ, L. H. 1854. Fauna chilena. Moluscos. In: Historia fisica y politica de Chile, por Claudio Gay. Zoologia 8: 499 pp.

INGLE, R. M., and D. P. DE SYLVA. 1955. The red tide. Florida State Bd. Conserv., Univ. Miami, Marine Lab., Educ. Ser. 1: 1–30, figs. (Rev.).

KOJIMA, S. 1959. Fishing conditions for squid off the Oki Islands, III. Effect of the surface current on formation of fishing grounds. Bull. Jap. Soc. Sci. Fish. 25(4): 249–258.

LAMONTE, F. R. 1955. A review and revision of the marlins, genus *Makaira*. Bull. Amer. Mus. Nat. Hist. 107(3): 323–358, pls. 4–12, 1 table.

——— and D. MARCY. 1941. Swordfish, sailfish, marlin and spearfish. Ichth. Contribs. Internatl. Game Fish Assoc., New York 1(2): 1–24, 5 pls.

LAVALLE Y GARCIA, J. A., DE. 1917*a*. La contracórriente equatorial como causa determinante del fenómeno marino conocido con el nombre de "aguaje." Bol. Soc. Geogr. Lima 33: 313–330.

——— 1917*b*. Informe prelíminar sobre la causa de la mortalidad de las aves ocurrida en el mes de marza del presente año. Mem. Compañia Administradora del Guano 8a: 61–88, 4 figs.

——— 1924. Communication on: Emigration and mortality of guano birds in the months of April, May and June 1923. Mem. Compañia Administradora del Guano 15a: 94–107.

MCGOWAN, J. 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif. Fish Game 40(1): 47–54, figs.

MANN, G. 1954. La vida de los peces in aguas chileñas. Ministerio de Agricultura, Santiago. 342 pp., figs.

MANNING, J. A. 1957. Summary of investigations on the pelagic fish survey of Chilean waters with special reference to the swordfish, marlins and tunas. Univ. Miami, Marine Lab., Tech. Ref. 57–4: 65 pp. (Duplicated.)

MIAMI, UNIVERSITY OF. 1955. Lou Marron–University of Miami Pacific Billfish Expedition, Preliminary report for 1954. Univ. Miami, Marine Lab., Ref. 55-8: 65 pp., 22 figs.

MURPHY, R. C. 1926. Oceanic and climatic phenomena along the west coast of South America during 1925. Geogr. Rev. 16(1): 26–54, 16 figs.

ORBIGNY, A., D'. 1835–43. Voyage dans l'Amérique Méridionale, 5, pt. 3. Mollusques. P. Bertrand, Paris. 758 pp., 85 pls.

PFEFFER, G. 1912. Die Cephalopoden der Plankton-Expedition. Ergebn. Plankton Exp. Humboldt-Stift., vol. 2, 815 pp., 48 pls.

POSNER, G. 1957. The Peru Current. Bull. Bingham Oceanogr. Coll. 16(2): 106–155, figs.

RAHM, G. 1937. Zoologische Probleme an der südamerikanischen Westküste besonders über das Massensterben im Pazifik. C.R. 12e Cong. Int. Zool., Lisboa, 1935, vol. 2, 1237–47.

ROJAS, E. B. 1953. Estudios preliminares del contenido estomacal de las anchovetas. Bol. Cient. Compañia Administradora del Guano 1(1): 33–42, tables.

SCHNEIDER, C. O. 1930. Notas sobre la jibia chilena (*Ommastrephes gigas,* Hupé). Bol. Soc. Biol. Concepcion 3:117–124.

SCHWABE, G. H. 1951. Sobre las mortandades de peces en la Bahía de San Vicente y sus causas. Bol. Soc. Biol. Concepcion 26: 31–40, 2 figs.

SCHWEIGGER, E. 1949. Der Perustrom nach zwölfjährigen Beobachtungen. Erdkunde 3: 121–132, 229–240.

SEARS, MARY. 1954. Notes on the Peruvian coastal current. 1. An introduction to the ecology of Pisco Bay. Deep-Sea Res., 1(3): 141–169, 4 figs., 3 tables.

STIGLICH, G. 1925. El fenómeno maritimo del Aguaje. Rev. Mar. Perú, 10(1): 25–40.

SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING. 1942. The Oceans. Prentice Hall, Inc., New York. 1,077 pp., 265 figs., 7 charts.

U.S. NAVY HYDROGRAPHIC OFFICE. 1938. Sailing Directions for South America. Vol. 3. Publ. 174: 484 pp.

WILHELM, G. O. 1930. Las mortandades de jibias (*Omastrephes gigas*) en la Bahía de Talcahuano. Bol. Soc. Biol. Concepcion 3: 23–38, 10 figs.

——— 1932. Das Massensterben von Tintenfischen in der Bucht von Talcahuano. Atti 11° Congr. Internaz. Zool. Padova: 334–339, pls. 6–9.

——— 1954. Algunas observaciones acerca de las mortandades de jibias (*Dosidicus gigas* D'Orb) en el litoral de Concepcion. Rev. Biol. Mar. Valparaiso 4: 196–201, figs.

WOOSTER, W. 1959. Yearly changes in the Peru Current. Paper, Pacif. Section, Amer. Soc. Limnol. Oceanogr., San Diego, Calif., June 17, 1959.

Studies on the Embryology of *Pycnopodia helianthoides* (Brandt) Stimpson

DONALD L. GREER[1]

THE EMBRYONIC DEVELOPMENT of *Pycnopodia helianthoides,* the 20-rayed sea star, which has a small egg (120μ), an indirect form of development, and larval metamorphosis, has not been previously reported in detail. Mortensen (1921) was able to rear only the early gastrula. No other references to the development of *Pycnopodia* have been found. Species of other multi-rayed sea stars with a yolky egg (and in consequence a more direct form of development) are much better known, e.g., *Solaster endeca* (Gemmill, 1912), *Leptasterias hexactis* (Osterud, 1918), and *Crossaster papposus* (Gemmill, 1920).

The main problems requiring study were the developmental stages between Mortensen's gastrula and metamorphosis, and the number of rays formed by the newly metamorphosed sea star. This latter problem arises from Ritter and Crocker (1900), who studied fixed material from the Harriman Alaska Expedition and gave a good description of a series of stages showing ray interpolation starting from a young specimen with eight rays. Nevertheless, in referring to the larval and post larval origin of rays, Ritter and Crocker (1900: 253) "assumed that at least five, probably all, of the *six rays of our youngest specimens* are, as in other starfishes, of larval beginning." The other two rays of their youngest specimen were small and were considered post larval in origin.

The purpose of this study is to report the continuous observation under laboratory culture of the development of *Pycnopodia* from fertilization to completion of metamorphosis. The newly metamorphosed larva has five arms.

This study was conducted at the Friday Harbor Marine Laboratories of the University of Washington, Friday Harbor, Washington. The author wishes to thank Dr. Robert L. Fernald, director of the Laboratories, for providing facilities and Dr. Dixy Lee Ray for reading the manuscript. Appreciation also is expressed to Mr. David Chase for his photographs of the living larvae.

MATERIALS AND METHODS

Adult animals were collected from the intertidal zone on San Juan Island, Washington, and were kept at the Friday Harbor Laboratories in tanks of running sea water. The animals thrived under these conditions, feeding on a variety of mollusks and sea urchins. In order to determine the sex of the animals without sacrificing them, a biopsy was performed by using a hypodermic needle to extract and examine a small amount of gonadal material. The sex and degree of ripeness of the gonad thus determined, a pair of animals was placed in each tank.

On the morning of Apr 8, 1960, the animals in captivity spawned; the male spawned first in each tank. One large female had been observed to spawn earlier during the latter part of Mar. No other spawning occurred although the animals were kept under constant observation. Mortensen (1921) reported the spawning of *Pycnopodia* at Nanaimo, British Columbia, in May and June.

To ensure natural fertilization, gametes were collected with a clean glass pipette as they emerged from the gonopores. They were then washed in filtered sea water. A sperm suspension was added to the eggs and the time of fertilization recorded. The zygotes were cultured in shallow glass dishes containing filtered sea water maintained at a temperature of 10–12 C on shallow sea water tables. The sea water in the dishes was changed daily until the swimming blastula stage was reached. The larvae were fed on a mixture of the solitary diatom *Nitzschia,* and the unicellular alga *Dunaliella.* The older bipin-

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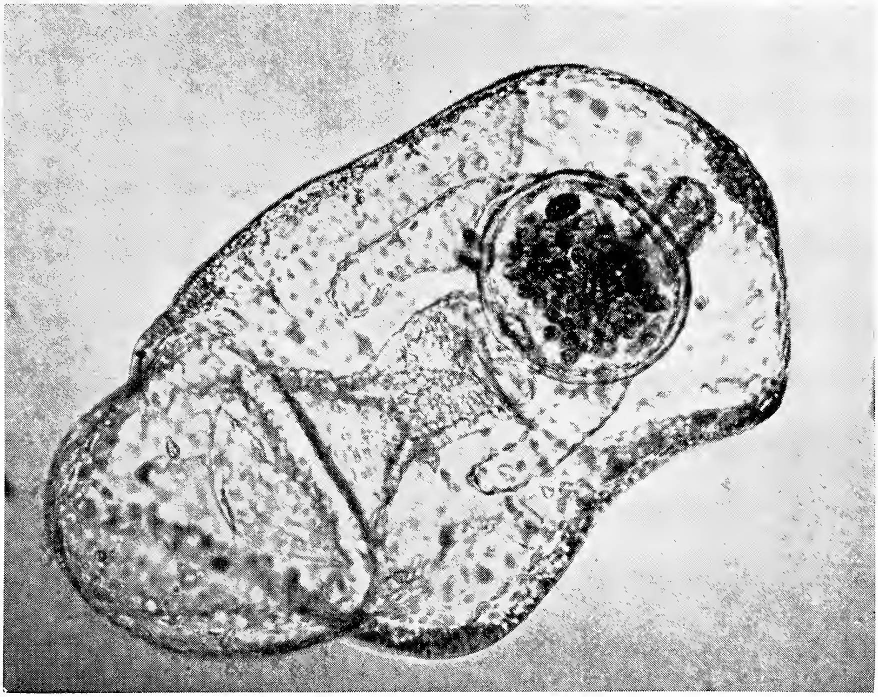

FIG. 1. Photograph of living bipinnarian larva, approximately 23 days old. Dorsal view. Note coelomic sacs and food in stomach. × 200.

narian and brachiolarian larvae were fed additional food materials in the form of marine protozoa and diatoms collected from small tide pools. This variety of food with the occasional supplementation from chance bacterial invasion provided even better results than *Nitzschia* alone. Under these conditions, 12 embryos were reared through metamorphosis. After metamorphosis, the 12 minute sea stars were placed in an aquarium which prevented their escape but allowed a continuous flow of fresh sea water. A variety of food materials was offered to the small sea stars, but none was observed to feed, and no satisfactory food material could be found. Their survival for 5 months after metamorphosis was apparently due to their feeding on debris that accumulated on the bottom of their aquarium.

Samples of the culture were removed for study at intervals throughout the period of development. Early samples were made frequently. They were preserved in Bouin's fixative. Later samples of the large bipinnarian and brachiolarian larvae, taken less frequently, were fixed in 10% formalin in sea water to minimize shrinkage. As it was hoped to follow the growth rate of post-metamorphic specimens for as long as possible and the material was not abundant, only 1 animal out of the 12 was fixed at the time of metamorphosis. Eleven specimens remained with which it was hoped to study growth and further development at least up to Ritter and Crocker's earliest specimens. As explained above, it proved impossible to find the right food. Such growth as did occur over the 5 months of laboratory culture (from approximately 1 mm diameter to 3 mm diameter) could hardly be considered normal. It was noteworthy that there was no further morphological development. Observation during this period had to be restricted to weekends, and the young which died during the interval had dispersed in the culture vessels. Thus there is no fixed material for this phase of the study. The fixed material obtained was stained with Grenacher's Borax Carmine method (Pantin, 1960: 23–24), after which whole mounts were made.

OBSERVATIONS

The embryos within the culture showed a wide variation in size. Even though the exact time of fertilization was known, crowding, feeding, temperature, and other similar factors appeared to influence the growth of the embryos. Despite these variations, the development of *Pycnopodia* closely resembles that of other sea stars having an indirect form of development, e.g., cleavage is holoblastic and almost equal, resulting in a typical blastula and gastrula. Of special interest during the early developmental period, however, is the appearance of large spaces between the blastomeres at the 4-cell stage, causing the blastomeres to appear loosely connected. The blastocoel itself begins to form at the 8- or 16-cell stage. Repeated cell divisions produce a well-formed ciliated blastula which rotates within the fertilization membrane. The blastulae soon "hatch" or break away from this membrane and swim freely. Gastrulation is by embolic invagination. Formation of mesenchyme does not occur until gastrulation is well advanced or completed. The appearance of a mouth completing the digestive system in the bipannarian larva denotes the beginning of feeding (Fig. 1). This stage is reached about 5 days after fertilization. The early development and the features of the larvae resemble those of *Asterias rubens* (Gemmill, 1914); i.e., preoral and post oral ciliated bands, complete digestive system, hydroporic canal and pore development from the left enterocoelic pouch, and the complete and elaborate development of the enterocoelae. The bipinnarian stage is prolonged and the elaborations of the enterocoelae occur late during this stage. The appearance of the brachiolarian arms about the fiftieth day marks the beginning of the brachiolarian larva (Fig. 2). The short brachiolarial arms appear anteriorly surrounding the sucker and provide temporary attachment prior to metamorphosis. Permanent attachment of the larvae is by means of the sucker. Metamorphosis occurs approximately 60–70 days after the onset of development. A summary of the chronological development is given below.

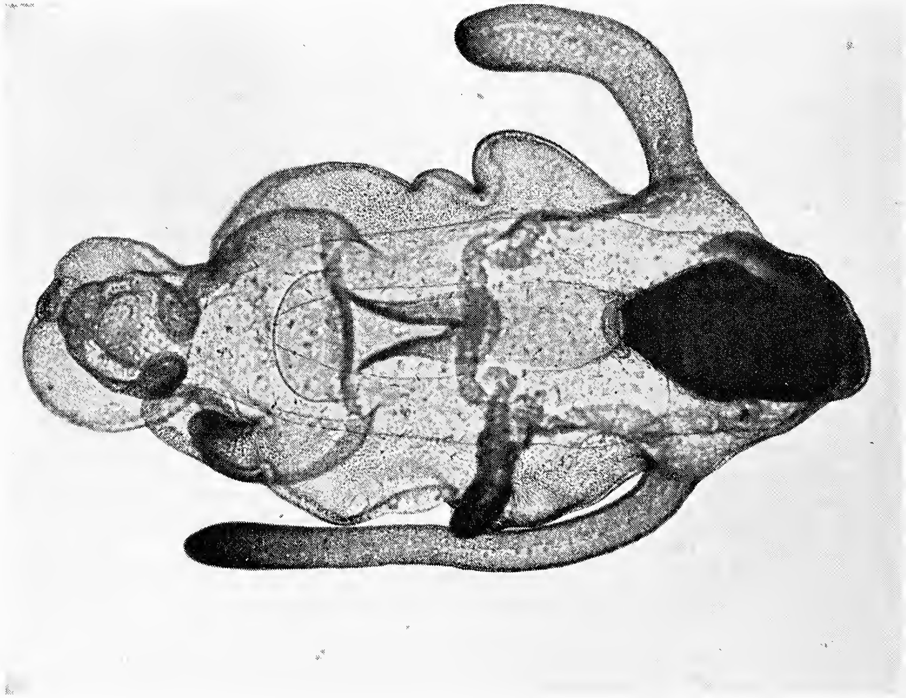

FIG. 2. Photograph of living brachiolarian larva, approximately 7 weeks old. Dorsal view. Note beginning of arm rudiments. × 55.

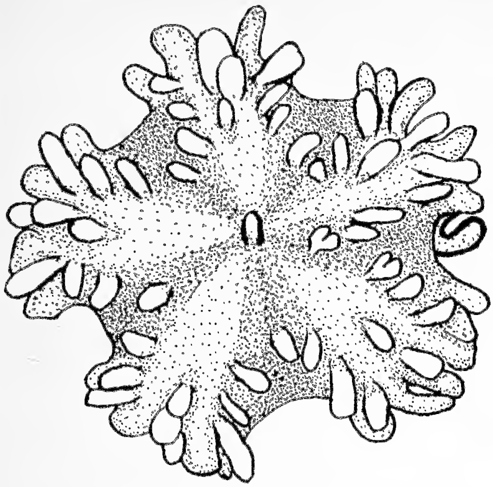

FIG. 3. Aboral view of young 5-rayed *Pycnopodia.* (Camera lucida drawing, × 100.)

1st day: cleavage completed.
2nd day: swimming blastulae.
3rd day: gastrulation completed.
4th day: beginning of mesenchymal formation; formation of enterocoelic sacs.
5th day: early bipinnarian larvae; regions of digestive canal distinct.
6th day: hydroporic canal and pore formed.
12th day: distinct forward and backward extensions of enterocoelic sacs.
32nd day: fusion of right and left anterior coeloms in preoral lobe.
7th week: brachiolarian larvae; formation of brachiolarian arms.
9th week: first metamorphosed animal.
10th week: metamorphosis of all specimens completed.

Shortage of material for sectioning prevented a detailed study of the internal changes during metamorphosis. The development of *Pycnopodia* prior to metamorphosis closely resembles that of *Asterias rubens;* it is therefore probable that this similarity of development also continues through to metamorphosis. Once permanent fixation by larval sucker has occurred, changes in the external morphology of the larva during metamorphosis are rapid. In general, a reabsorption of the larval elements occur, revealing the rudimentary disc and arms of the young sea star. The anterior and middle regions of the larva including "all the larval ciliated processes, as well as the larval anus for the short period during which it can still be recognized, are now on the oral side of the starfish disc" (Gemmill, 1914: 252). The arm rudiments are now clearly visible from the aboral surface of the disc. The young star remains attached by its sucker for 3 or 4 days. When two to three pairs of tube feet have appeared on each arm the sucker is ruptured near the disc and the young sea star begins its free life. The number of arm rudiments clearly visible in this stage of the multi-rayed *Pycnopodia* is *five* (Fig. 3).

The number of primary arms in *Pycnopodia* at the time of metamorphosis has been an open question. Ritter and Crocker's (1900: 260) interpretation of ray multiplication in *Pycnopodia* was made, as they said, "in the absence of knowledge of the embryology of the species." Indeed, no studies of ray formation in other multi-rayed sea stars had been reported at the time. Even though, as reported, *Pycnopodia* is a five-rayed individual at the time of metamorphosis, the question raised by Ritter and Crocker (1900: 260), "What is the relation of ray A [the sixth ray] to the five rays of the asterid ground plan?" still needs an answer. They showed that the sixth ray had a unique relationship to the two bud-

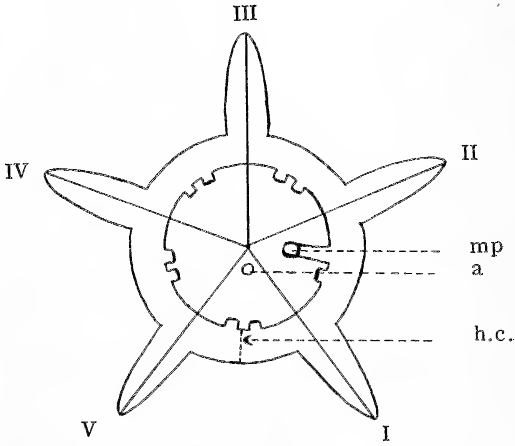

FIG. 4. Aboral view to illustrate numbering of rays and position of hydrocoel closure in 5-rayed asteroids. (Redrawn from Gemmill, 1914.) *mp*, Madreporite; *a*, anus; *h.c.*, hydrocoel closure and position of larval stalk.

ding zones which give rise to all the secondary arms. These secondary arms are interpolated in pairs on each side of the sixth ray. The origin of the sixth ray they supposed to arise from a radial closure of the hydrocoel, i.e., the sixth ray would rise from the exact point of closure. Ritter and Crocker (1900: 265) also suggested "that the two budding zones of the new rays correspond to the region of closure of the hydrocoel ring."

The closure of the hydrocoel ring, so far as is known in five-rayed asteroids, occurs inter-radially (Fig. 4). Information on the embryology of the multi-rayed asteroids *Solaster endeca* (Gemmill, 1912), *Leptasterias hexactis* (Osterud, 1918), and *Crossaster papposus* (Gemmill, 1920) shows that the closure of the hydrocoel is also inter-radial. According to Gemmill (1914), the stalk, hydrocoel closure, and the anus all occur in the same inter-radium in *Asterias.* Therefore, taking the stalk as a point of reference, the hydrocoel closure is inter-radial in *Pycnopodia* (Fig. 5). It is at this point that, if Ritter and Crocker's (1900) hypothesis is true, one would expect to find the sixth ray. However, neither the newly metamorphosed animals nor later forms showed any indication of a sixth ray. The appearance of the sixth ray at this point of closure would still be radial in reference to the hydrocoel itself. Unfortunately, we still have no information of the place and time of origin of the sixth ray. The thickened area shown in oral view in the region of the hydrocoel closure (Fig. 6) is thought to be the disintegrating larval sucker and stalk. The evidence that the "larval organ" in *Pycnopodia* is found at the point of closure is in support of Ritter and Crockers' (1900) suggestion that the sixth ray is in some way possibly related with the "larval organ" of other asteroids.

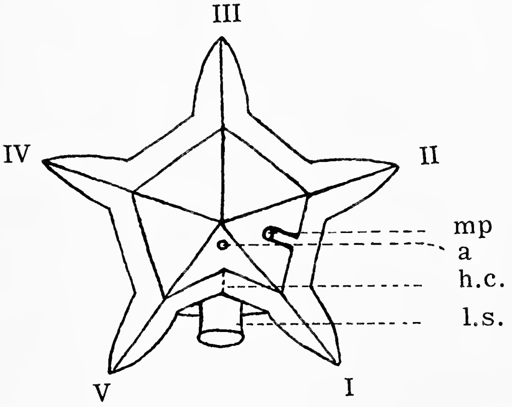

FIG. 5. Aboral view (diagrammatic) to show relationship of hydrocoel closure to larval stalk in *Pycnopodia. mp,* Madreporite; *a,* anus; *h.c.,* hydrocoel closure; *l.s.,* larval stalk.

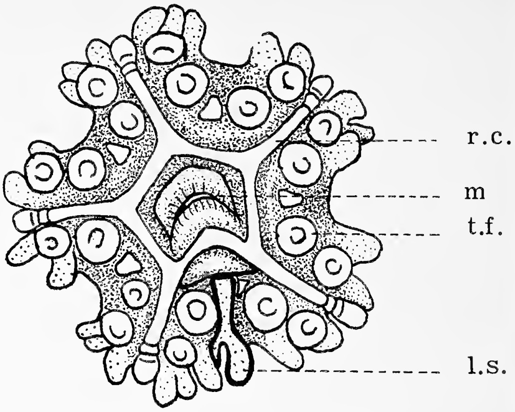

FIG. 6. Oral view of young *Pycnopodia.* Note larval stalk. *l.s.,* Larval stalk; *m,* mouth; *r.c.,* radial canal; *t.f.,* tube feet. (Camera lucida drawing, × 100.)

SUMMARY

This contribution reports that only five primary rays are present in the multi-rayed sea star *Pycnopodia helianthoides* at the time of metamorphosis and suggests that the hydrocoel closure is inter-radial in position. The relationship of the sixth ray to the primary rays and the hydrocoel closure is still unsolved. However, the fact that the five-rayed condition exists for a time after metamorphosis, even though this time may have been lengthened by laboratory culture conditions, demonstrates that the appearance of the sixth ray is secondary to the original five of the asteroid ground plan.

REFERENCES

GEMMILL, J. F. 1912. The development of the starfish *Solaster endeca* Forbes. Trans. Zool. Soc. Lond. 20(1): 1–72, 5 pls.

——— 1914. The development and certain points in the adult structure of the starfish *Asterias rubens,* L. Phil. Trans. Roy. Soc. ser. B, 205: 213–294, 7 pls., 1 fig.

——— 1920. The development of the starfish *Crossaster papposus,* Muller and Troschel. Quart. J. Micr. Sci. 64: 155–190.

MORTENSEN, T. H. 1921. Studies of the Development and Larval Forms of Echinoderms. G. E. C. Gad, Copenhagen. 261 pp., 33 pls., 102 figs.

OSTERUD, H. L. 1918. Preliminary observations on the development of *Leptasterias hexactis.* Publ. Puget Sound Biol. Sta. 2(32): 1–15, 5 pls.

PANTIN, C. F. A. 1960. Notes on microscopical technique for Zoologists. Cambridge Univ. Press, Cambridge. 76 pp.

RITTER, W. E., and G. R. CROCKER. 1900. Multiplication of rays and bilateral symmetry in the 20-rayed star-fish, *Pycnopodia helianthoides* (Stimpson). Proc. Wash. Acad. Sci. 2: 247–274, 2 pls.

Predation on the California Sea Hare, *Aplysia californica* Cooper, by the Solitary Great Green Sea Anemone, *Anthopleura xanthogrammica* (Brandt), and the Effect of Sea Hare Toxin and Acetylcholine on Anemone Muscle

LINDSAY R. WINKLER and BERNARD E. TILTON[1]

BECAUSE THERE ARE NO KNOWN PREDATORS to feed on them in their adult state, the sea hares do not seem to enter into the prey-predator relationships of the sea. They do, however, appear to have a place in the food economy in certain limited ways. Great numbers of larvae are produced by the sea hares (MacGinitie, 1934), which presumably are consumed in large numbers by predaceous plankton and filter-feeders. Large quantities of sea weed are masticated, partially digested, and passed in the fecal pellets, thus somewhat abbreviating the process by which sea weed becomes detritus. Finally, when the adults die their bodies become a part of the marine economy by providing nutrition for bacterial flora, or perhaps for scavengers such as *Pachygrapsus,* which on occasion have been observed feeding on the bodies of dead sea hares.

Fitch of the California Fish and Game Laboratories (1961) virtually eliminates predation by fish; he and his staff have examined the stomach contents of approximately 10,000 fish representing 100 or more species, many of which live in close association with *Aplysia,* and have as yet found no evidence of any *Aplysia* remains. No other animal is known to prey on postmetamorphic *Aplysia.*

The probability of any more direct contribution of *Aplysia* to the food economy of the sea or to a prey-predator relationship seemed more removed by the demonstration of a toxin with cholinergic (acetylcholinelike) action from the digestive glands of the California sea hares (Winkler, 1961; Winkler, Tilton and Hardinge, in press). In addition to any effects of the strongly persistent, musky odor and of the protective secretions of these animals to be dealt with in an ensuing paper, this toxin would seem to make them a questionable article of predator diet, at least during the postmetamorphic adult stages.

While a specimen of the Solitary Great Green Anemone, *Anthopleura xanthogrammica* (Brandt), was being removed from the rocks in a lagoon at Lunada Bay, Palos Verdes, California (during mid-Nov), it regurgitated a young partially-digested specimen of *Aplysia californica* Cooper. Since these young sea hares were present in considerable numbers in the lagoon, other anemones were immediately examined. Five sea hare remains were obtained from the first six anemones checked. A further check of other anemones outside the lagoon, where fewer young sea hares were found, produced sea hare remains less frequently but doubled the number of *Aplysia* remains for study. One crab cheliped was the only other evidence of enteric contents recovered from the anemones.

This find showed an ecological relationship not previously reported and led to experiments to determine if the toxin-containing digestive gland was retained and digested, and, if retained, what the effect of the cholinergic activity of the *Aplysia* toxin (aplysin) might be on the anemone.

MATERIALS AND METHODS

All field studies were carried out and specimens were routinely obtained at Lunada Bay, Palos Verdes, California. Anemones were checked for enteric contents by inserting the index finger through the mouth, exploring the enteron therewith and extricating any solid matter found. Remains recovered were preserved in formol-alcohol. After preservation, remains were sketched, photographed, and weighed, and the digestive gland was carefully removed and reweighed separately.

In order to calculate the approximate original weight of a sea hare from the weight of its digestive gland, data obtained from previous observations were used (Winkler, 1961). A similar study was made with *A. vaccaria* Winkler.

The digestive glands of *A. vaccaria* and *A. californica* may readily be distinguished by their form and histology. The gland of the former is

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diffuse, composed of convoluted folds with large and numerous sulci interspersed; while the latter is compact, without folds or convolutions. The histology is distinguished by the appearance of large numbers of oval brown granules of approximately 100 μ in *A. californica,* while granules are only rarely found as sparse, irregular objects in an occasional specimen of *A. vaccaria.*

Studies on the intact animal were carried out both in the field and in laboratory–maintained specimens. Specimens were fed small living sea hares and pieces of digestive gland. Field specimens were injected with aplysin and the results noted.

Three types of isolated anemone muscle were used: (1) The septum retractor muscle, an internal vertical muscle near the medial margin of the septa; (2) The internal walls of the pharynx, removed and used in isolated baths; (3) Strips of the external circular muscle, 1 × 6 cm, cut from the body wall just below the tentacles. The latter specimens were cut from the living animals which were then replaced in the aquarium and soon recovered, regenerating the lost tissues.

The muscular tissue was ligated at both ends. One end was tied to a solid plastic support while the other activated a pressure transducer the output of which was fed through an amplifier into a Grass electronic recorder. The muscles were immersed in an aerated 30 ml sea water bath to which small amounts of the aplysin and acetylcholine were added. Aplysin was prepared as described by Winkler (1961) and Winkler, Tilton, and Hardinge (in press). Acetylcholine was used in 1% solution in all cases.

RESULTS

The condition of the partially digested remains of 10 sea hares (*Aplysia californica*) is shown on Figure 1, and the weights of the remains and those of the digestive glands with the calculated probable weights of the living animals are listed in Table 1. The per cent of total body weight of the digestive glands from 15 living *A. californica* were calculated in a previous experiment but are first reported herewith. The average of 10.8% (standard deviation ± 1.73%) is somewhat lower than that for *A. vaccaria* which averages 18% (standard deviation ± 3.83%). Since this present study utilized only preserved specimens on which no other data were available, all weights were calculated on the basis that the digestive gland represents 10% of the total weight. This figure may vary somewhat from fact but is probably quite close and seems to be adequate for the present study.

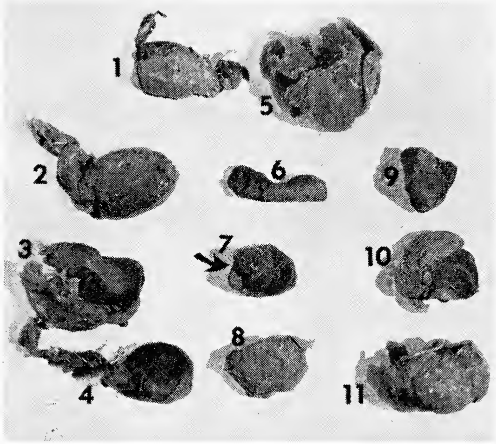

FIG. 1. Remains of *Aplysia californica* Cooper obtained from enteric cavities of the sea anemone, *Anthopleura xanthogrammica* (Brandt). Numbers correspond with those of analysis in Table 1.

In the field, experimental feeding of digestive gland to three anemones resulted in ingestion but in two cases expulsion took place during the limited period of observation. These experiments were supplemented by numerous feedings to four specimens maintained in an aerated, cooled salt water aquarium. The ingestion was immediate, followed by a slow regurgitation in 5–10 min. (Anemones were normally fed on frog muscle, which was not regurgitated). The regurgitated material was covered with an envelope of thick mucus.

Small sea hares were fed alive to anemones; and although ingested, in all except the case of a weakened animal (no. 1), the sea hares were able to escape. The fact remains, however, that in nature some at least do not escape.

The anemones in the field, when injected with aplysin, gave inconclusive results. The most uniform reaction was contraction of the area injected for a period of time, but it was difficult to interpret this as being greatly different from the effect of a simple puncture except that it was more persistent. When aplysin was released in the enteron the anemone would close in a few minutes, but part of the tentacles might maintain their expanded positions.

The isolated septum retractor muscle of the anemone was slightly contracted by aplysin, while the wall of the enteron (including the pharynx) was insensitive to large doses of both aplysin and acetylcholine. Regular jagged contractions were initiated in the former by acetylcholine but not by aplysin. These contractions disappeared upon washing and returned when acetylcholine was again added. The wall of the enteron and pharynx did not show a response when stimulated with glass rods inserted in the mouth of living sea anemones as long as the external oral margin was not touched. However, stimulation of the external oral margin yielded an unfailing response. Apparently the internal enteron wall is devoid of tactile receptors or ganglia producing contractatory responses.

Arcs of tissue taken from the external body wall and suspended in a tissue bath were very sensitive to acetylcholine and to aplysin. Strong responses were elicited which were of added interest in that, without the washing, the height of response fell off rapidly and returned to the base line or below it in 3–5 min (Fig. 2). Upon adding acetylcholine to such an aplysin-excited preparation, no renewed response could be elicited, even though the muscle had relaxed (Fig. 2*a*). The same was true when aplysin was added to an acetylcholine-excited strip (Fig. 2*b*). Washing did not immediately renew sensitivity. When aplysin was applied first, the washing time required before sensitivity returned was ½ hr or more, as compared to 2–6 min in the case of acetylcholine. These time periods reflect quite accurately the relative washing times required for aplysin and for acetylcholine in the frog rectus abdominis assay procedure of Chang and Gaddum (1933).

DISCUSSION AND CONCLUSIONS

The extent to which *Anthopleura xanthogrammica* was preying on young *A. californica* in this particular location is interesting relative to the position of *Aplysia* in the food chains of life in the sea.

The anemones, however, appear to be a nearly "dead-end street" as far as a food chain is concerned, since some species of anemones are known to have lived in captivity at least 70 years (Annandale, 1912; MacGinitie, 1949) and apparently are not greatly preyed upon. In addition, the predator in this case is of a lower order of life than the prey. Thus the enormous numbers of larvae produced (MacGinitie, 1934) would seem to be the principal contribution of *Aplysia* to the food cycles of the sea. According to this concept the adult sea hares serve largely as reproductive machines increasing the supply

TABLE 1

ANALYSIS OF REMAINS OF *A. californica*
TAKEN FROM ENTERIC CAVITIES OF *Anthopleura xanthogrammica*

NUMBER*	SOURCE OF ANIMAL	WEIGHT IN GRAMS				% CONSUMED
		Remains	Digestive Gland	Approximate Original Weight of Animal	Amount Consumed	
1	fed animal	10	2	20	10	50
2	reef	21	10	100	79	79
3	animal	20	6	60	40	67
4	animal	13	5	50	37	74
5	reef	30	9	90	60	67
6	animal	3	1	10	7	70
7†	animal	7	4.5	45	38	85
8	animal	9	4	40	31	73
9	animal	7	3.5	35	28	79
10	animal	11	4	40	29	72
11	animal	25	8	80	55	69

* Number corresponds to those on photographs.
† The only specimen in which the taut translucent membrane surrounding the digestive gland had been penetrated.

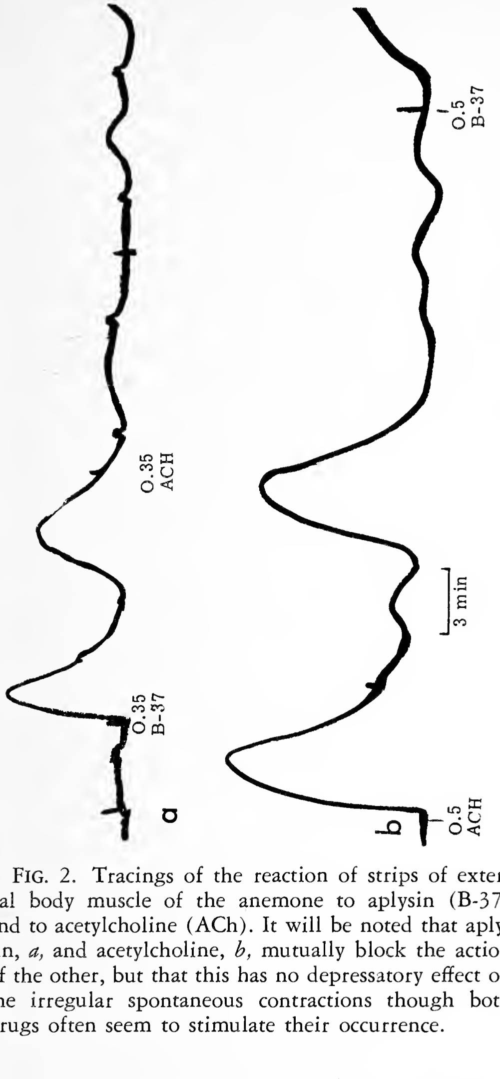

FIG. 2. Tracings of the reaction of strips of external body muscle of the anemone to aplysin (B-37) and to acetylcholine (ACh). It will be noted that aplysin, *a,* and acetylcholine, *b,* mutually block the action of the other, but that this has no depressatory effect on the irregular spontaneous contractions though both drugs often seem to stimulate their occurrence.

of microscopic organisms available as food. The findings of the present paper modify but little this latter concept.

Apparently the sea anemone consumes the sea hare without becoming a victim of the sea hare's digestive gland toxin because (1) the digestive gland appears usually to be regurgitated and (2) the toxin has only a transitory effect on the simple organ systems of the anemone. Study of the sea hares recovered from anemones suggested that the digestive gland is attacked by the digestive fluids of the anemone only after almost the entire sea hare has been consumed. The digestive gland of *A. californica* is consolidated and protected by a transparent membrane, which was found to be consistently exposed over a considerable area before it was finally penetrated. Thus most of the sea hare is digested and absorbed before sufficient irritation from the toxin is produced to stimulate rejection or to cause much effect on the anemone's system. The secretion of the thick mucus with which the sea hare digestive gland is coated by the anemone prior to its ejection is perhaps stimulated by local irritant qualities of the toxin, though Hyman (1940) states that this mucus is a normal reaction to any material ingested. The ejection itself is accomplished by a slow steady movement of the undesired material out of the mouth and over the surface of the perioral disk, at the margin of which it is finally released.

Aplysia toxin is a powerful cholinergic agent (Winkler, Tilton, and Hardinge, in press) acting upon both ganglia and parasympathetic nerve endings as well as on the neuromuscular junction in higher animals. The effect of acetylcholine on the external anemone muscle suggests that either acetylcholine or a similar agent is the transmitter substance. The spontaneous relaxation of anemone muscle experimentally contracted with either aplysin or acetylcholine is probably not the result of enzymatic destruction of the agent, as might occur with small amounts in higher animals, since no new contraction can be initiated by either acetylcholine or aplysin. Only after adequate washing can the muscles again respond.

The mutual antagonism would seem to indicate the same mechanism of action for aplysin as for acetylcholine. Certain cholinergic agents such as aplysin operate by mimicking the natural nerve transmitter substance, acetylcholine, but each has its own peculiar characteristics. In this case acetylcholine may be washed out in about 3 min, while aplysin takes ½ hr or more. The nerve receptors appear to be completely paralyzed and unable to be excited again until the transmitter substance has been completely removed.

According to Hyman (1940), the nervous system of anemones consists of two plexi: one, the epidermal plexus throughout the exterior body surface; the other, the gastrodermal plexus in the septa.

The epidermal plexus contains ganglion cells in the tentacles, oral disk, and pharynx. According to the Hertwigs, the ganglion cells are most numerous in the oral disc at the base of the tentacles where they form a centralized ring. Later workers have failed to verify this statement and Groselj (1909) locates the greatest concentration of the second nerve plexus in the upper end of the pharynx.

Thus considerable uncertainty as to the innervation of the sea anemones already exists—which may of course reflect species differences. These workers have probably correctly analyzed the species with which each worked. For the present species it seems obvious that the pharynx lacks nervous tissue sensitive to the tactile and chemical stimuli used, or that these agents initiate reactions other than contraction or relaxation (such as increased secretion of mucus or increased directional ciliary activity) which were not under study in the present paper. If these anemones are insensitive to acetylcholine it would then be likely that a chemical mediator other than acetylcholine may occur naturally, though neither epinephrine nor serotonin caused contraction of the pharynx in tissue bath.

The tactile sense is acute in the lips, which in this species consists of the scalloped margin of the mouth where it connects to the pharynx with an abrupt change of tissue color as well as of texture. The tactile sensitivity commences abruptly as a glass probe is passed onto the colored external tissue at the lips. This perioral disk area and the tentacles are very sensitive to tactile stimuli. These findings agree with the first innervation mentioned by Hyman (1940), as well as with her later discussion of the areas sensitive to tactile stimulation.

SUMMARY

1) Remains of *Aplysia californica* Cooper in various stages of digestion were taken from the enteron of various specimens of *Anthopleura xanthogrammica* (Brandt).

2) The estimated per cent of consumed material, in the case of 10 specimens taken from anemone digestive tracts, ran between 67 and 85%.

3) In no case was the digestive gland attacked by the digestive process.

4) In tissue baths aplysin and acetylcholine produced contractatory response of the external surface muscle, and no effect was noted on the internal wall of the enteron.

5) Tactile- or chemo-receptors, sensitive to acetylcholine and initiating contractatory responses, appear to be absent in the enteron and pharynx.

6) Segments of the external wall reacting completely to either acetylcholine or aplysin would relax to the starting level in 3–5 min. Subsequent application of the other agent showed the muscle to be unable to respond.

7) After washing, those treated initially with acetylcholine quickly regained their ability to respond. However, those treated initially with aplysin would respond again only after repeated washing.

8) It appears that the anemones may reject the digestive gland after having digested away the animal itself. However, if absorbed, aplysin would probably cause only a temporary contraction followed by relaxation and temporary paralysis.

REFERENCES

ANNANDALE, N. 1912. Aged sea anemones. Nature 89: 607.

CHANG, C. H., and J. H. GADDUM. 1933. Cholinesters in tissue extracts. J. Physiol. 79: 255.

FITCH, JOHN E. 1961. Personal communication.

GROSELJ, P. 1909. In quotation from Hyman, 1940.

HYMAN, L. H. 1940. The Invertebrates: Protozoa through Ctenophora. McGraw-Hill, New York. Pp. 583, 596.

MACGINITIE, G. E. 1934. The egg-laying activities of the sea hare, *Tethys californica* (Cooper). Biol. Bull. 67: 300.

——— 1949. Natural History of Marine Animals. McGraw-Hill, New York. P. 132.

WINKLER, LINDSAY R. 1961. Preliminary tests of the toxin extracted from California sea hares of the genus *Aplysia*. Pacific Sci. 15(2): 211.

WINKLER, LINDSAY R., BERNARD E. TILTON, and MERVYN G. HARDINGE. In press. A cholinergic extracted from sea hares. Arch. Int. Pharmacodyn.

Revision of the Genus *Pandanus* Stickman, Part 12
Queensland *Pandanus*

Harold St. John[1]

In 1958, under a grant from the National Science Foundation, the writer made an expedition in search of *Pandanus* in New Guinea and in Queensland, Australia. Most of the following novelties were collected on that trip, in company with Dr. Stanley T. Blake of the Botanic Museum, Brisbane.

SECTION *Pandanus*

Pandanus angulatus sp. nov. (sect. *Pandanus*) Figs. 107B, 109*a*

DIAGNOSIS HOLOTYPI: Arbor 7 m alta 2 dm diametro, radicibus fulturosis nullis, cortice cum radicillis adpresse adscendentibus, foliis 1.60–1.62 m longis 6.5–7 cm latis coriaceis in sectione mediali cum 63–65 nervis secundariis in quaque latere, gladiformibus ex base in apice subulato diminuentibus eo in puncto 10 cm ex apice 2 mm lato in sectione M-formatis basi amplexicauli inermi sed ex 22–25 cm marginibus cum aculeis 2.8–3.5 mm longis 8–14 mm distantibus graciliter subulatis adscendentibus apice brunneo, midnervo infra per partem 4/5 inferiorem inermi, in sectione mediali margine uno cum aculeis 1.8–2 mm longis 6–19 mm distantibus adpresse adscendentibus, margine alter inermi, proxima apicem marginibus inermibus sed midnervo infra cum serris 0.2 mm longis 5–8 mm distantibus, phalangibus 5–5.6 cm longis 4.7–6.1 cm latis 3.9–5.1 cm crassis luteo-aurantiacis late ellipsoideis basi truncata apice depresse convexo, parte ½ supera libera, suturis lateralibus profundis et V-formatis, lateribus dense papillosis et 7–9-angulatis et carpella quaque cum 3–8 angulis secundariis, suturis lateralibus evidentis angustis, sinibus apicalibus centralibus 7–12 mm profundis V-formatis, carpellis 9–14 apicibus centralibus pyramidalibus et multiangulatis, apicibus marginalibus pyramidalibus compressis et angulatis, in apice cum regione concava cartilaginea lucida et sub margine hoc stigmate 1.5–2.5 mm longo suborbiculari ad oblato cordato obscure brunneo sulcato obliquo, sinibus proximalibus ½–¾ ad fondam extentis, endocarpio submediali 2.5–3 cm longo solido osseoso brunneo lateribus 4–5 mm crassis, seminibus 15 mm longis 3 mm diametro ellipsoideo, mesocarpio apicali 8–20 mm longo cavernoso cum fibris membranisque, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 7 m tall, 2 dm in diameter; no prop roots; bark with appressed ascending rootlets; leaves 1.60–1.62 m long, 6.5–7 cm wide, coriaceous, at midsection with 63–65 secondary veins on each side, sword-like, tapering from the base to the subulate tip which about 10 cm down is 2 mm wide, 1-ribbed, but in section flattened M-shaped, the base amplexicaul and unarmed but beginning 22–25 cm from the base the margins with slender subulate prickles 2.8–3.5 mm long, 8–14 mm apart, ascending, brown tipped; the midrib below unarmed for lower 4/5 part; at the midsection one margin with prickles 1.8–2 mm long, 6–19 mm apart, closely appressed ascending, the other margin unarmed; near the apex the margins unarmed but the midrib below with serrae 0.2 mm long, 5–8 mm apart; phalanges 5–5.6 cm long, 4.7–6.1 cm wide, 3.9–5.1 cm thick, yellow-orange, broadly ellipsoid with a broad truncate base and a broad, low convex apex, upper ½ free, lateral sutures deep and V-shaped, the sides closely minutely papillose, with 7–9 principal angles and on each carpel with 3–8 secondary ridges and valleys; lateral sutures pronounced, narrow; apical central sinuses 7–12 mm deep, V-shaped; carpels 9–14, the apices of the central ones pyramidal but with numerous longitudinal ridges and valleys and mortised with the neighboring ones, the

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[1] B. P. Bishop Museum, Honolulu 17, Hawaii, U. S. A. Manuscript received June 26, 1961.

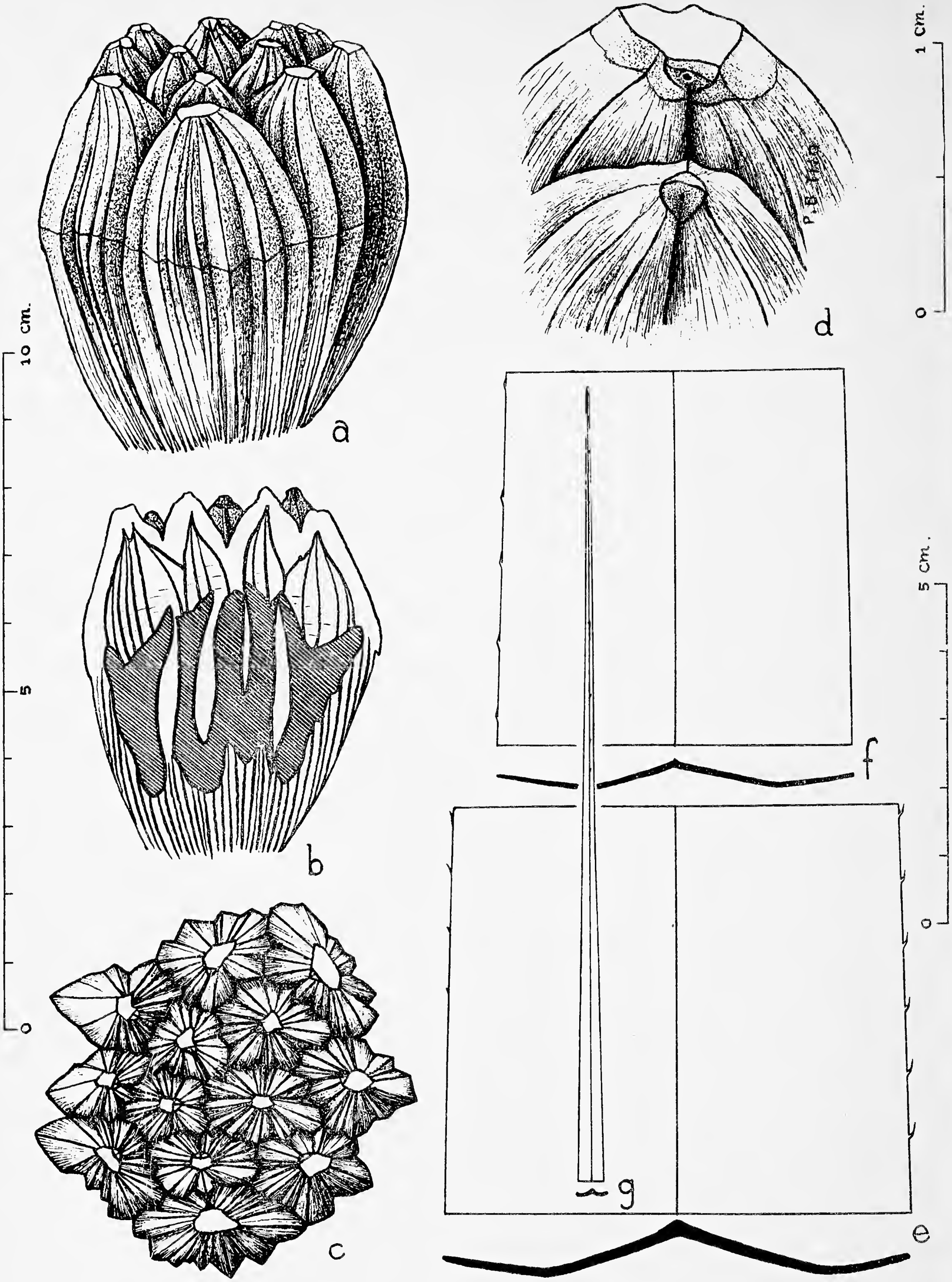

FIG. 107B. *Pandanus angulatus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices and stigmas, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

marginal ones pyramidal but flattened distally, similarly ridged, the apex with a cartilaginous, shiny concavity, under the proximal edge of which is the centripetal, steeply oblique stigma 1.5–2.5 mm long, suborbicular to oblate cordate, dark brown, creased; proximal crease in a narrow valley, running ½–¾ way to the mortised valley bottom; endocarp inframedian, 2.5–3 cm long, massive, bony, brown, the lateral walls 4–5 mm thick; seeds 15 mm long, 3 mm in diameter, ellipsoid; apical mesocarp cavernous in each carpel, 8–20 mm long, with numerous strong, longitudinal fibers and white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, 10 miles s.s.e. of Cooktown, towards Archer Point savanna, 20 ft. alt., Feb. 1, 1958, *H. St. John 26,242* (BISH).

DISCUSSION: *P. angulatus* is a member of the section *Pandanus,* and finds there its closest relative, *P. Solms-Laubachii* F. Muell. of Queensland, which has the phalanges 5–7 cm long, 2.5–4 cm wide, and the carpel apices semiorbicular-conic. In contrast, *P. angulatus* has the phalanges 5–5.6 cm long, 4.7–6.1 cm wide, and the carpel apices pyramidal and deeply many sulcate.

The new epithet is the Latin adjective meaning angled, in reference to the angled sides of the phalange and carpels.

Pandanus australiensis sp. nov. (sect. *Pandanus*)

Figs. 108, 109*b–d*

DIAGNOSIS HOLOTYPI: Arbor 13 m alta 2 dm diametro sparse furcata in corona laxa, cortice cum radicillis multis adscendente adpressis ramosis eis 3–4 cm longis et cum *Bryophytis* et *Pteridophytis* epiphyticis, radicibus fulturosis nullis, foliis 1.84–2.27 m longis 7.5–8 cm latis coriaceis in sectione mediali cum 68–72 nervis secundariis in quoque latere, in sectione oblate M-formatis gladiformatis ex basi in apice subulato diminuentibus eo in puncto 10 cm ex apice 3 mm lato basi amplexicauli et inermi sed ex 25–28 cm marginibus cum aculeis 1.5–2.5 mm longis 4–11 mm distantibus valide subulatis adscendentibus basibus pallidis apicibus rubrobrunneis, midnervo infra inermi excepta in apice, in regione mediali marginibus inermibus, circa apicem marginibus cum serrulis 0.1 mm longis 2–10 mm distantibus, midnervo infra cum serrulis simulantibus pluribus remotis, syncarpio inviso, phalangibus 5.6–6.1 cm longis 4.7–5.9 cm latis 4.1–5.4 cm crassis rotundato-obovoideis 5–6-subangulatis in sicco brunneo sed obscure rubro-tincto lateribus subconvexis sed cum dorsis longitudinalibus multis et papillosis rugosisque exlucidis parte ⅓ supera libera, apice depresse convexo, suturis lateralibus angustis sed prominentibus, sinibus centralibus apicalibus 5–8 mm profundis late V-formatis, carpellis 7–10 plerumque 8 apicibus semiorbiculari-pyramidalibus angulosis et cum dorsis secundariis supra punctatis et exlucidis infra rugosis et sublucidis lateribus distalibus cum 2–8 angulis et interobserratis, in apice cum concavite horizontali et ab eo cum projectioni proximali et infra eam stigmati 1.5–3 mm longo ovali vel suborbiculari nigri valde obliqui vel perpendiculari sulcato centripetali eis marginalibus plerumque truncatis, sinibus proximalibus prominentibus et cum labiis protrusis ¼–½ ad fondam extentis, endocarpio in parte 2/5 infera osseoso solido brunneo marginibus lateralibus 8–10 mm crassis, seminibus 20–22 mm longis 2 mm diametro sublinearibus, mesocarpio apicali cavernoso cum fibris validis multis et membranis medullosis aliquis et pilis, mesocarpio basali pauci sed fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 13 m tall, 2 dm in diameter, sparsely forked to form an open crown; bark with abundant appressed ascending branching rootlets 3–4 cm long, bearing moss and ferns as epiphytes; prop roots none; leaves 1.84–2.27 m long, 7.5–8 cm wide, coriaceous, at midsection with 68–72 secondary veins on each side, in section low M-shaped, swordlike, tapering from base to the subulate apex which 10 cm down is 3 mm wide, the base amplexicaul and unarmed, but beginning at 25–28 cm the margins with prickles 1.5–2.5 mm long, 4–11 mm apart, arcuate, stout subulate, ascending, pale below, the tips red-brown; midrib below unarmed except at very tip; at midsection the margins unarmed; near the tip the margins with serrulations 0.1 mm long, 2–10 mm apart, and the midrib below with several, remote similar serrulations; syncarp not seen; phalanges 5.6–6.1 cm long, 4.7–5.9 cm wide, 4.1–5.4 cm thick,

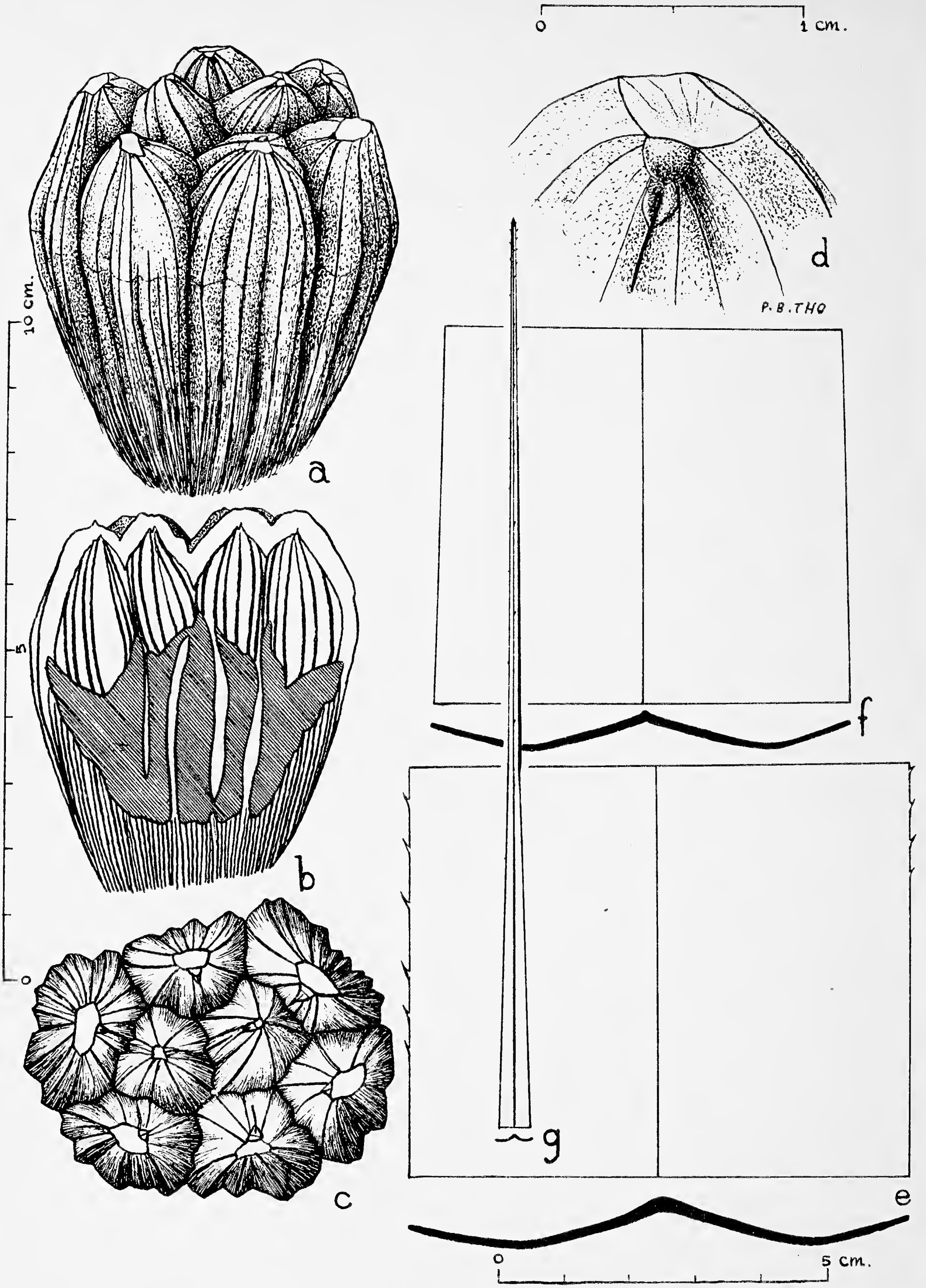

FIG. 108. *Pandanus australiensis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex and stigma, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

rounded obovoid, with 5–7 obscure angles, when dried brown but with traces of dark red, the sides gently convex but with many longitudinal ridges, the surface papillose and wrinkled, rather dull, upper ⅓ free, the apex low convex; lateral sutures well marked but narrow; central apical sinuses 5–8 mm deep, broad V-shaped; carpels 7–10, usually 8, the apices semiorbicular-pyramidal, angled and ridged on all sides, above the surface punctate and dull, below wrinkled and a little shiny, the distal sides of each with 2–8 angles and valleys, mortised with the neighbors, on the apex a prominent horizontal concavity leading to a visor over the stigma which is 1.5–3 mm long, oval to suborbicular, black, steeply oblique to perpendicular, creased, centripetal, the marginal ones mostly truncate; proximal sinus prominent and with protruding lips, running ¼–½ way to valley bottom; endocarp centering in lower 2/5, bony, massive, brown, the lateral margins 8–10 mm thick; seeds 20–22 mm long, 2 mm in diameter, almost linear; apical mesocarp cavernous, with numerous strong fibers and some medullary membranes and hairs; basal mesocarp of small extent, fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, 10 miles s.s.e. of Cooktown, towards Archer Point, rainforest in gully, 100 ft. alt., Feb. 1, 1958, *H. St. John 26,243* (BISH).

DISCUSSION: *P. australiensis* is a member of the section *Pandanus.* Its closest relative, *P. Whitei* Martelli of Queensland has the phalanges 7–7.3 cm long, 6–6.5 cm wide, the surface not punctate or rough, central apical sinuses 3–5 mm deep, the carpel apices obscurely pentagonal, rounded pyramidal; and the stigmas apical. On the other hand, *P. australiensis* has the phalanges 5.6–6.1 cm long, 4.7–5.9 cm wide, the surface papillose and wrinkled, the central apical sinuses 5–8 mm deep, the carpel apices sharply angled, semiorbicular-pyramidal, with the apex concave; and the stigma on the distal face.

Pandanus Blakei sp. nov. (sect. *Pandanus*)

Fig. 110

DIAGNOSIS HOLOTYPI: Arbor 6 m alta 18 cm diametro, cortice sparse muricatuli, radicibus fulturosis 1 m longis 4 cm diametro sparse muricatulis, foliis 1.45–1.5 m longis 8–8.5 cm latis coriaceis supra viridibus infra pallidis in sectione depresse M-formatis in apice subulato longe diminuentibus eo in puncto 10 cm ex apice 3.5 mm lato, basi inermi sed ex 6 cm marginibus cum aculeis 2–2.5 mm longis 3–20 mm distantibus pallidis subulatis adscendentibus, midnervo infra inermi ex basi et ultra mediam, in sectione mediali marginibus cum aculeis 1.5–2 mm longis 3–8 mm distantibus simulantibus adpressis vel in regionibus aliquis nullis, proxima apicem marginibus et midnervo infra cum serrulis 0.2–0.3 mm longis 2–6 mm distantibus, pedunculo 34 cm longo trigono bracteoso, syncarpio terminali solitario 20 cm longo 15 cm diametro ellipsoideo obtuse trigono cum 79 phalangibus eis 5.1–5.5 cm longis 3.2–4.6 cm latis 2.2–3.5 cm crassis (sed in geminis 5.5 cm latis) obovoideis subcompressis basi cuneata 5–6-angulosis lateribus sublucidis subcurvatis parte ½ supera libera apice oblato-convexo, suturis lateralibus nullis, sinibus centralibus apicalibus 1.5–3 mm profundis, carpellis 9–12 apicibus oblato-pyramidalibus ad pyramidalibus eis marginalibus minime majoribus valleculis latis vel angustis et V-formatis, stigmatibus 1–1.5 mm longis ovalibus ad obovatis sulcatis obliquis centripetalibus pallide brunneis, suturis proximalibus profundis et ½ ad fondam extentis, endocarpio mediali 2 cm longo osseoso obscure brunneo lateribus 3–4 mm crassis, seminibus 11–13 mm longis 4–5 mm diametro ellipsoideis vel obliquiter ellipsoideis, mesocarpio supero in carpella quaque cavernam rotundatam cum fibris paucis et membranis albis medullosis formato, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 6 m tall, 18 cm in diameter; bark sparingly muriculate; prop roots 1 m long, 4 cm in diameter, sparingly muriculate; leaves 1.45–1.5 m long, 8–8.5 cm wide, coriaceous, green above, pale beneath, in section perceptibly M-shaped, long tapering to the subulate apex, the tip 10 cm down 3.5 mm wide, the base unarmed for 6 cm, then the margins with prickles 2–2.5 mm long, 3–20 mm apart, pale, subulate, ascending; the midrib below unarmed near the base and essentially so to beyond the middle; at the midsection the mar-

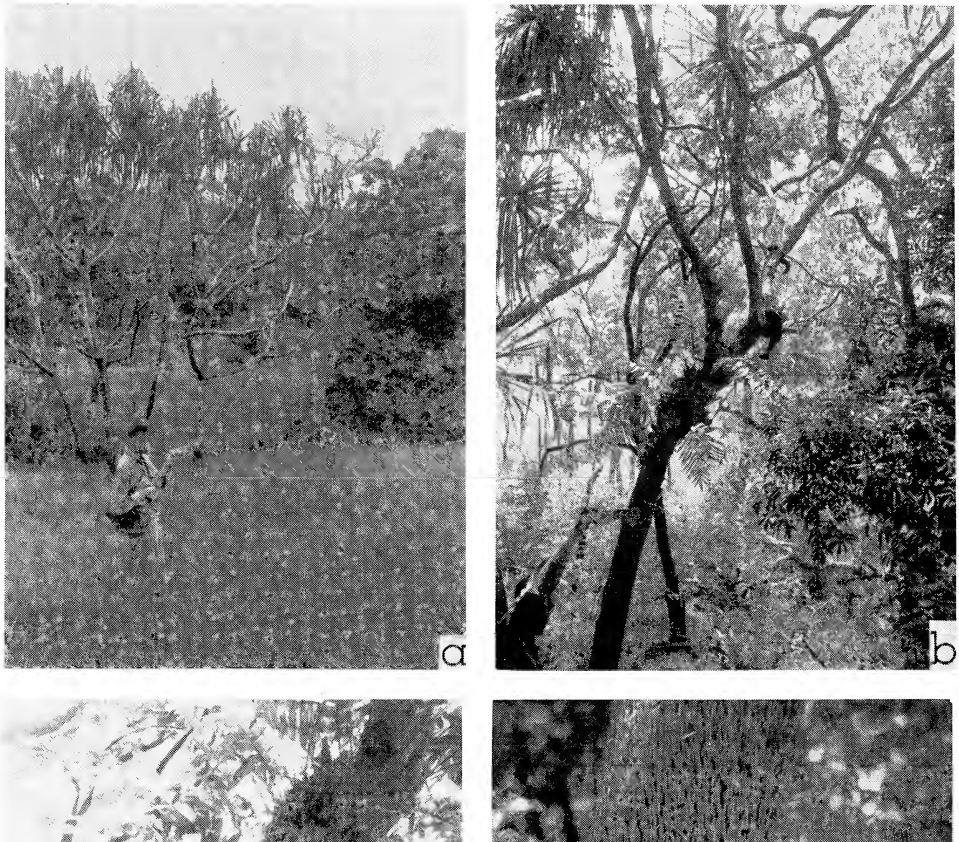

FIG. 109. *a, Pandanus angulatus* St. John, holotype, habit. *b, P. australiensis* St. John, holotype, branches and crown; *c,* trunk with epiphytes, and portrait of S. T. Blake; *d,* trunk covered by appressed ascending, adventitious rootlets.

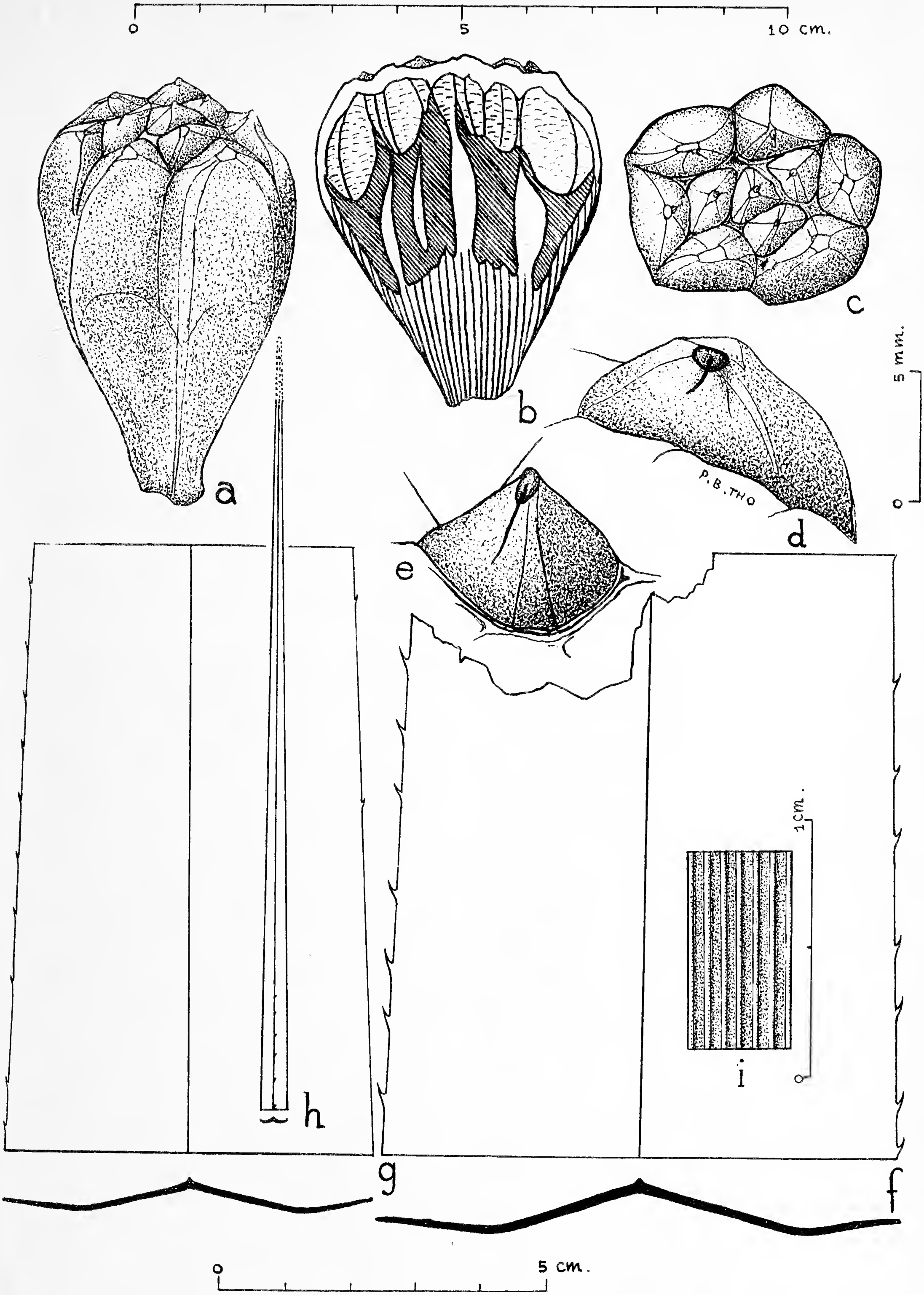

FIG. 110. *Pandanus Blakei* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* marginal carpel apex and stigma, oblique view, × 4; *e,* narrower central carpel apex, and stigma, oblique view, × 4; *f,* leaf base, lower side, × 1; *g,* leaf middle, lower side, × 1; *h,* leaf apex, lower side, × 1; *i,* secondary veins at midsection, lower side, × 4.

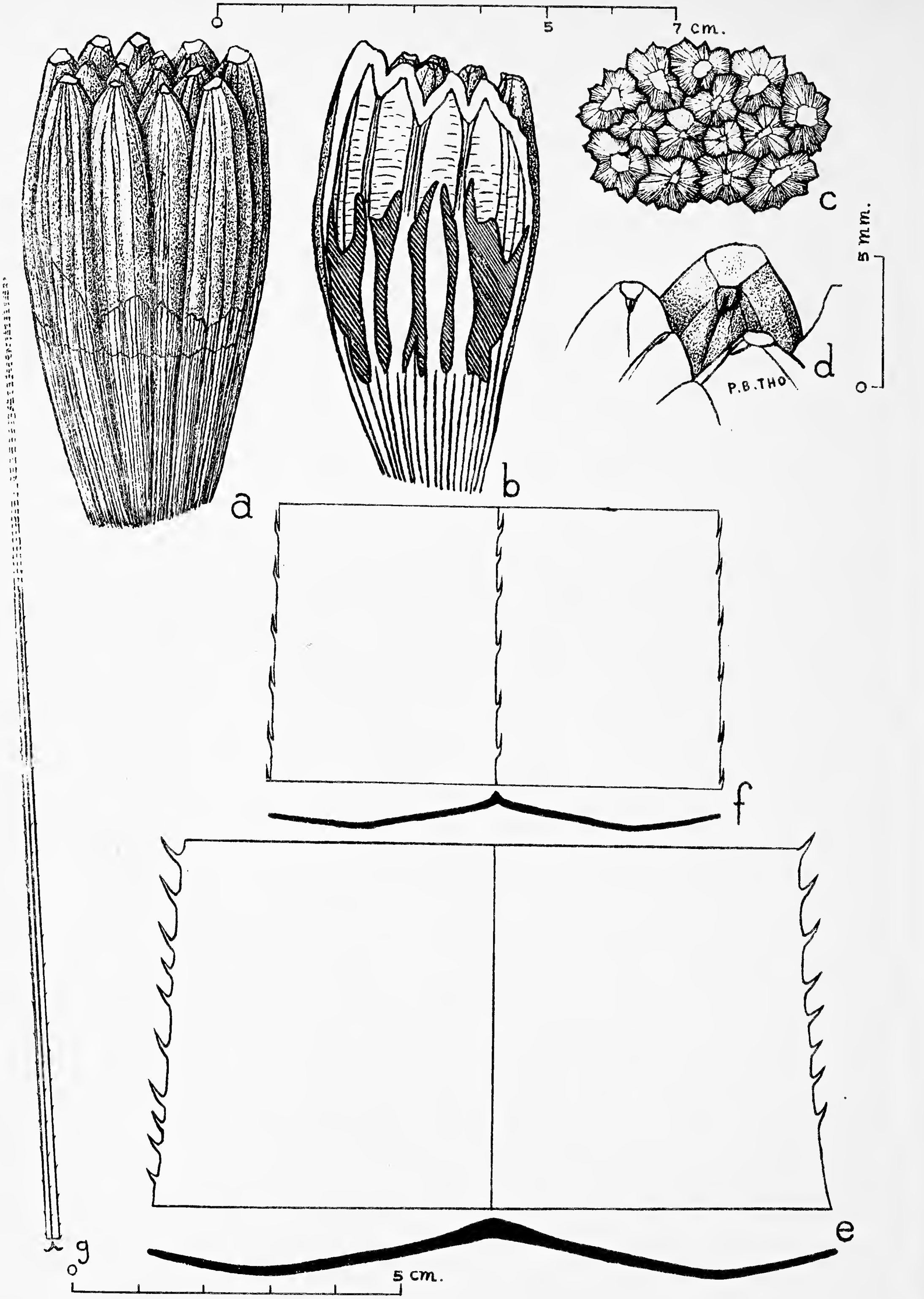

FIG. 111. *Pandanus citraceus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices and stigmas, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

gins with prickles 1.5–2 mm long, 3–8 mm apart, similar, appressed or for some distance wanting; near the tip the margins and midrib below with serrations 0.2–0.3 mm long, 2–6 mm apart; peduncle 34 cm long, trigonous, leafy bracted; syncarp terminal, solitary, 20 cm long, 15 cm in diameter, ellipsoid, 3-sided, bearing 79 phalanges, these 5.1–5.5 cm long, 3.2–4.6 cm wide, 2.2–3.5 cm thick, (in a double 5.5 cm wide), obovoid, somewhat compressed, the base cuneate, 5–6-angled, the sides smooth, somewhat shining, gently curved, upper ½ free, apex low convex, lateral sutures none, apical central sinuses 1.5–3 mm deep; carpels 9–12, their apices from low pyramidal to pyramidal, the marginal ones a little the larger, the valleys broad or narrow V-shaped; stigmas 1–1.5 mm long, oval to obovate, sulcate, oblique, centripetal, light brown; proximal crease deep, running ½ way to valley bottom; endocarp median, 2 cm long, bony, dark brown, the lateral margins 3–4 mm thick; seeds 11–13 mm long, 4–5 mm in diameter, ellipsoid or obliquely so; apical mesocarp forming in each carpel a rounded cavern with a few longitudinal fibers and filled with white, medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, Yule Point, 27 miles n. of Cairns, top of sea beach with *Scaevola frutescens, Clerodendron inerme, Vitex trifolia* var. *ovalifolia, Ipomoea pes-caprae* ssp. *brasiliensis,* Feb. 5, 1958, *H. St. John 26,260* (BISH).

DISCUSSION: *P. Blakei* is a member of the section *Pandanus.* Its closest relative is *P. somersetensis* St. John, of Queensland, which has the phalanges 4–5.1 cm wide, upper ¼ free, the apical central sinuses 0.5–1 mm deep; carpels 7–9, the apices of the marginal almost flat, but of the central perceptibly depressed conic; stigmas 1.5–3 mm long; leaves 6.8–7.2 cm wide, and at midsection unarmed, the leaf tip 10 cm down 7 mm wide. In contrast, *P. Blakei* has the phalanges 3.2–4.6 cm wide, upper ½ free, the apical central sinuses 1.5–3 mm deep; carpels 9–12, their apices from low pyramidal to pyramidal; stigmas 1–1.5 mm long; leaves 8.3–8.5 cm wide, and at midsection the margins armed with prickles 1.5–2 mm long, and the leaf tip 10 cm down 3.5 mm wide.

This species is named in honor of Dr. Stanley T. Blake, of the Brisbane Botanic Gardens.

Pandanus citraceus sp. nov. (sect. *Pandanus*)
Figs. 111, 139A*a–c*

DIAGNOSIS HOLOTYPI: Arbor 10–15 m alta 25–28 cm diametro, cortice cum radicillis multis adpresse adscendentibus, radicibus fulturosis nullis, foliis 2.3–2.85 m longis 7–8 cm latis coriaceis in sectione mediali cum 67–70 nervis secundariis in quoque latere, gladiformibus ex basi in apice subulato circa 30 cm longo diminuentibus eo in puncto 10 cm ex apice 2 mm lato, basi amplexicauli et inermi sed 12–26 cm ex basi marginibus cum aculeis 3–5 mm longis 6–12 mm distantibus subulatis arcuatis adscendentibus dimidio externo mahogani-brunneo, midnervo infra plerumque inermi, regioni mediali marginibus cum aculeis 3–3.5 mm longis 5–8 mm distantibus, simulantibus, midnervo infra acute salienti et cum aculeis 2.5–3 mm longis adscendentibus simulantibus, proxima apicem marginibus et midnervo infra cum aculeis 0.5–0.7 mm longis 2–6 mm distantibus subulatis adscendentibus, folio juvenali 2.7 m longo 10 cm lato et spinosiori marginalibus basalibus cum spinis 4–5.5 mm longis 4–11 mm distantibus subrectis crasse subulatis, midnervo infra ex 30 cm cum aculeis 3–4 mm longis 6–16 mm distantibus subulatis obscure mahogani-brunneis inferioribus reflexis alteris adscendentibus; inflorescentia foeminea terminali cernua foliosa, syncarpio solitario 23 cm longo 17 cm lato late ovoideo, phalangibus 6–7 cm longis 2.8–4.1 cm latis 2.2–3 cm crassis cuneatis vel oblanceo-cuneatis 5–6-angulatis in sicco rubro-brunneis, lateribus subcurvatis sed cum dorsis multis papillosis sublucidis et cutim Citri simulantibus, parte ⅗ supera libera apice truncato simulante sed in verite vadose concava, suturis lateralibus angustis in dimidia supera notatis, sinibus centralibus apicalibus 6–9 mm profundis anguste V-formatis, carpellis 9–16 (in geminis 19) apicibus anguste pyramidalibus eis centralibus symmetricalibus sed marginalibus distaliter compressis et cum apice concavo parvo inflexo, lateribus cum dorsis et valleculis pluribus, stigmatibus 1.5–2 mm longis ellipticis subnigris papillosis sulcatis valde obliquis ad verticalibus centripetalibus, sinibus proximalibus ⅔ distantia ad fondam extentis, endocarpio minime submediali 25–30 mm longo osseoso obscure mahogani-colorato paginis interioribus lucidis lateribus 3–4 mm crassis, seminibus 17–22 mm longis 3–4 mm diametro ellipsoideis, mesocarpio supero in carpella quaque cavernam cum in lateribus fibris et in centro membranis medullosis transversis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 10–15 m tall, 25–28 cm in diameter; bark with many appressed ascending rootlets; prop roots none; leaves 2.3–2.85 m long, 7–8 cm wide, coriaceous, at midsection with 67–70 secondary veins on each side, swordlike, tapering from base to the subulate apex about 30 cm long, and about 10 cm down 2 mm wide, the base amplexicaul and unarmed but beginning 12–26 cm up the margins with prickles 3–5 mm long, 6–12 mm apart, subulate, arcuate, ascending, the outer half mahogany brown; the nearby midrib below mostly unarmed; at midsection the margins with prickles 3–3.5 mm long, 5–8 mm apart, similar; the midrib sharply salient below and with similar ascending prickles 2.5–3 mm long; near the apex the margins and midrib below with subulate ascending prickles 0.5–0.7 mm long, 2–6 mm apart; the leaf of a juvenile sprout is 2.7 m long, 10 cm wide, and in general with more spiny margins, those near the base being 4–5.5 mm long, 4–11 mm apart, nearly straight, stout subulate; and the midrib below beginning 30 cm from the base has prickles 3–4 mm long, 6–16 mm apart, subulate, wholly dark mahogany brown, the lower ones reflexed, the others ascending; pistillate inflorescence terminal, nodding, leafy bracted; syncarp solitary, 23 cm long, 17 cm wide, broadly ovoid; phalanges 6–7 cm long, 2.8–4.1 cm wide, 2.2–3 cm thick, cuneate or oblance-cuneate, 5–6-angled, when dried reddish brown, the sides gently curving but with many longitudinal ridges, papillose, almost shiny, resembling Citrus skin, upper 3/5 free, apex appearing truncate but actually usually shallowly concave, lateral sutures narrow, distinct at least in upper free part, central apical sinuses 6–9 mm deep, narrow V-shaped; carpels 9–16 (in a double 19), the apices narrowly pyramidal, the central ones symmetric, the lateral ones laterally compressed and with a small, oblique, concave apex slanting inward, the sides ridged and mortised with adjacent ones, the outer side of each with 3–9 secondary sharp ridges and valleys; stigmas 1.5–2 mm long, elliptic, blackish, papillose, creased, sharply oblique to vertical, centripetal; proximal sinus running ⅔ to all the way to the valley bottom; endocarp slightly submedian, 25–30 mm long, bony, dark mahogany colored, the inner surfaces shining, the lateral margins 3–4 mm thick; seeds 17–22 mm long, 3–4 mm in diameter, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with on the sides longitudinal fibers and within transverse medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, ½ mile w. of Trinity Beach, n. of Cairns, by small creek in *Eucalyptus* forest with *Melaleuca viridiflora, Dillenia alata, Eucalyptus alba,* 15 ft. alt., grove of *Pandanus,* Feb. 6, 1958, *H. St. John 26,265* (BISH).

DISCUSSION: *P. citraceus* is a member of the section *Pandanus.* Its closest relative is *P. mossmanicus* St. John. For a statement of the characteristic differences, see the treatment of that species.

The new epithet is from the generic name *Citrus,* plus the Latin adjectival ending *-aceus,* meaning citrus-like, in reference to the surface of the phalanges which is rugose, half shiny, appearing glandular, like the skin of an orange fruit.

Pandanus endeavourensis sp. nov. (sect. *Pandanus*)

Fig. 112

DIAGNOSIS HOLOTYPI: Arbor 7 m alta 2 dm diametro, cortice cum radicillis adpresse adscendentibus dense obtecto, radicibus fulturosis nullis, foliis 1.6–1.79 m longis 6–7.5 cm latis coriaceis in sectione mediali cum 59–61 nervis secundariis in quoque latere, in sectione depresse M-formatis ex basi in apice subulato diminuentibus eo gracili sed in parte perdito, basi amplexicauli et inermi sed ex 15–40 cm marginibus cum aculeis 2.5–4 mm longis 7–13 mm distantibus gracilibus subulatis brunneis adpresse adscendentibus, midnervo toto inermi, in sectione mediali et ad apicem marginibus iner-

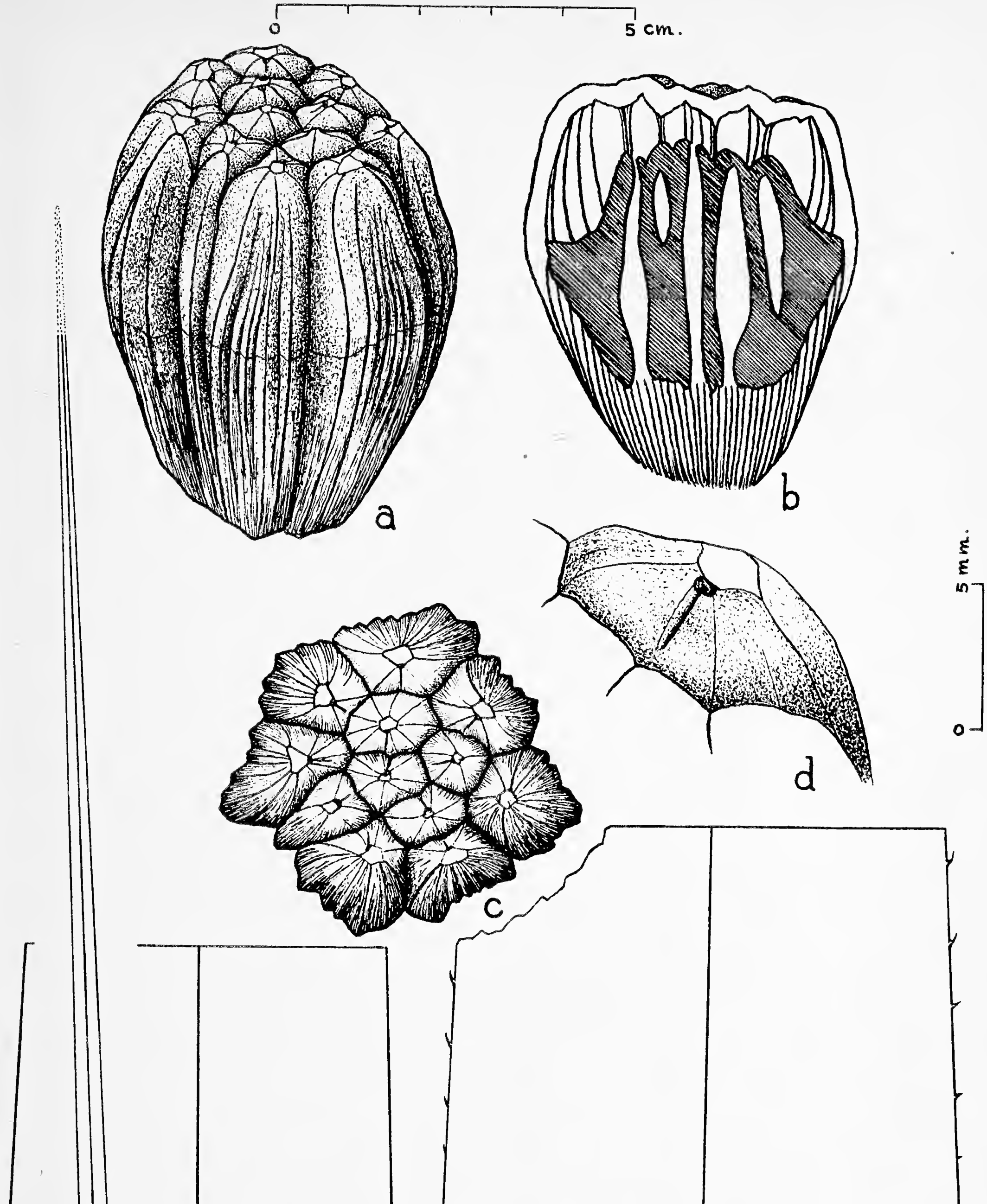

FIG. 112. *Pandanus endeavourensis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

mibus, phalangibus 5–5.8 cm longis 4.1–4.8 cm latis 3.7–4.5 cm crassis late obovoideis 5–6-angulatis in sicco brunneis lateribus punctatis et subscabris exlucidis sensim convexis sed cum angulis multis, parte ½ supera libera, apice oblato convexo vel enim truncato, suturis lateralibus distinctis, sinibus apicalibus centralibus 2–4 mm profundis curvatis vel sinuosis, carpellis 11–14 plerumque 12 apicibus subaequalibus oblato-pyramidalibus et cum concavite horizontali, stigmatibus 1–1.5 mm longis ovatis vel reniformibus brunneis sulcatis obliquis centripetalibus, sinibus proximalibus ½–⅔ ad fondam extentis, endocarpio minime supramediali 3.5 cm longo solido osseoso mahogani-brunneo intra lucido lateribus 8–9 mm crassis, seminibus 20 mm longis 4–5 mm diametro ellipsoideis, mesocarpio in apice carpella quaque cavernam cum fibris et medulla formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 7 m tall, 2 dm in diameter; bark densely covered with appressed ascending rootlets; prop roots none; leaves 1.6–1.79 m long, 6–7.5 cm wide, coriaceous, at midsection with 59–61 secondary veins on each side, depressed M-shaped in section, sword-shaped, tapering from the base to the subulate apex which is slender but the tip not preserved, the base amplexicaul and unarmed, but the margins beginning 15–40 cm up with prickles 2.5–4 mm long, 7–13 mm apart, slender subulate, brown, appressed ascending; midrib unarmed throughout; at the midsection and from there to the tip the margins unarmed; inflorescence and syncarp not seen; phalanges 5–5.8 cm long, 4.1–4.8 cm wide, 3.7–4.5 cm thick, broadly obovoid, 5–6-angled, when dried brown, the sides punctate and slightly roughened, dull, gently convex but with many angles, upper ½ free, the apex very low convex or even truncate; lateral sutures distinct; central apical sinuses 2–4 mm deep, wide, curved or sinuous; carpels 11–14, mostly 12, the apices subequal, much depressed pyramidal, the actual apex with a mostly horizontal concavity, the distal sides with 4–8 sharp angles and valleys, running almost to the apex and thus mortised with the adjacent ones; stigmas 1–1.5 mm long, ovate to reniform, brown, creased, oblique, centripetal; proximal sinus in a valley, running ½–⅔ way to the bottom; endocarp slightly supramedian, 3.5 cm long, massive, bony, mahogany-brown, the seed cavities shining, the lateral walls 8–9 mm thick; seeds 20 mm long, 4–5 mm in diameter, ellipsoid; upper mesocarp forming in each carpel apex a cavity with stout fibers and pith; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, by airstrip, 5 miles w.n.w. of Cooktown, savanna, 10 ft. alt., Feb. 1, 1958, *H. St. John 26,251* (BISH).

DISCUSSION: *P. endeavourensis* is a member of the section *Pandanus*. Its closest relative is *P. orbicularis* St. John, of Queensland, which has the leaves 1.15–1.3 m long, 5.5–5.6 cm wide, the marginal prickles near the base 1.3–1.8 mm long; phalange 5.4–6.5 cm wide, subglobose, the sides almost smooth, a little shiny, the apex rounded; central apical sinuses 5–8 mm deep; and the carpels 7–12. In contrast, *P. endeavourensis* has the leaves 1.6–1.79 m long, 6–7.5 cm wide, the marginal prickles near the base 2.5–4 mm long; phalange 4.1–4.8 cm wide, broadly obovoid, the sides punctate and roughened, dull, the apex very low convex or even truncate; central apical sinuses 2–4 mm deep; and the carpels 11–14.

The species is named for the type locality, which is within a few miles of the Endeavour River, a name reminiscent of the ship commanded by Captain James Cook on his first world voyage. After stoving in its hull on the Great Barrier Reef, he managed to make the shore and beach his craft, H.M.S. "Endeavour," in the bay watered by the river that he named after the ship.

Pandanus exarmatus sp. nov. (sect. *Pandanus*)
Fig. 113

DIAGNOSIS HOLOTYPI: Arbor 9 m alta 20 cm diametro, cortice cum radicillis adpresse adscendentibus, radicibus fulturosis nullis, foliis 2.1 m longis 7.6–8.4 cm latis coriaceis in sectione mediali cum 62–65 nervis secundariis in quaque latere, in sectione depresse M-formatis gladiformatis ex basi in apice subulato diminuentibus sed apice non conservato, basi amplexicauli et inermi sed ex 24–41 cm marginibus cum aculeis 1.5–3 mm longis 6–25 mm distantibus, midnervo toto inermi, ex medio ad apicem marginibus inermibus, inflorescentia et syncarpio invisa, phalangibus 5.1–5.5 cm longis 3.1–4.8 cm latis 3.5–4.5 cm crassis late obovoideis 5–6-angulosis in sicco brunneo lateribus gradatim curvatis laevibus et lucidis in partibus expositis, apice subconvexo parte ½ supera libera suturis lateralibus angustis sed evidentis plerumque ad basim, sinibus apicalibus centralibus 7–10 mm profundis V-formatis exinterobseratis, carpellis 8–11, plerumque 9 apicibus centralibus ovoideo-pyramidalibus eis marginalibus semiorbiculari-pyramidalibus in latere distali compresso et cum 3–7 angulis et valleculis solum in parte mediali et cum apice subdivergenti, stigmatibus 2–3 mm longis ellipsoideis apicalibus sulcatis brunneis obliquis centripetalibus, sinibus proximalibus ½–⅔ ad fondam extentis, endocarpio submediali solido osseoso mahogani-brunneo intra lucido lateribus lateralibus 6–7 mm crassis, mesocarpio super in apice carpellae quoque cavernoso et cum fibris et membranis medullosis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 9 m tall, 20 cm in diameter; bark with appressed ascending rootlets; prop roots none; leaves 2.1 m long, 7.6–8.4 cm wide, coriaceous, at midsection with 62–65 secondary veins on each side, in section low M-shaped, sword-shaped, tapering from the base to the subulate apex, but the actual tip not preserved, base amplexicaul and unarmed, but the margins beginning at 29–41 cm with prickles 1.5–3 mm long, 6–25 mm apart, the midrib unarmed throughout; from the middle to the tip the margins unarmed; inflorescence and syncarp not seen; phalanges 5.1–5.5 cm long, 3.1–4.8 cm wide, 3.5–4.5 cm thick, broadly obovoid, 5–6-angled, when dried brown, the sides gently sloping, smooth and shiny almost throughout the exposed part, the apex moderately convex, upper ½ free, lateral sutures narrow but distinct all or nearly all the way; central apical sinuses 7–10 mm deep, V-shaped, not mortised; carpels 8–11, mostly 9, the apices of the central ones ovoid-pyramidal, of the marginal ones semiorbicular-pyramidal, the distal side compressed and with 3–7 perceptible angles and valleys just in the median part, and the apex somewhat diverging; stigmas 2–3 mm long, apical, ellipsoid, creased, brown, oblique and centripetal; proximal sinus prominent, running ½–⅔ way to valley bottom; endocarp submedian, massive, bony, mahogany-brown, in inner surfaces shining, the lateral walls 6–7 mm thick; upper mesocarp forming in the apex of each carpel a cavern with many fibers and with medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, by airstrip, 5 miles w.n.w. of Cooktown, savanna, 10 ft. alt., Feb. 1, 1958, *H. St. John 26,250* (BISH).

DISCUSSION: *P. exarmatus* is a member of the section *Pandanus.* Its closest relative is *P. australiensis* St. John, of Queensland, which has the phalanges 5.6–6.1 cm long, 4.7–5.9 cm wide, the sides with many longitudinal ridges running to the tip, the upper ⅓ free; central apical sinuses 5–8 mm deep, mortised; apices of the central carpels semiorbicular-pyramidal, the outer ones erect, and all bearing an apical concavity. *P. exarmatus* has the phalanges 5.1–5.5 cm long, 3.1–4.8 cm wide, the sides with longitudinal ridges only near the middle, upper ½ free; central apical sinuses 7–10 mm deep, straight or curving; apices of the central carpels ovoid-pyramidal, the outer ones somewhat divergent, all acute or obtuse.

The new epithet is the Latin word *exarmatus,* unarmed, chosen because of the nearly spineless leaves.

Pandanus medialinermis sp. nov. (sect. *Pandanus*)

Fig. 114

DIAGNOSIS HOLOTYPI: Arbor 7 m alta 15 cm diametro, cortice cum papillis adscendentibus, foliis 1.5–1.65 m longis 5–5.3 cm latis in sectione depresse sinuose M-formatis in sectione mediali cum 50 nervis secundariis in quoque latere, gladiformatis ex basi in apice subulato diminuentibus eo circa 10 cm ex puncto 4 mm lato basi amplexicauli et inermi sed ex 28–34 cm marginibus cum aculeis 2–2.5 mm longis 11–21 mm distantibus graciliter subulatis adscendentibus adpressis brunneis in margine uno per 1 dm productis, in altero per 2 dm productis, midnervo toto inermi, marginibus ex sec-

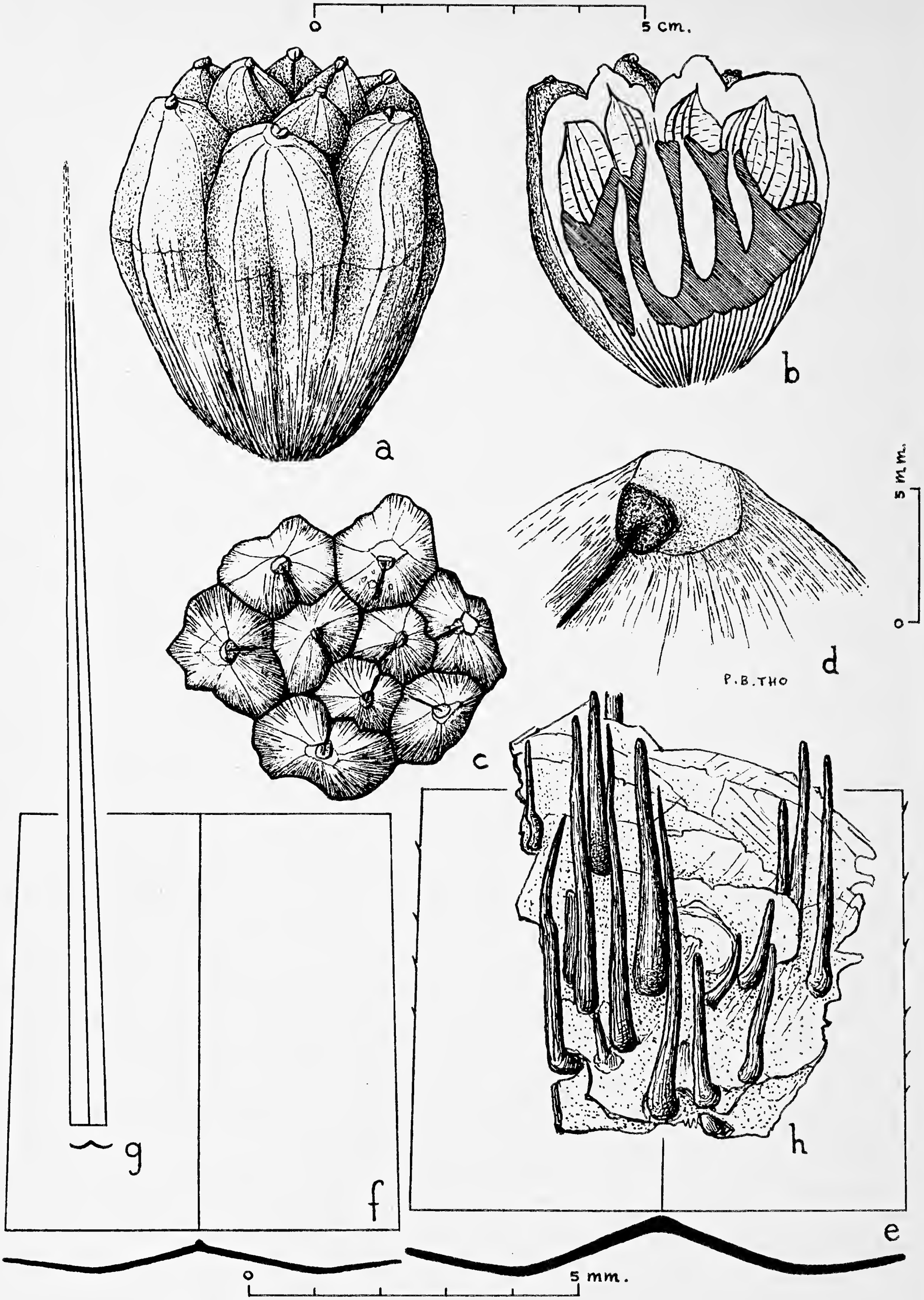

FIG. 113. *Pandanus exarmatus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex and stigma, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1; *h,* bark with appressed ascending adventitious rootlets, × 1.

tione mediali ad apicem inermibus, phalangibus 4.5–5 cm longis 5.8–7.4 cm latis 4.2–5.3 cm crassis late turbinatis subcompressis basi lata et truncata in sicco brunneis 4–6-angulosis apice alto-convexo lateribus subrugosis et cum rimosis longitudinalibus brunneis pluribus parte ½ supera libera, suturis lateralibus angustis in dimidia supera distinctis, sinibus centralibus apicalibus 1–2 mm profundis latis subcurvatis vel rectis, carpellis 8–11 (in geminis 16 et phalangio 8 cm lato) apicibus carpellarum centralium oblato-pyramidalibus cum concavite apicali parvo, eis marginalium cum apicibus tantum projectionibus laterum phalangium apicibus subangulatis et cum concavite majore, stigmatibus 1.5–2 mm longis obdeltoideis vel obovoideis et multis truncatis obscuris sulcatis centripetalibus eis centralibus obliquis et inflexis illis marginalibus plerumque in concavite sitis et divergentibus, sinibus proximalibus ¾ vel tota ad fondam extensis, endocarpio 3 cm longo mediali solido osseoso obscure mahogani-brunneo intra lucido lateribus lateralibus 7–8 mm crassis, seminibus 15–18 mm longis 4–5.5 mm diametro ellipsoideis, mesocarpio supera in apice carpella quaque cavernoso cum fibris fortibus et membranis pallidis medullosis, mesocarpio basali parvo fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 7 m tall, 15 cm in diameter; bark with ascending papillae; leaves 1.5–1.65 m long, 5–5.3 cm wide, in section low sinuous M-shaped, at midsection with 50 secondary veins on each side, swordlike, tapering from the base to the subulate apex, this about 10 cm down 4 mm wide, the base amplexicaul and unarmed, but beginning at 28–34 cm the margins with prickles 2–2.5 mm long, 11–21 mm apart, slender subulate, ascending, closely appressed, brown, produced for about 1 cm on one side, and 2 dm on the other; midrib unarmed throughout; from the midsection to the tip the margins unarmed; phalanges 4.5–5 cm long, 5.8–7.4 cm wide, 4.2–5.3 cm thick, broad turbinate, a little compressed, the wide base truncate, when dried brown, 4–6-angled, the apex high convex, the sides slightly rough and with several longitudinal, brown cracks, upper ½ free, lateral sutures narrow, distinct in upper half; central apical sinuses 1–2 mm deep, wide, gently curved or straight; carpels 8–11 (16 in a double and its phalange 8 cm wide), apices of central carpels flattened pyramidal, with a small apical concavity, those of the marginal carpels having the apices mere curved continuations of the sloping sides and not clearly separable from them, the sinuses no deeper, the apex slightly angled and with a larger concavity; stigmas 1.5–2 mm long, obdeltoid to obovoid, many truncate, dark, creased, centripetal, the central ones oblique and canted inwards, the marginal ones mostly in the concavity and canted outwards; proximal sinus running ¾ way to all the way to the valley bottom; endocarp 3 cm long, median, massive, bony, dark mahogany brown, the inner surfaces shining, the lateral walls 7–8 mm thick; seeds 15–18 mm long, 4–5.5 mm in diameter, ellipsoid; upper mesocarp forming in each carpel apex a small cavern with heavy fibers and pale medullary membranes; basal mesocarp sparse, fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, Six Mile Creek, 6 miles w. of Cooktown, fringing forest on small creek in *Eucalyptus* forest, 20 ft. alt., Jan. 3, 1958, *H. St. John 26,239* (BISH).

DISCUSSION: *P. medialinermis* is a member of the section *Pandanus.* In that section is its closest relative, *P. somersetensis* St. John, of Queensland, which has the bark muriculate; leaves 0.93 m long, 6.8–7.2 cm wide, near the tip the midrib below with ascending prickles 0.3 mm long; phalanges 5–5.5 cm long, 4–5.1 cm wide, narrowly obpyramidal, upper ¼ free, apex low convex, lateral sutures mostly none, central apical sinuses 0.5–1 mm deep, almost imperceptible; carpels 7–9, the apices depressed conic; and the endocarp walls 2–3 mm thick. *P. medialinermis* has the bark with ascending papillae; leaves 1.5–1.6 m long, 5–5.3 cm wide, midrib unarmed throughout; phalanges 4.5–5 cm long, 5.8–7.4 cm wide, broad turbinate, upper ½ free, apex high convex, lateral sutures distinct in upper half, central apical sinuses 1–2 mm deep; carpels 8–11, the apices with a terminal concavity; and the endocarp lateral walls 7–8 mm thick.

The new epithet is from the Latin *medialis,* middle; *inermis,* unarmed, in reference to the unarmed midrib.

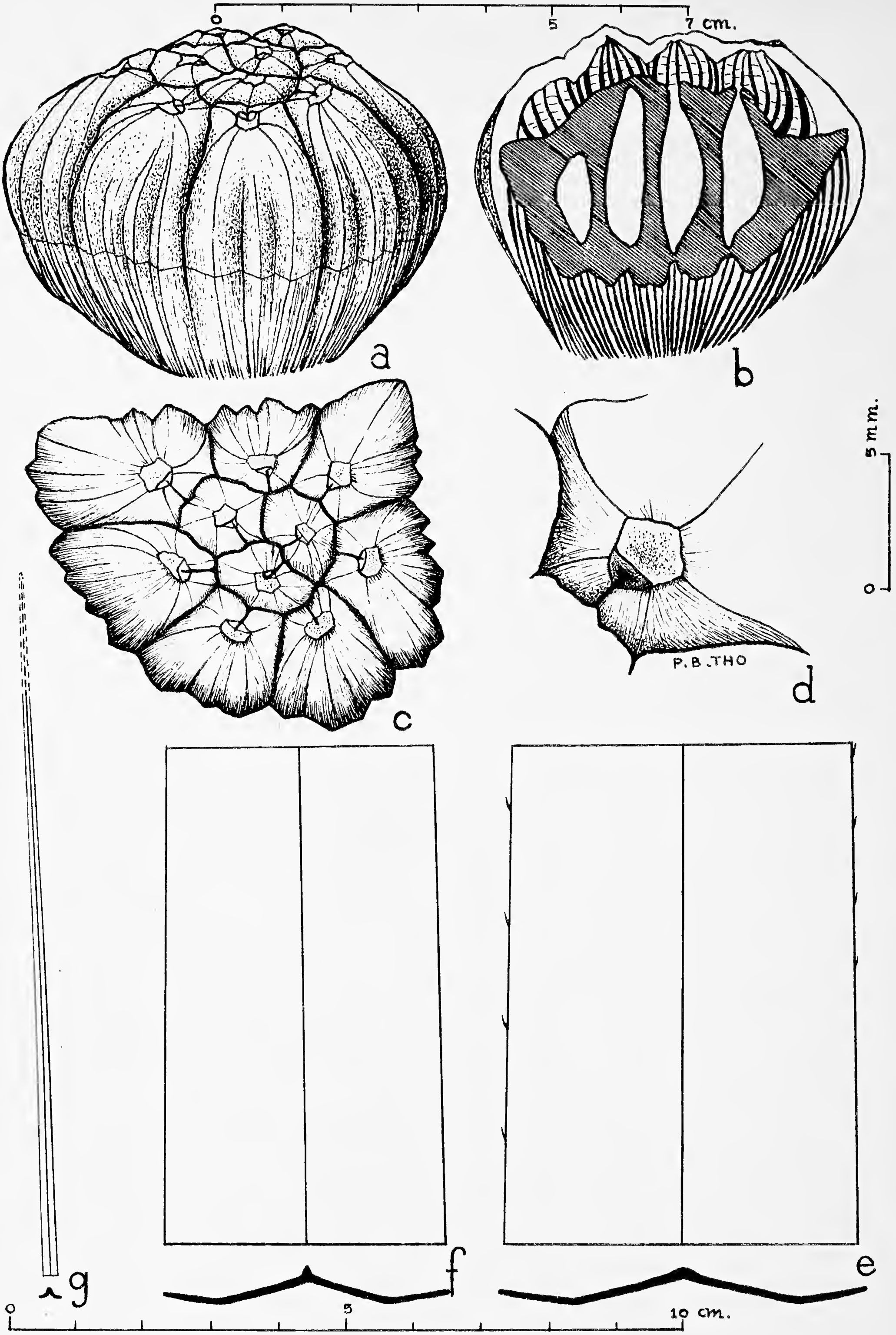

FIG. 114. *Pandanus medialinermis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex and stigma, apical view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

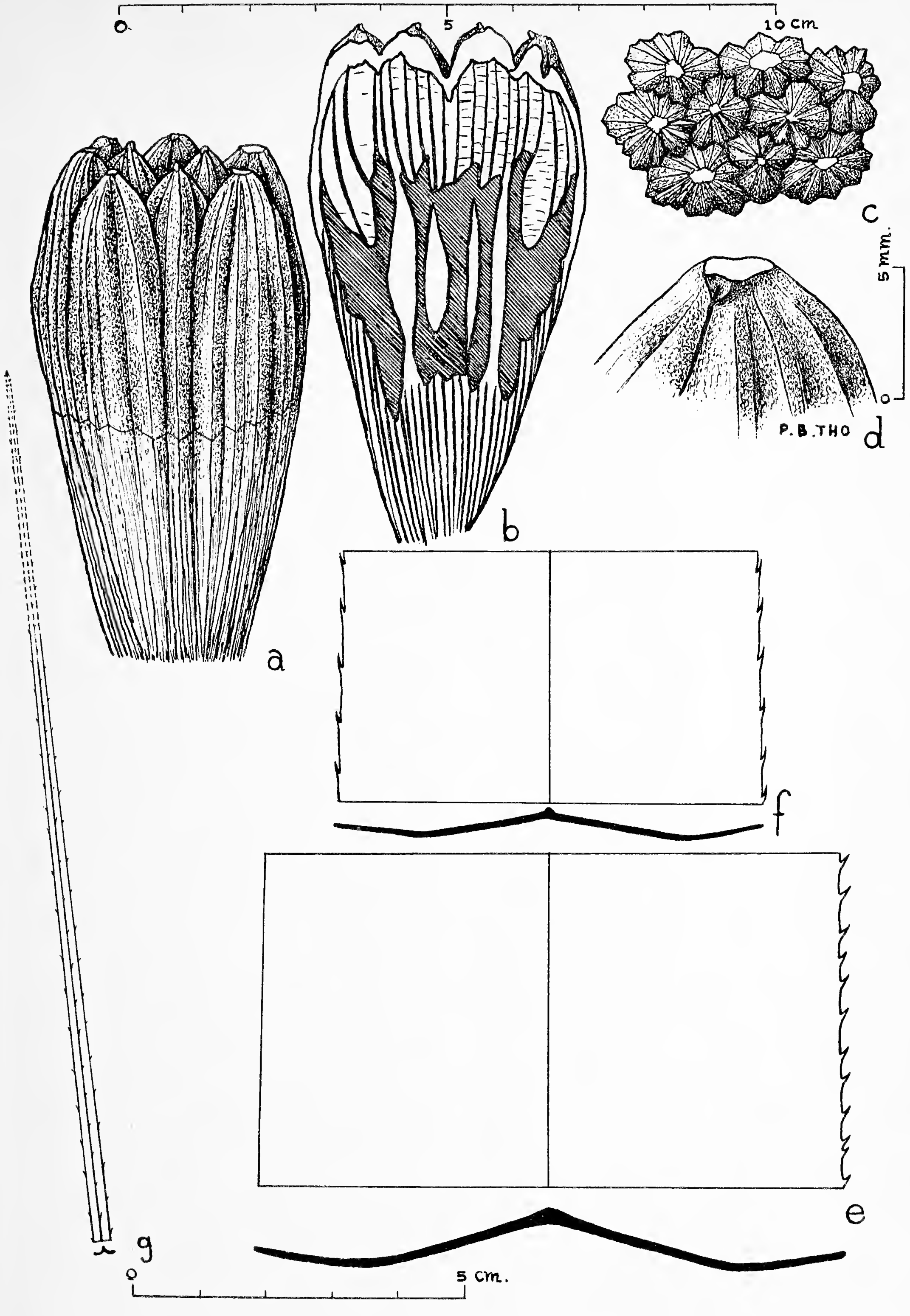

FIG. 115. *Pandanus mossmanicus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

Pandanus mossmanicus sp. nov. (sect. *Pandanus*)

Figs. 115, 116*a*

DIAGNOSIS HOLOTYPI: Arbor 13 m alta 22 cm diametro, trunco per 8–9 m singulo, cortice cum radicillis adpresse adscendentibus dense obtecto, radicibus fulturosis nullis, foliis 2.43–2.50 m longis 9.5–10 cm latis coriaceis in sectione mediali cum 67–74 nervis secundariis in quoque latere, gladiformibus ex basi in apice longo subulato diminuentibus eo in puncto approximato 10 cm ex apice 3–4 mm lato, basi amplexicauli inermi sed ex 20–25 cm marginibus cum aculeis 1.5–3 mm longis 3–11 mm distantibus validis subulatis adscendentibus apice brunneo, midnervo infra inermi in regione basali et mediali, in regione mediali marginibus cum aculeis 2–2.2 mm longis 5–12 mm distantibus crassiter subulatis subadpressis adscendentibus, proxima apicem marginibus cum serris 0.2–0.5 mm longis 2–5 mm distantibus, midnervo infra cum serris simulantibus sed gracilioribus, inflorescentia foeminea terminali cernua foliosa, syncarpio unico globoso, phalangibus 7.3–7.8 cm longis 3.7–4.7 cm latis 2.5–4.2 cm crassis elliptico-obovoideis in basi cuneatis 4–5 angulosis, dimidia supera mahogani-rubra lateribus subcurvatis papillosis et dense plicatis sublucidis et cuti. Citri simulantibus parte ½ supera libera apice truncato vel rare paene convexo-truncato, suturis lateralibus distinctis sed angustis, sinibus centralibus apicalibus 6–12 mm profundis V-formatis, carpellis 7–11 plerumque 8–9 apicibus anguste angulosis marginalibus semiorbiculari-pyramidalibus et pluribus in lateribus distalibus compressis, marginibus exterioribus cum 5–12 dorsis angustis longitudinalibus, lateribus interioribus item cum dorsis valleculisque, apice minime truncato vel concavo, apicibus centralibus plerumque lanceoloideo-pyramidalibus symmetricalibus, stigmatibus 1.5–2 mm longis sulcatis subnigris ovalibus vel marginalibus ceteribus in apice truncatis centripetalibus obliquis vel verticalibus proximalibus, sinibus proximalibus ad fondam extentis, endocarpio minime supramediali solido osseoso mahogani-colorato 35–38 mm longo summibus interioribus lucidis lateribus lateralibus 6–8 mm crassis, seminibus 13–15 mm longis 4 mm diametro ellipsoideis, mesocarpio supero in carpella quaque cavernam apicalem cum fibris plerumque marginalibus et cum membranis pallidis medullosis formanti, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 13 m tall, 22 cm in diameter; the trunk unbranched for 8–9 m; bark densely covered with appressed ascending rootlets; prop roots none; leaves 2.43–2.50 m long, 9.5–10 cm wide, coriaceous, at midsection with 67–74 secondary veins on a side, swordlike, tapering from the base to the long subulate apex, this about 10 cm down 3–4 mm wide, the base unarmed, amplexicaul, but beginning 20–25 cm up the margins with prickles 1.5–3 mm long, 3–11 mm apart, stout subulate, ascending, brown tipped; the midrib below unarmed till well beyond the middle; at midsection the margins with prickles 2–2.2 mm long, 5–12 mm apart, stout subulate, subappressed ascending; near the apex the margins with serrae 0.2–0.5 mm long, 2–5 mm apart; the midrib below with similar but more

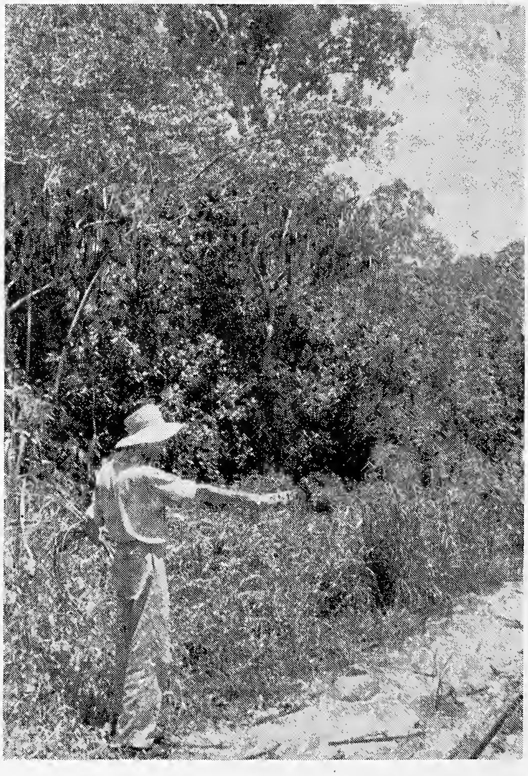

FIG. 116*a*. *Pandanus mossmanicus* St. John, holotype, habit and habitat, with S. T. Blake.

FIG. 116*b–d*. *b*, *P. pluriangulatus* St. John, holotype, habit; *c*, foliage and syncarp. *d*, *P. punctatus* St. John, holotype, habit.

slender serrae; pistillate inflorescences terminal, nodding, leafy bracted; syncarp single, when half grown green, globose; ripe, fallen phalanges 7.3–7.8 cm long, 3.7–4.7 cm wide, 2.5–4.2 cm thick, elliptic-obovoid, cuneate towards the base, 4–5-angled, upper half deep mahogany-red, the sides gently curved, papillose and closely wrinkled, somewhat shiny, somewhat resembling the skin of a *Citrus* fruit, free in upper ½, the apex truncate, or rarely slightly convex-truncate, lateral sutures distinct but narrow; central apical sinuses 6–12 mm deep, V-shaped below; carpels 7–11, mostly 8–9, their apices sharply angled, the marginal ones semiorbicular-pyramidal and some of them flattened on the distal side, the outer margins with 5–12 sharp, longitudinal ridges, thus mortised with their neighbors, the inner sides also with sharp angles and valleys, and mortised, and at the apex with a small area truncate or shallowly concave, the central carpel apices mostly lanceoloid-pyramidal, symmetric; stigmas 1.5–2 mm long, creased, blackish, oval or some of the marginal ones truncate at summit, centripetal and oblique to vertical on proximal face of tip; proximal sinus running to valley bottom; endocarp slightly supramedian, massive, bony, mahogany-colored, 35–38 mm long, the inner surfaces shining, the outer lateral walls 6–8 mm thick; seeds 13–15 mm long, 4 mm in diameter, ellipsoid; upper mesocarp forming in apex of each carpel a cavern with the longitudinal fibers mostly marginal and with pale medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, Drovandi Bridge, 3½ miles n. of Mossman, swamp forest with *Dillenia alata, Melaleuca, Stenochlaena scandens,* 20 ft. alt., common 2nd. story tree, Feb. 5, 1958, *H. St. John 26,261* (BISH).

SPECIMENS EXAMINED: Queensland, Mourilyan, Nov. 19, 1924, *W. H. Amundsen* (BRI): Daintree River, 1876, *Fitzalan,* bearing an unpublished new specific epithet by von Mueller (MEL).

DISCUSSION: *P. mossmanicus* is a member of the section *Pandanus.* Its closest relative is *P. citraceus* St. John, from Queensland. The latter species has the leaves 7–8 cm wide, near the base the margins with prickles 3–5 mm long, at midsection the midrib below with ascending prickles 2.5–3 mm long; phalanges 6–7 cm long, 2.8–4.1 cm wide, the apex shallowly concave; carpels 9–16, the apices narrowly pyramidal; and the endocarp 25–30 mm long, the lateral walls 3–4 mm thick. On the other hand, *P. mossmanicus* has the leaves 9.5–10 cm wide, near the base the margins with prickles 1.5–3 mm long, from the base to well beyond the middle the midrib unarmed; phalanges 7.3–7.8 cm long, 3.7–4.7 cm wide, the apex truncate; carpels 7–11, the marginal apices semiorbicular-pyramidal, the central ones mostly lanceoloid-pyramidal; endocarp 35–38 mm long, the lateral walls 6–8 mm thick.

The new epithet is an adjective formed from the name of the type locality.

Pandanus oblatiapicalis sp. nov. (sect. *Pandanus*)

Fig. 117

DIAGNOSIS HOLOTYPI: Arbor 8 m alta 12 cm diametro, cortice verruculoso, radicibus fulturosis 1 m longis 3–4 cm diametro sparse verruculosis, foliis 1.7 m longis 5.7–6.5 cm latis subcoriaceis in sectione mediali cum 57 nervis secundariis in quoque latere, in sectione depresse sinuositer M-formatis gladiformatis ex basi in apice subulato diminuentibus basi amplexicauli inermi sed ex 9–12 cm marginibus cum aculeis 2–3 mm longis 5–14 mm distantibus subulatis adscendentibus apice brunneo, midnervo infra ex 12–15 cm cum aculeis 1.5–2.5 mm longis 8–27 mm distantibus simulantibus sed reflexis, in regione mediali marginibus cum serris subulatis 1–1.3 mm longis 8–15 mm distantibus, midnervo infra cum aculeis 1.3–1.5 mm longis 8–25 mm distantibus adscendentibus subulatis, circa apicem marginibus cum serris 0.2 mm longis 4–6 mm distantibus, midnervo infra cum aculeis 0.6–0.8 mm longis 3–6 mm distantibus subulatis adscendentibus, syncarpio inviso, phalangibus 3.8–4.3 cm longis 2–3 cm latis 1.6–2.6 cm crassis cuneato-obovoideis vel-oblanceoloideis compressis in sicco pallide brunneis 5–6-angulosis lateribus gradatim curvatis vel planatis laevibus lucidis parte ⅓ supera libera apice convexo, suturis lateralibus in media vel totis partibus liberae, sinibus centralibus apicalibus 2–4 mm profundis parte basali angusto recto vel subcurvato, carpellis 8–15 plerumque 11–12 apicibus subaequalibus oblato-semiorbicularibus marginalibus plerumque asymmetricalibus et latere distali complanato sed paucis majoribus cum concavite distali subterminali vadoso, stigmatibus 1–1.5 mm longis subcircularibus vel late ellipticis sulcatis apicalibus elevatis obliquis centripetalibus vel paucis marginalibus extra inclinatis, sinibus proximalibus stigmati aequalibus, endocarpio minime supramediali 18–19 mm longo obscure brunneo osseoso lateribus lateralibus 1 mm crassis, seminibus 10-12 mm longis 3–5 mm diametro obliquiter ellipsoideis, mesocarpio apicali in carpella quaque cavernam cum fibris paucis longitudinalibus et membranis albis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 8 m tall, 12 cm in diameter; bark warty; prop roots 1 m long, 3–4 cm in diameter, sparsely warty; leaves 1.7 m long, 5.7–6.5 cm wide, subcoriaceous, at midsection with 57 secondary veins on each side, in section low, sinuous M-shaped, sword-shaped, tapering from the base to the subulate apex, the base amplexicaul and unarmed, but beginning at 9–12 cm the margins with prickles 2–3 mm long, 5–14 mm apart, subulate, ascending, brown-tipped; the midrib below beginning at 12–15 cm up with prickles 1.5–2.5 mm long, 8–27 mm apart, similar but reflexed; at the midsection the margins with prickles 1–1.3 mm long, 8–15 mm apart, subulate serrae; the midrib below with prickles 1.3–1.5 mm long, 8–25 mm apart, ascending, subulate; near the apex the margins with serrae 0.2 mm long, 4–6 mm apart; the midrib below with prickles 0.6–0.8 mm long, 3–6 mm apart, subulate, ascending; syncarp not seen; phalanges 3.8–4.3 cm long, 2–3 cm wide, 1.6–2.6 cm thick, cuneate-obovoid or -oblanceoloid, compressed, when dried pale brown, 5–6-angled, the sides gently curved or plane, smooth, shining, free in upper ⅓, the apex convex; lateral sutures distinct in half or all of the upper free portion; central apical sinuses 2–4 mm deep, the lower part narrow, straight or gently curved; carpels 8–15, mostly 11–12, the apices subequal, oblate semiorbicular, the marginal ones mostly asymmetric and flattened distally, but a few of the larger ones with a nearly terminal, distal, shallow concavity; stigmas 1–1.5 mm long, subcircular to broad elliptic, creased, apical, raised, oblique, centripetal or a few of the marginal ones slanted outwards; proximal sinus not longer than the stigma; endocarp slightly supramedian, 18–19 mm long, dark brown, bony, the lateral walls 1 mm thick; seeds 10–12 mm long, 3–5 mm in diameter, obliquely ellipsoid; upper mesocarp forming in each carpel apex a cavern with a few longitudinal fibers and with white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, Green Island, off Cairns, in forest at top of beach, with *Scaevola frutescens, Thespesia populnea, Planchonella obovata, Mimusops parviflora,* Feb. 9, 1960, *H. St. John 26,267* (BISH).

DISCUSSION: *P. oblatiapicalis* is a member of the section *Pandanus.* Its closest relative is *P. duriocarpus* Martelli, of Palau, a species which has the leaves 7.8 cm wide; phalanges 4.5–4.8 cm long, 2.5–4 cm wide; carpel apices acutely narrow pyramidal; apical central sinuses 5–7 mm deep; and the endocarp in the upper third. *P. oblatiapicalis* has the leaves 5.7–6.5 cm wide; phalanges 3.8–4.3 cm long, 2–3 cm wide; carpel apices oblate-semiorbicular; apical central sinuses 2–4 mm deep; and the endocarp slightly supramedian.

Pandanus orbicularis sp. nov. (sect. *Pandanus*)
Figs. 118, 139A*d*

DIAGNOSIS HOLOTYPI: Arbor 8 m alta 15 cm diametro pauciter ramosa in corona laxa, cortice cum radicillis adpresse adscendentibus, radicibus fulturosis nullis, foliis 1.15–1.3 m longis 5.5–5.6 cm latis coriaceis in sectione mediali cum 50 nervis secundariis in quoque latere, in sectione oblatiter M-formatis gladiformatis ex basi in apice subulato diminuentibus eo 10 cm ex apice 6 mm lato basi amplexicauli et inermi sed ex 10–28 cm marginibus cum aculeis 1.3–1.8 mm longis 5–15 mm distantibus valde subulatis adscendentibus brunneis, midnervo toto inermi, in sectione mediali et ad apicem marginibus inermibus, phalangibus 5.4–6.5 cm longis 5.4–6.5 cm latis 4.3–4.8 cm crassis subglobosis compressis 5–6-angulatis in sicco brunneo et pauciter subrubro lateribus sublaevibus et sublu-

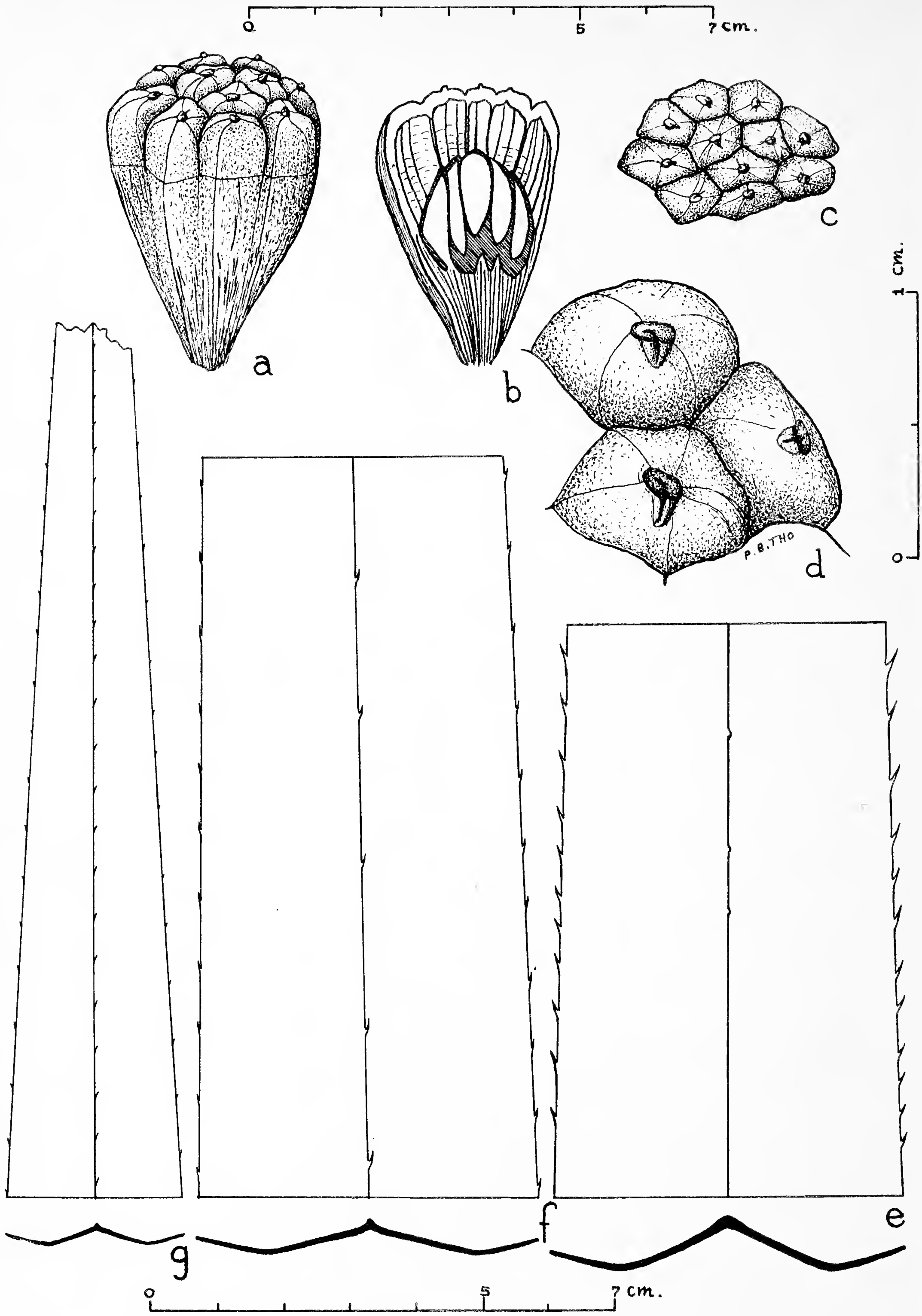

FIG. 117. *Pandanus oblatiapicalis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apices, stigmas, and proximal sinuses, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

cidis subcurvatis sed cum dorsis multis parte ½ supera libera apice rotundato, suturis lateralibus profundis et conspicuis, sinibus centralibus apicalibus 5–8 mm profundis late V-formatis curvatis vel subsinuosis, carpellis 7–12 plerumque 9–10 (sed geminis cum 14 et 8.2 cm latis) apicibus pyramidali-semiorbicularibus subaequalibus angulosis in apice concavitate parva, stigmatibus 2–3 mm longis obdeltoideis vel oblanceolatis sulcatis obliquis centripetalibus, sinibus proximalibus ⅔ ad fondam extentis, endocarpio 3.4 cm longo solido mediali osseoso mahogani-colorato intra lucido lateribus 9–11 mm crassis, seminibus 20–23 mm longis 5–6 mm diametro ellipsoideo, mesocarpio supero in apice carpellae quaeque cavernam cum fibris longitudinalibus fortibus et membranis albis medullosis formanti, mesocarpio basali sparso fibroso carnosoque.

DIAGNOSIS OF HOLOTYPE: Tree 8 m tall, 15 cm in diameter, few branched to form an open crown; bark with appressed ascending rootlets; prop roots none; leaves 1.15–1.3 m long, 5.5–5.6 cm wide, coriaceous, at midsection with 50 secondary veins on each side, in section low M-shaped, swordlike, tapering from the base to the subulate tip, this about 10 cm down 6 mm wide, the base amplexicaul and unarmed, but beginning at 10–28 cm the margins with prickles 1.3–1.8 mm long, 5–15 mm apart, stout subulate, ascending, brown; the midrib unarmed throughout; at midsection the margins unarmed and likewise from there to the tip; inflorescence and syncarp not seen; phalanges 5.4–6.5 cm long, 5.4–6.5 cm wide, 4.3–4.8 cm thick, subglobose, compressed, 5–6-angled, when dried brown with a trace of pink, the sides almost smooth, a little shiny, gently sloping but cut by numerous longitudinal ridges, upper ½ free; apex rounded; lateral sutures deep and prominent; central apical sinuses 5–8 mm deep, wide V-shaped, curved or slightly sinuous; carpels 7–12, mostly 9–10 (but in a twin 14 and the phalange 8.2 cm wide), the apices pyramidal semiorbicular, subequal, angled, the actual apex with a small concavity; stigmas 2–3 mm long, obdeltoid to oblanceolate, creased, oblique, centripetal; proximal sinus running ⅔ way to valley bottom; endocarp 3.4 cm long, massive, median, bony, mahogany-colored, the inner surfaces shining, the lateral margins 9–11 mm thick; seeds 20–23 mm long, 5–6 mm in diameter, ellipsoid; upper mesocarp forming in each carpel apex a cavern with strong longitudinal fibers and white medullary membranes; basal mesocarp sparse, fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, south bank of Annan River, 4 miles s.s.w. of Cooktown, savanna with *Eucalyptus alba, E. leptophleba,* Feb. 3, 1958, *H. St. John 26,252* (BISH).

DISCUSSION: *P. orbicularis* is a member of the section *Pandanus*. Its closest relative is *P. Whitei* Martelli, of Queensland, which has the leaves more than 1.5 m long, 8 cm wide; phalanges 7–7.3 cm long, 6–6.5 cm wide; central apical sinuses 3–5 mm deep, zigzag and adjacent carpels strongly mortised. In contrast, *P. orbicularis* has the leaves 1.1–1.3 m long, 5.5–5.6 cm wide; phalanges 5.4–6.5 cm long, 5.4–6.5 cm wide; central apical sinuses 5–8 mm deep, and gently curved or slightly sinuous.

The new epithet is the Latin adjective *orbicularis,* orbicular, given in reference to the nearly orbicular phalanges of this species.

Pandanus papillosus sp. nov. (sect. *Pandanus*) Fig. 119

DIAGNOSIS HOLOTYPI: Arbor 10 m alta 2 dm diametro, trunco cum radicillis adpresse adscendentibus obtecto, radicibus fulturosis nullis, foliis 1.75–1.83 m longis 8 cm latis coriaceis in quoque latere cum 71 nervis secundariis in sectione depresse M-formatis gladiformatis ex basi in apice licet subulato sensim diminuentibus, basi amplexicauli et inermi sed ex 12–14 cm marginibus cum aculeis 3–4 mm longis 5–9 mm distantibus valide arcuate subulatis adscendentibus in apice brunneo, midnervo affini inermi, in sectione mediali marginibus cum subulato-serris 1–1.5 mm longis 3–8 mm distantibus, midnervo infra cum aculeis 1.5–2 mm longis 6–18 mm distantibus graciliter subulatis adpresse adscendentibus, circa apicem marginibus et midnervo infra cum serris 0.2–0.4 mm longis 1.5–3 mm distantibus, phalangibus 4.3–4.8 cm longis 2.3–2.9 cm latis 2.1–2.4 cm crassis late cuneatis parte ½ supera libera apice truncato (vel minime convexo) suturis lateralibus dis-

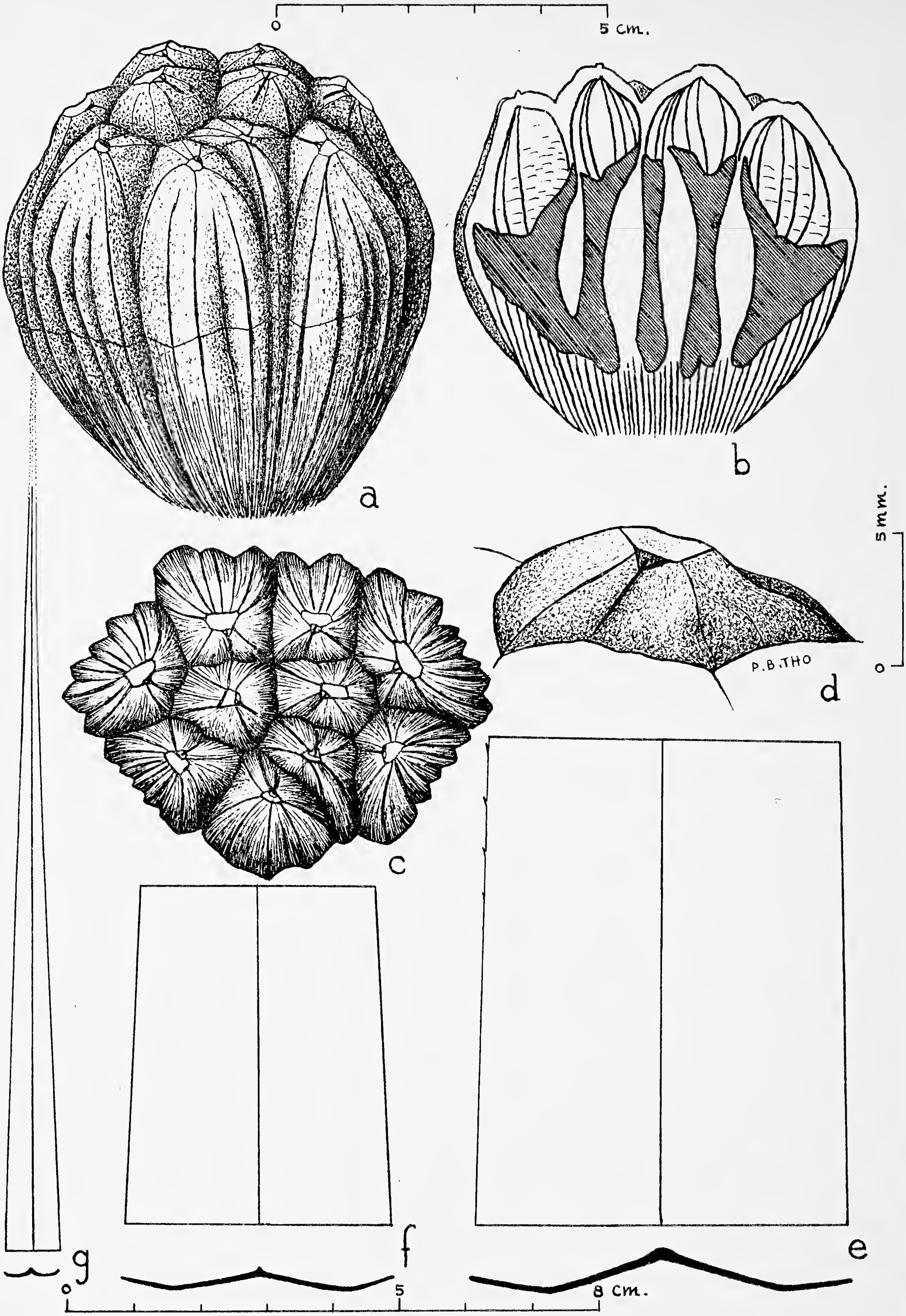

FIG. 118. *Pandanus orbicularis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex with stigma and proximal sinus, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

tinctis sed angustis, lateribus densiter minute papillosis cum 4–7 angulis majoribus et carpella quaque cum 3–10 dorsis et valleculis secundariis angustis, sinibus centralibus apicalibus 5–12 mm profundis anguste V-formatis, carpellis 5–7 apicibus pyramidalibus eis marginalibus omnibus truncatis, stigmatibus 1.5–2 mm longis distalibus obliquis centripetalibus ovatis vel deltoideis sulcatis nigris, sinibus proximalibus vel in dorso ½ ad fondam vel in vallecula tota ad fondam extentis, endocarpio mediali 3–3.3 cm longo osseoso obscure brunneo lateribus lateralibus 2 mm crassis, seminibus 20–25 mm longis 4 mm diametro fusiformibus, mesocarpio supero in apice carpella quaque cavernoso cum fibris fortibus paucis et membranis albis medullosis multis, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 10 m tall, 2 dm in diameter; trunk covered with appressed ascending rootlets; prop roots none; leaves 1.75–1.83 m long, 8 cm wide, coriaceous, on each side with 71 secondary parallel nerves, in section low M-shaped, sword-shaped, tapering gradually from the base to the apparently subulate apex, the base amplexicaul and unarmed, but beginning 12–14 cm up the margins with prickles 3–4 mm long 5–9 mm apart, stout subulate arcuate ascending, brown-tipped; the nearby midrib unarmed; at midsection the margins with subulate-serrae 1–1.5 mm long, 3–8 mm apart; the midrib below with prickles 1.5–2 mm long, 6–18 mm apart, slender subulate, appressed ascending; near the tip the margins and midrib below with serrae 0.2–0.4 mm long, 1.5–3 mm apart; phalanges 4.3–4.8 cm long, 2.3–2.9 cm wide, 2.1–2.4 cm thick, broad cuneate, upper ½ free, apex truncate (or very low convex), lateral sutures distinct narrow cracks, the sides closely and minutely papillose, with 4–7 principal angles and on each carpel with 3–10 sharp secondary ridges and valleys, apical central sinuses 5–12 mm deep, narrow V-shaped; carpels 5–7, their apices pyramidal, and all the marginal ones with an apical horizontal or slightly oblique truncate plane, then on the distal face is the oblique, centripetal stigma 1.5–2 mm long, ovate to deltoid, creased, black; proximal crease if on a ridge running ½ way, if in a valley running quite to the valley bottom; endocarp median, 3–3.3 cm long, bony, dark brown, the lateral walls 2 mm thick; seeds 20–25 mm long, 4 mm in diameter, fusiform; apical mesocarp cavernous in each carpel, with a few strong fibers and many white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, 9 miles w.s.w. of junction of McIvor and Morgan Rivers, fringing forest along swampy creek, with *Dillenia, Cassia, Planchonella,* 100 ft. alt., Feb. 1, 1958, *H. St. John 26,249* (BISH).

DISCUSSION: *P. papillosus* is a member of the section *Pandanus.* Its closest relative is *P. ferrimontanus* St. John, of Queensland. The latter has the leaves 5.8 cm wide; phalanges 4.2 cm wide, 3.4–3.5 cm thick, the apex rounded; central apical sinuses 3.5–4.5 mm deep; carpels 8–12, and their apices semiorbicular. *P. papillosus* has leaves 8 cm wide; phalanges 2.3–2.9 cm wide, 2.1–2.4 cm thick, the apex truncate; central apical sinuses 5–12 mm deep; carpels 6–8, and their apices conic.

The new epithet is the Latin adjective *papillosus,* with papillae, in reference to the papillose surface of the phalanges.

Pandanus pluriangulatus sp. nov. (sect. *Pandanus*)

Figs. 120, 116*b, c*

DIAGNOSIS HOLOTYPI: Arbor 7 m alta 2 dm diametro, corona vadosa lata pauce ramosa, cortice cum radicillis multis adpresse adscendentibus, radicibus fulturosis nullis, foliis 1.5 m longis 7 cm latis coriaceis in sectione depresse M-formatis in quoque latere cum 63–65 nervis secundariis, gladiformatis in apice subulato diminuentibus basi amplexicauli inermi marginibus et midnervo infra tota inermibus, inflorescentia foeminea 5 dm longa, syncarpio ⅔ maturo 18 cm longo subgloboso, phalangibus 5.7–6.5 cm longis 4–5 cm latis 3.7–4.3 cm crassis late ellipsoideis 4–6-angulosis in sicco brunneis sed pauce rubris, lateribus subcurvatis papillosis rugosis exlucidis parte ½ supera libera, apice depresse convexo, suturis lateralibus distinctis sed angustis, sinibus centralibus apicalibus 4–7 mm profundis V-formatis angulosis et interobseratis, carpellis 9–12 apicibus subaequalibus eis centralibus lanceoloideis vel lanceo-ovoideis acute angulosis lateribus cum 3–7 dorsis et valleculis longitudinalibus angustis, apicibus mar-

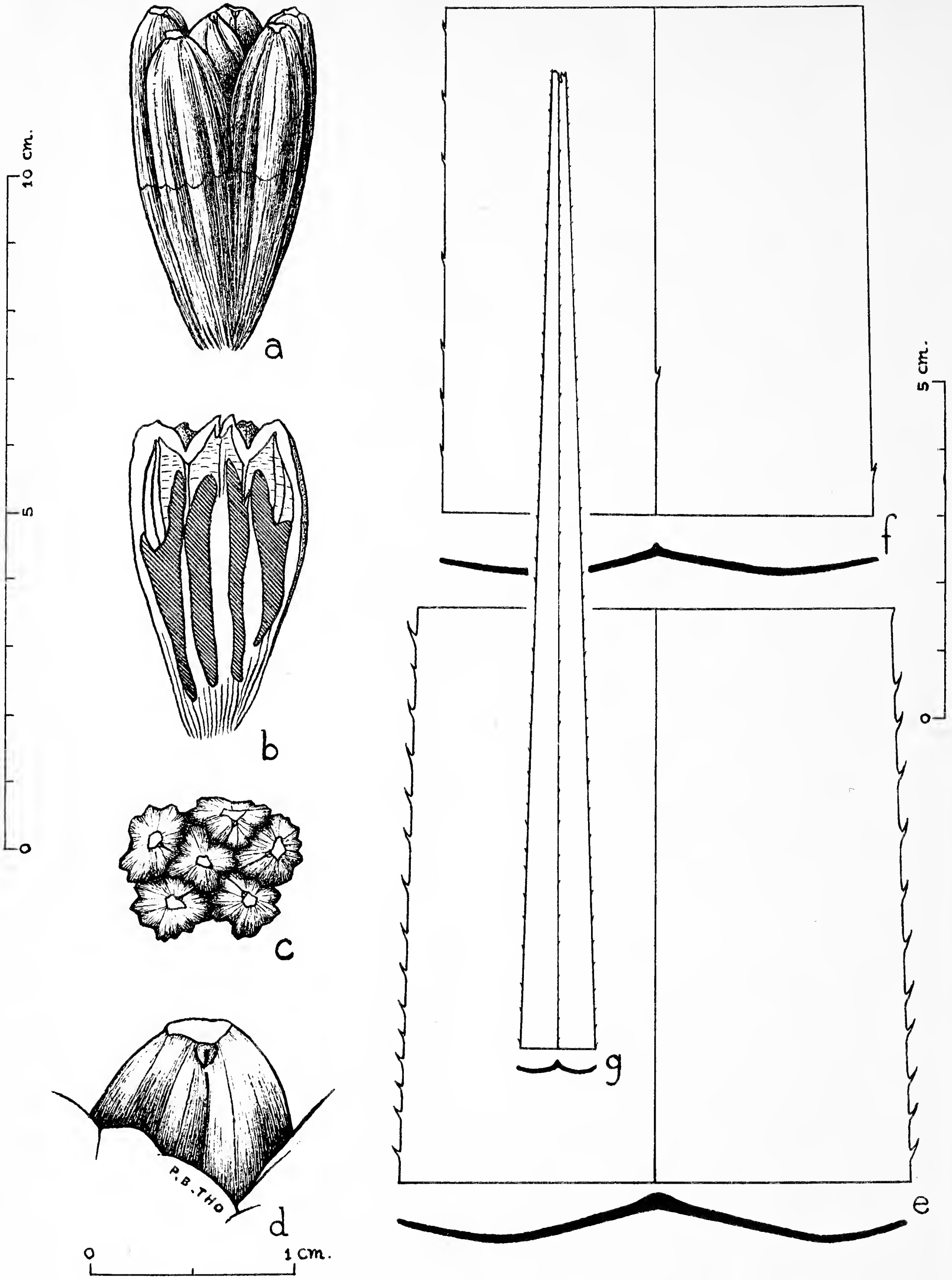

FIG. 119. *Pandanus papillosus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

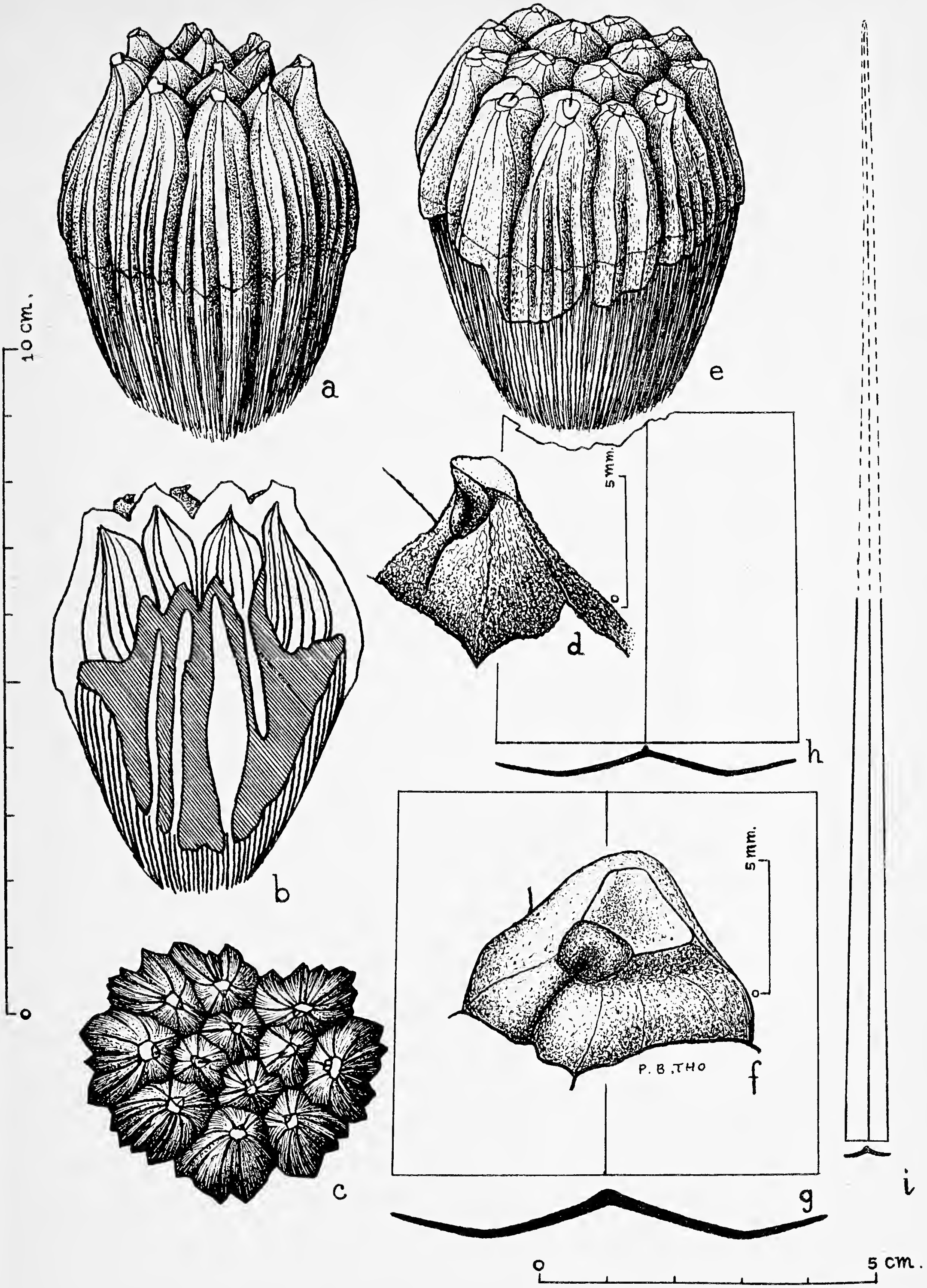

FIG. 120. *Pandanus pluriangulatus* St. John, holotype. *a,* Typical phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* typical phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, × 4; *e,* one of the few broader phalanges, lateral view, × 1; *f,* carpel apex of *e,* × 4; *g,* leaf base, lower side, × 1; *h,* leaf middle, lower side, × 1; *i,* leaf apex, lower side, × 1.

ginalibus lanceo-ovoideis vel semiorbiculari-pyramidalibus et multis a latere compressis et subdivergentibus, enim phalangibus paucis cum apicibus carpellarum oblato-pyramidalibus, stigmatibus 2–3.5 mm longis ellipsoideis sulcatis, eis marginalis plerumque obliquis truncatis centripetalibus apicalibus vel in aliquis marginalibus subapicalibus et distalibus regionis truncatae vel convexae, sinibus proximalibus ½ ad fondam extentis, endocarpio 3.8–4 cm longo solido osseoso mahogani-colorato intra lucido lateribus lateralibus 5–7 mm crassis, seminibus 22 mm longis 5.5 mm diametro ellipsoideo; mesocarpio supero in apice carpellae quoque cavernam cum fibris fortibus et membranis pallidis delicatis medullosis formanti, mesocarpio basali exili fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 7 m tall, 2 dm in diameter; crown low and broad, due to the few, widespreading branches; bark with many appressed ascending rootlets; prop roots none; leaves 1.5 m or more long, 7 cm wide, coriaceous, in section low M-shaped, on each side with 63–65 secondary parallel veins, swordlike, tapering to a subulate tip not wholly preserved in our specimen, the base amplexicaul, unarmed, and the leaf margins and midrib unarmed throughout; pistillate inflorescence 5 dm long; a syncarp observed ⅔ mature 18 cm long, subglobose; phalanges 5.7–6.5 cm long, 4–5 cm wide, 3.7–4.3 cm thick, broad ellipsoid, 4–6-angled, when dried brown, but with traces of red, the sides gently curved, papillose and rough, dull, upper ½ free, apex low convex, lateral sutures distinct but narrow, central apical sinuses 4–7 mm deep, V-shaped, zigzag from the mortised carpels; carpels 9–12, the apices subequal, the central apices lanceoloid or lance-ovoid, sharply angled, the sides with 3–7 sharp longitudinal ridges and valleys, the marginal ones lance-ovoid- to semiorbicular-pyramidal and many of them laterally compressed and slightly divergent, and even a few of the phalanges with the carpel apices oblate pyramidal; stigmas 2–3.5 mm long, ellipsoid, creased, the marginal mostly truncate, oblique, centripetal, apical or on some marginal ones subapical and distal of an apical truncate or convex area; proximal sinus running half or all the way to the valley bottom; endocarp 3.8–4 cm long, massive, bony, slightly inframedian, mahogany-colored, the inner surfaces shining, the lateral walls 5–7 mm thick; seeds 22 mm long, 5.5 mm in diameter, ellipsoid, upper mesocarp forming in the apex of each carpel a cavern with strong fibers and delicate, pale, medullary membranes; basal mesocarp thin, fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, 9.3 miles n. of Mossman, open forest near sea beach, with *Terminalia, Acacia aulaeocarpa, Hibiscus tiliaceus,* Feb. 5, 1958, *H. St. John 26,262* (BISH).

Also observed by the writer on the same expedition, in open forest near the sea shore, Port Douglas, Queensland.

DISCUSSION: *P. pluriangulatus* is a member of the section *Pandanus.* In that section is its closest relative, *P. angulatus* St. John, of Queensland, which has its leaves with the margins near the base with prickles 2.8–3.5 mm long, 8–14 mm apart, slender subulate; near the tip the midrib below with serrae 0.2 mm long, 5–8 mm apart; phalanges 5–5.6 cm long, 4.7–6.1 cm broad, yellow-orange, lateral sutures deep, apical central sinuses 7–12 mm deep; and the seeds 3 mm in diameter. *P. pluriangulatus* has the leaves unarmed throughout; phalanges 5.7–6.5 cm long, 4–5 cm wide, when dried reddish brown, lateral sutures distinct but narrow, apical central sinuses 4–7 mm deep; and the seeds 5.5 mm in diameter. For comparison with the few phalanges with low, broad carpel apices, the most similar species is *P. endeavourensis* St. John, of Queensland, which has the leaves sparsely prickly; phalanges 5–5.8 cm long, central apical sinuses 2–4 mm deep; and the stigmas 1–1.5 mm long. *P. pluriangulatus* has the leaves wholly unarmed; phalanges 5.7–6.5 cm long, central apical sinuses 4–7 mm deep; and the stigmas 2–3.5 mm long.

The new epithet is from the Latin *pluris,* of many; *angulatus,* angled, in reference to the numerous, prominent, lateral angles of the phalanges.

Pandanus punctatus sp. nov. (sect. *Pandanus*)
Figs. 121, 122, 116*d*, 123*a*

DIAGNOSIS HOLOTYPI: Arbor 17 m alta 25 cm diametro, cortice cum radicillis adpresse adscendentibus obtecto, radicibus fulturosis 5–10 dm longis 1–3 cm diametro muricatis, foliis 2.2–2.33 m longis 10–12 cm latis coriaceis in sectio M-formatis in sectione mediali in quoque latere cum 78–82 nervis secundariis ligulatis sensim ex basi in apice longe subulato diminuentibus eo in puncto 10 cm ex apice 1 mm lato basi amplexicauli inermi sed ex 15–40 cm marginibus inaequaliter cum aculeis 2–3 mm longis 3–15 mm distantibus adscendentibus subulatis arcuatis apice brunneo, midnervo infra per 95–120 cm inermi, in sectione mediali marginibus cum aculeis 2.5–3.5 mm longis 4–8 mm distantibus simulantibus sed adpresse adscendentibus, midnervo infra cum aculeis 1.5–2 mm longis 15–45 mm distantibus simulantibus adpressis, proxima apicem marginibus cum aculeis 0.3–0.7 mm longis 2–4 mm distantibus subulatis adscendentibus vel subadpressis brunneis, midnervo inermi, inflorescentiis foemineis terminalibus, pedunculo 25 cm longo 15 mm crasso subdeltoideo folioso, syncarpio terminali 25 cm longo 20 cm diametro ovoideo, phalangibus 5.8–6.2 cm longis 3.2–4.2 cm latis 2.6–3.1 cm crassis subrubris oblongo-obovoideis lateribus papillosis in sicco rubro-mahoganicoloratis apice pallide subviridibus lateribus 4–6-angulosis et carpella quaque cum 2–6 angulis et valleculis parvis et interobseratis parte ½ supera libera apice valde plano-truncato suturis lateralibus angustis sed ad basim distinctis, sinibus apicalibus centralibus 3–6 mm profundis angustis, carpellis 8–10 apicibus plerumque subtruncatis et eis marginalis valde truncatis et cum concavite apicali et stigmate proximali apicibus cum angulis pluribus supra rotundatis infra prominentibus et interobseratis, apicibus centralibus pyramidalibus cum concavitis minoribus vel nullis, stigmatibus 1.5–2 mm latis cordatis vel subcircularibus apice saepe truncato papillosis nigris sulcatis obliquis centripetalibus, sinibus proximalibus ½ ad fondam extentis, endocarpio mahogani-colorato osseoso solido 3.2 cm longo lateribus lateralibus 3–4 mm crassis, seminibus 15 mm longis 4 mm diametro ellipsoideo, mesocarpio apicali in carpella quaque cum caverna cum membranis medullosis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 13–17 m tall, 20–25 cm in diameter, erect; bark covered with appressed ascending rootlets; prop roots absent or 5–10 dm long and 1–3 cm in diameter, muricate; leaves 1.7–2.33 m long, 8.5–12 cm wide, sword-shaped, coriaceous, in cross section M-shaped, in middle part with 78–82 secondary parallel veins on each side, gradually tapering to a long subulate apex, this 10 cm from the tip 1 mm wide, the base slightly widened and amplexicaul and unarmed, but beginning 15–40 cm up and at unequal distances the margins with prickles 2–3 mm long, 3–15 mm apart, ascending arcuate subulate, brown-tipped; the midrib below unarmed for 95–120 cm; near the midsection the margins with prickles 2.5–3.5 mm long, 4–8 mm apart, similar but appressed ascending, the midrib below with prickles 1.5–2 mm long, 15–45 mm apart, appressed, similar; near the tip the margins with teeth 0.3–0.7 mm long, 2–4 mm apart, subulate, ascending or subappressed, brown; the nearby midrib unarmed; pistillate inflorescences terminal; peduncle 25–60 cm long, 15 mm thick, slightly 3-sided, leafy bracted; syncarp solitary, terminal, 24–25 cm long 20 cm in diameter, ovoid; the core when dried 14 cm long, 4.5 cm in diameter, deltoid, bearing 117 phalanges 5.3–6.3 cm long, 2.6–4.2 cm wide, 2.3–3.2 cm thick, oblong-obovoid to oblanceoloid, compressed, the surface papillose, when ripe the apices greenish yellow, the sides to the middle burnt Sienna, the lower half yellow, the sides when dry reddish-mahogany colored, the apex pale greenish, the sides 3–9-angled and each carpel with 2–6 low angles and shallow valleys and thus mortised with their neighbors, upper ½ free, apex conspicuously flat truncate, or in a few of the largest ones very slightly convex, lateral sutures narrow but distinct to the base, apical central sinuses 2–6 mm deep, narrow; carpels 7–14, mostly 9, the apices rounded conic or mostly subtruncate, and the marginal ones markedly so with a prominent concavity (or plane) on the proximal side of which is the stigma, the apices with several angles ending in rounded shoulders, the angles prominent below and mortised with their neighbors, the central apices with smaller concavities or even none and pyramidal; stigmas 1–2 mm wide, cordate to subcircular to oblate reniform, the apex often truncate, papillose, blackish,

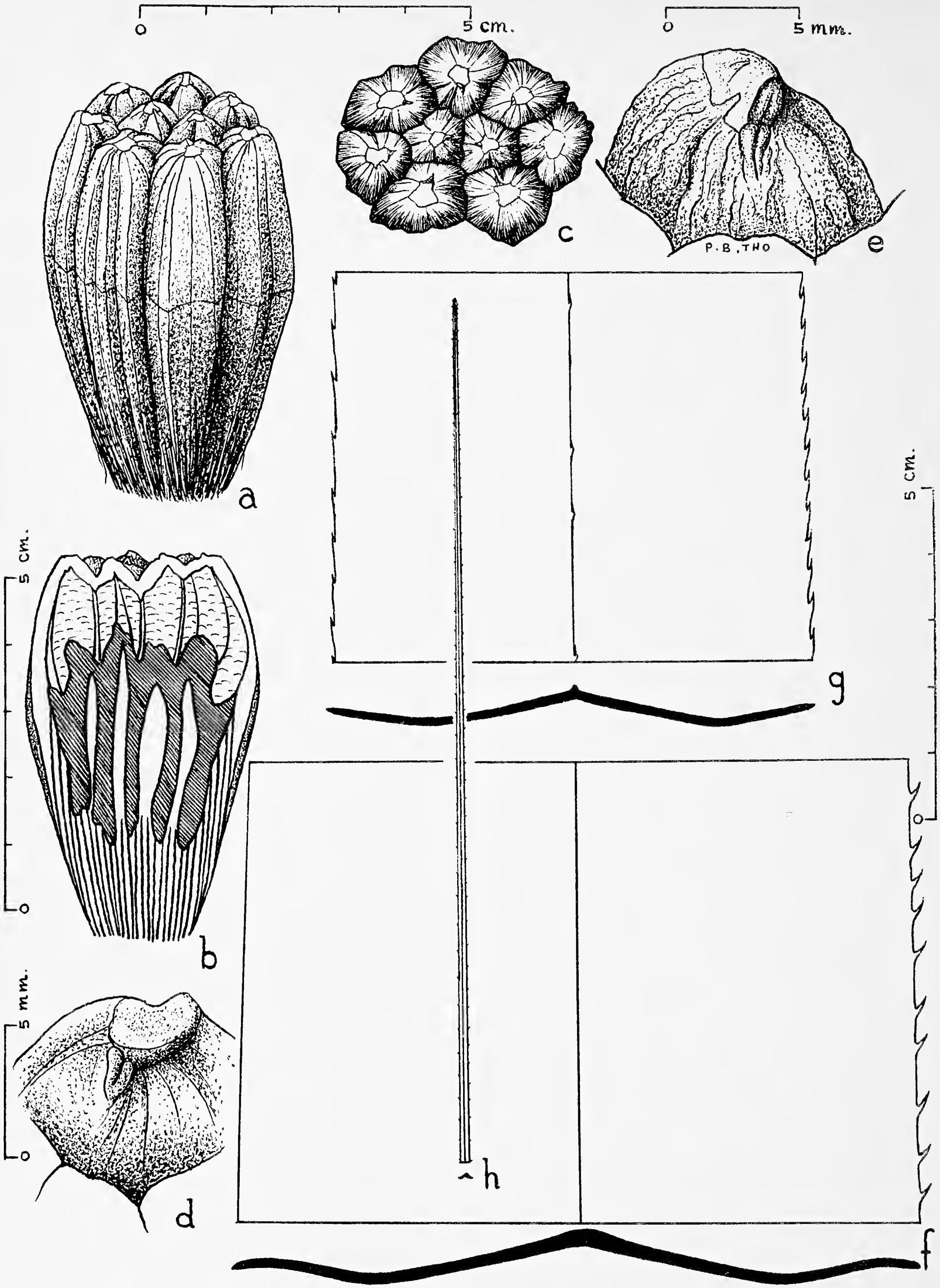

FIG. 121. *Pandanus punctatus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* occasional carpel apex with stigma lateral on the proximal sinus, × 4; *e,* typical carpel apex with stigma and proximal sinus, × 4; *f,* leaf base, lower side, × 1; *g,* leaf middle, lower side, × 1; *h,* leaf apex, lower side, × 1.

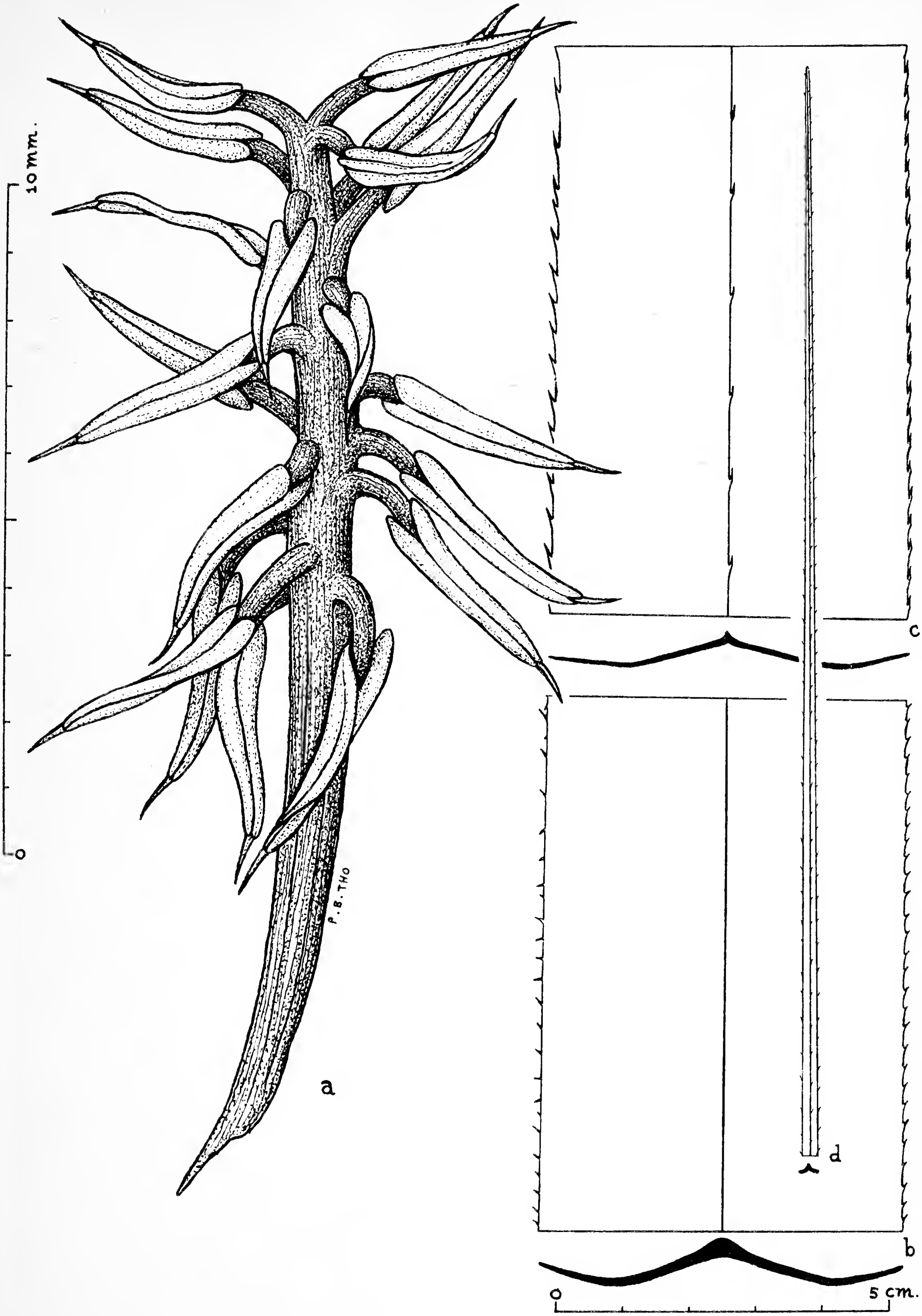

FIG. 122. *Pandanus punctatus* St. John, from *St. John 26,248. a,* Staminal column with anthers, × 10; *b,* leaf base, lower side, × 1; *c,* leaf middle, lower side, × 1; *d,* leaf apex, lower side, × 1.

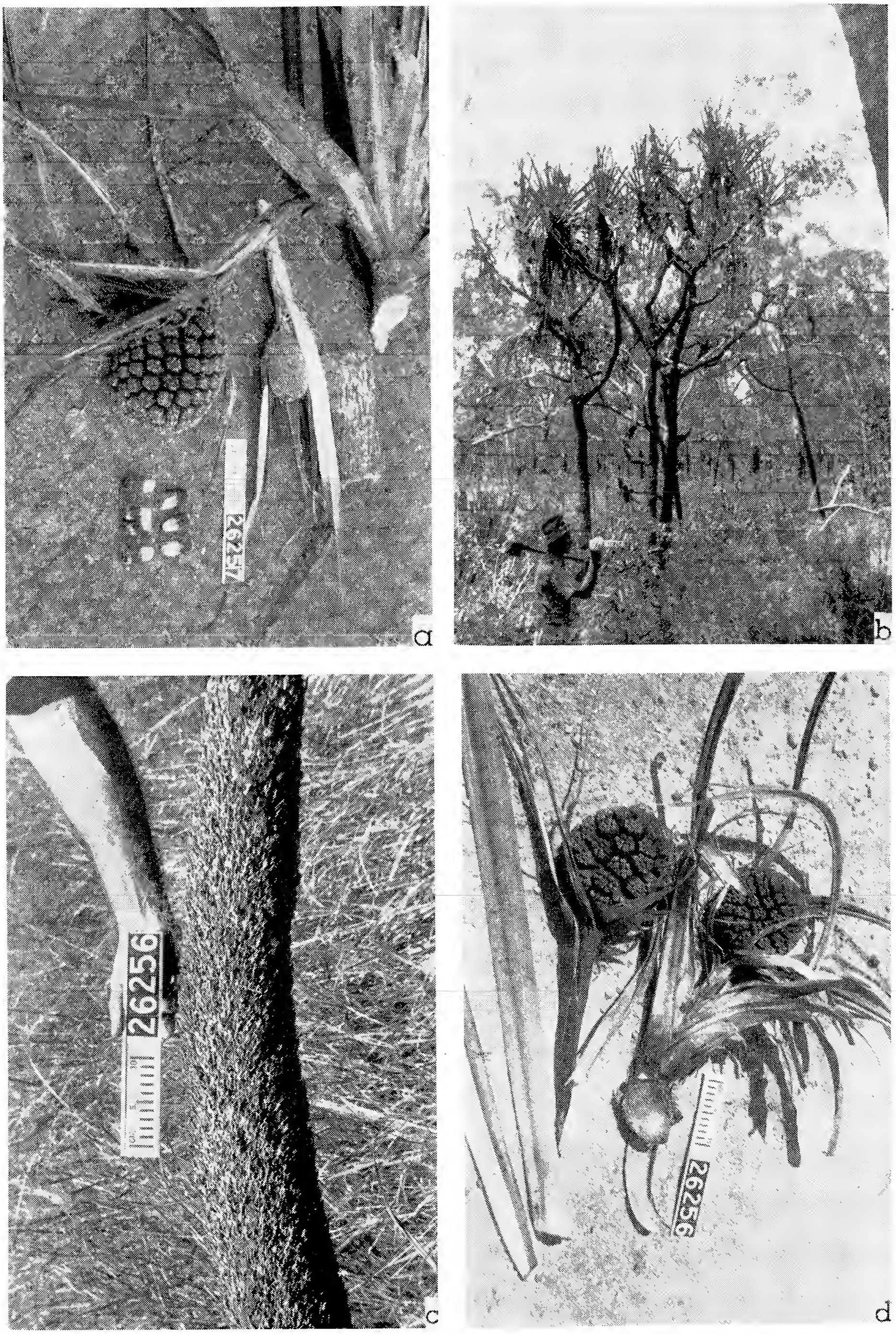

FIG. 123. *a, Pandanus punctatus* St. John, holotype, young and mature pistillate inflorescence. *b, P. radiciferus* St. John, holotype, habitat and habit; *c,* trunk with adventitious ascending rootlets; *d,* young and mature syncarps, with foliage.

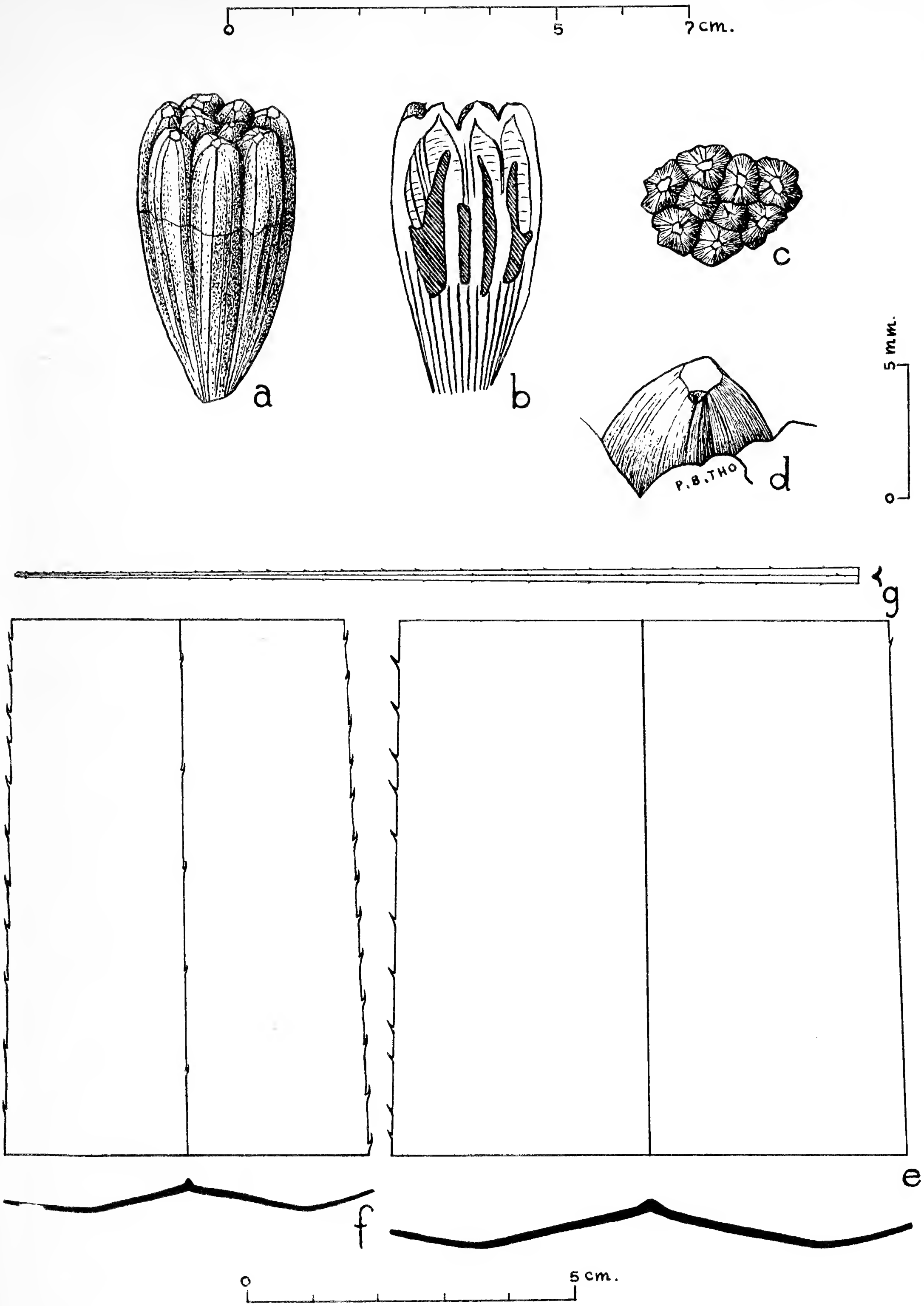

FIG. 124. *Pandanus radiciferus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

creased, centripetal, oblique; the proximal crease running about half way to the valley bottom; endocarp median or slightly inframedian, mahogany-colored, bony, massive, 2.5–3.2 cm long, the lateral margins 2–4 mm thick; seeds 13–15 mm long, 4 mm in diameter, ellipsoid; apical mesocarp forming in each carpel a cavern, these somewhat confluent and filled with white, medullary membranes; basal mesocarp fibrous and fleshy, the pulp fruity but astringent. Staminate trees appearing similar; staminate inflorescence 1.05 m long; peduncle 23 cm long, fleshy; lowest bracteal leaf (the one illustrated) 1.53 m long, 7 cm wide ⅓ from the base, narrowing to the base and tapering to the long subulate apex which 10 cm down is 1.2 mm wide; at midsection the margins with prickles 1.5–2 mm long, 2–8 mm apart, pale arcuate ascending, flattened subulate; the nearby midrib with similar prickles 1.3–1.5 mm long, 6–10 mm apart; near the apex the margins and midrib below with prickles 0.5–0.8 mm long, 2–7 mm apart, subulate, ascending, this bracteal one here described, as no true foliage one was preserved; floral part about 75 cm long, with 17–20 spikes, these 5–8 cm long, 2 cm in diameter, dense; staminal columns 12–18 mm long, with about 20 stamens, borne on the upper half; free filament tips 1–1.5 mm long; anthers 2.2–3.2 mm long, narrowly lanceoloid, bearing at the apex a subulate projection of the connective 0.7–0.9 mm long.

HOLOTYPUS: Australia, North Queensland, 5 miles w.n.w. of the junction of McIvor and Morgan Rivers, grove in wet savanna, with *Tristania suaveolens, Eucalyptus alba,* and *E. leptophleba,* Feb. 2, 1958, *H. St. John 26,247* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, McIvor and Morgan Rivers, same locality, habitat, and data as above, *H. St. John 26,248* (BISH); Smithfield, 10 miles n. of Cairns, at edge of fresh swampy stream bank, with *Melaleuca leucadendra, Albizzia procera, Hibiscus tiliaceus, Stenochlaena scandens,* Feb. 4, 1958, *H. St. John 26,257* (BISH).

DISCUSSION: *P. punctatus* is a member of the section *Pandanus.* In that section its closest relative is *P. rivularis* St. John, of Queensland, a species which has prop roots none; leaves 1.68–1.81 m long, 6–7.6 cm wide, the apex acute and 10 cm down 16 mm wide, at midsection the margins with prickles 1–2 mm long, 6–13 mm apart; phalanges 5.1–5.3 cm long, the side of each carpel with 2–4 angles; apical central sinuses 4–7 mm deep; and the endocarp with lateral walls 4–6 mm thick. *P. punctatus* has prop roots 5–10 dm long, 1–3 cm in diameter, or none; leaves 1.7–2.33 m long, 8.5–12 cm wide, the apex long subulate and 10 cm down 1 mm wide, at midsection the margins with prickles 2.5–3.5 mm long, 4–8 mm apart; phalanges 5.3–6.3 cm long, the side of each carpel with 2–6 angles; apical central sinuses 3–6 mm deep; and the endocarp with lateral walls 2–4 mm thick.

The new epithet is the Latin adjective *punctatus,* with points or dots, given in reference to the roughened surface of the sides of the phalanges.

Pandanus radiciferus sp. nov. (sect. *Pandanus*)
Figs. 124, 125, 123*b–d*, 126*a, b*

DIAGNOSIS HOLOTYPI: Arbor 13 m alta 20 cm diametro, corona late ellipsoidea, cortice ex radicillis 2–3 cm longis adpresse adscendentibus plerumque furcatis clausi, radicibus fulturosis nullis, foliis 1.6–2.1 m longis 7.5–8 cm latis coriaceis in sectione mediali cum 74 nervis secundariis in quaque latere, gladiformatis et ex basi in apice subulato 40 cm longo diminuentibus eo in puncto 10 cm ex apice 1.3 mm lato, basi amplexicauli et inermi sed ex 16–32 cm marginibus cum aculeis 1.5–2 mm longis 4–10 mm distantibus subulatis arcuatis adscendentibus brunneis, midnervo infra inermi in parte ⅔ infera, in sectione mediali uno margine cum aculeis 2–2.3 mm longis 4–9 mm distantibus simulantibus sed gracilibus et adpresse adscendentibus basi pallida, sed margine altero inermi vel subinermi, proxima apicem marginibus et midnervo infra cum aculeis 0.3–0.4 mm longis 3–5 mm distantibus subulatis adscendentibus brunneis, inflorescentia foeminea terminali, pedunculo 27 cm longo 15–20 mm diametro trigono folioso, syncarpio solitario 20–30 cm diametro globoso cum 127 phalangibus eis 4.4–4.7 cm longis 1.6–2.5 cm latis 1.6–2.1 cm crassis oblanceoloideis apice truncato 5–6-angulosis quando submaturis apicibus viridibus lateribus

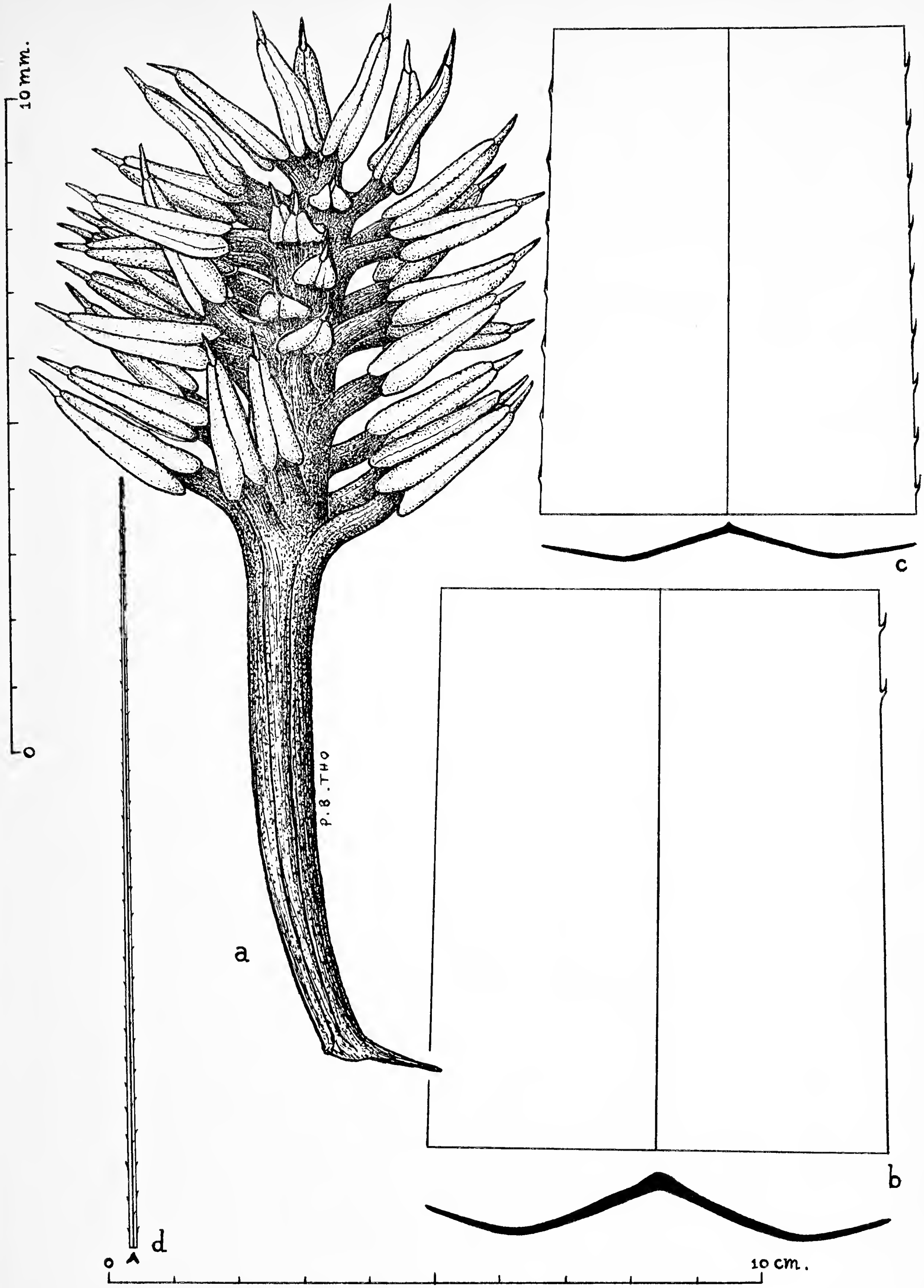

FIG. 125. *Pandanus radiciferus* St. John, from *St. John 26,255*. *a*, Staminate column with anthers, × 10; *b*, leaf base, lower side, × 1; *c*, leaf middle, lower side, × 1; *d*, leaf apex, lower side, × 1.

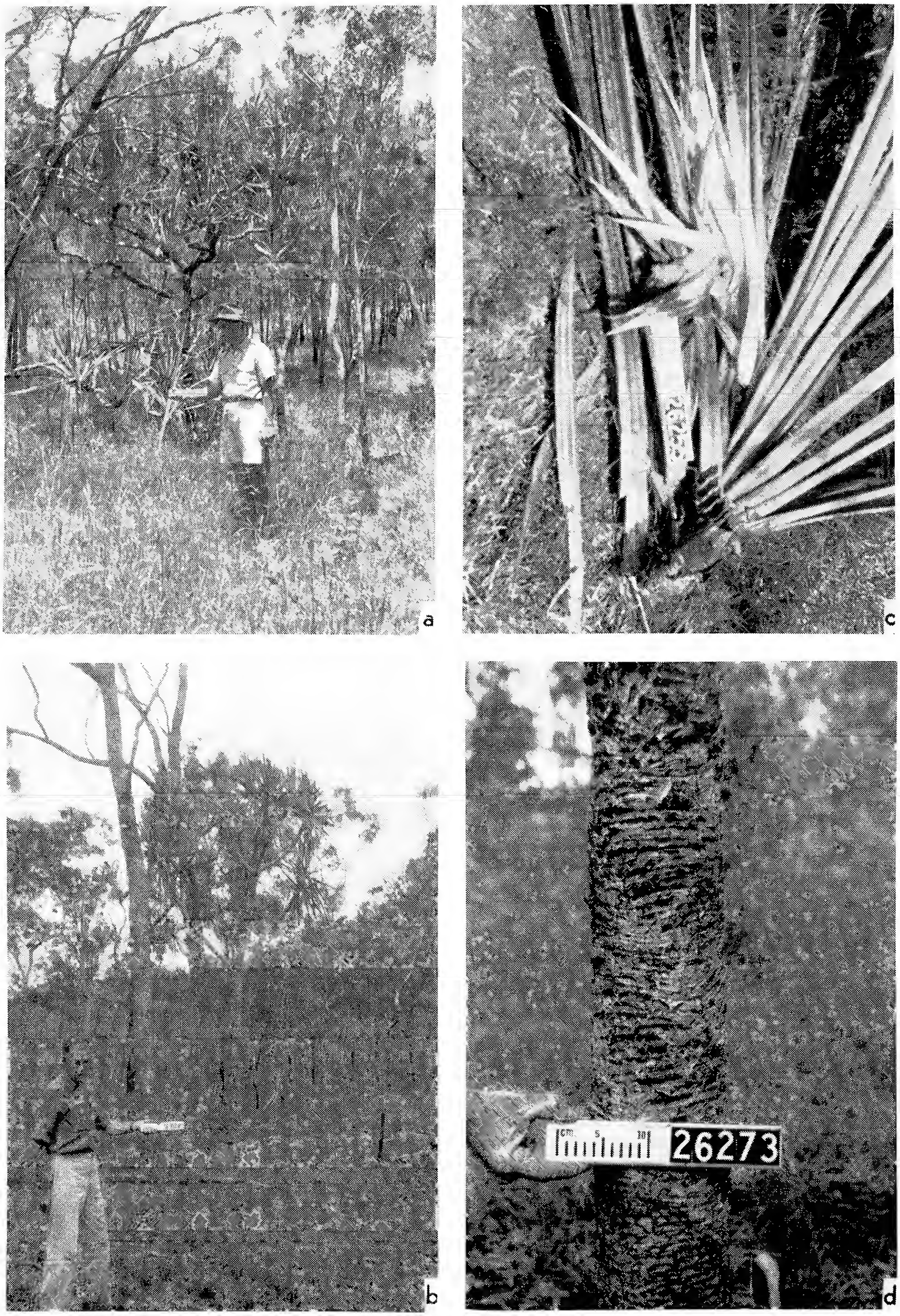

FIG. 126. *a, Pandanus radiciferus* St. John, staminate tree, habit from *St. John 26,255,* with S. Ernest Stevens; *b,* staminate inflorescence and foliage of same. *c, P. stoloniferus* St. John, from *St. John 26,273,* habit, with S. T. Blake; *d,* trunk with scorched bark.

exponitis cinnamoni-coloratis papillosis sed sublucidis gradatim convexis parte ⅓ supera libera, suturis lateralibus in parte ½–⅔ supera distinctis, sinibus centralibus apicalibus 2–5 mm profundis V-formatis, carpellis 5–10 plerumque 8–9 (sed in geminis 14–21 et phalangio 2.8–4.1 cm lato), apicibus ovoideis cum concavite vel plana terminali lucido, stigmatibus 1–2 mm longis ellipticis vel obovatis sulcatis apice saepe truncato obliquis proximis, sinibus proximalibus ½ vel tota ad fondam extentis, endocarpio mediali 18–20 mm longo osseoso obscure brunneo lateribus 1–2 mm crassis, seminibus 15 mm longis 3 mm diametro ellipsoideis, mesocarpio supero in carpella quaque cavernam cum fibris marginalibus et membranis pallidis medullosis formantibus, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 13 m tall, 20 cm in diameter; crown broadly ellipsoid, of few branches; bark concealed by abundant, appressed ascending rootlets, these often forked, 2–3 cm long; prop roots absent or present and 2–4 dm long, 2–4 cm in diameter, muricate; leaves 1.6–2.1 m long, 7–8 cm wide, coriaceous, at midsection with 59–74 secondary veins on each side, swordlike, tapering from the base to the 40 cm subulate apex, this at the point 10 cm down 1.3 mm wide, the base amplexicaul and unarmed, but beginning 16–32 cm up the margins with prickles 1.5–2 mm long, 4–10 mm apart, stout subulate, arcuate ascending, brown; the midrib below unarmed for the lower ⅔'s; at midsection the margins with prickles on one side 2–2.3 mm long, 4–9 mm apart, similar but slender and appressed ascending, and pale at base, but on the other margin few or none; near the apex the margins and midrib below with prickles 0.3–0.4 mm long, 3–5 mm apart, subulate, ascending, brown; pistillate inflorescence terminal; peduncle 27 cm long, 15–20 mm in diameter, trigonous, leafy bracted; syncarp solitary, 20–30 cm in diameter, globose, or subglobose and 14 cm long, 13 cm in diameter, bearing 90–127 phalanges, these 4.4–4.7 cm long, 1.6–2.9 cm wide, 1.6–2.7 cm thick, oblanceoloid with the apex truncate, 5–6-angled, when slightly immature the apices green, the exposed sides cinnamon, papillose but almost shiny, gently convex, upper ⅓ free, lateral sutures distinct down ½–⅔ way, central apical sinuses 2–5 mm deep, V-shaped; carpels 5–10, mostly 8–9 (but in doubles 14–21, and the phalanges 2.8–4.1 cm wide), the apices ovoid, with shallow, shining concavity or plane on the apex, distal of the stigma; stigmas 1–2 mm long, elliptic to obovate, creased, the apex often truncate, very oblique, on the proximal face of the carpel apex; proximal sinus wide, running half to all the way to the valley bottom; endocarp median, 18–20 mm long, bony, dark brown, the outer lateral walls 1–2 mm thick; seeds 15 mm long, 3 mm in diameter, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern outlined by fibers, crossed by delicate, pale, medullary membranes; basal mesocarp fibrous and fleshy. Staminate trees (no. 26,255) 10 m tall, 20 cm in diameter; prop roots none, but with a few spiny drop roots; at midsection the leaves with prickles 2–3 mm long, 5–13 mm apart on both margins; staminate inflorescences terminal, nodding, 60 cm long; peduncle 10 cm long, fleshy, leafy bracted; lowest floral bract 96 cm long, 6 cm wide, the lower fifth elliptic, white, mostly unarmed, the upper part swordlike, the margins and midrib below prickly, the apex long subulate; floral bracts white, the median one 30 cm long, 4 cm wide, chartaceous below, lanceolate, the exposed parts having on margins and midrib below prickles 0.5–1 mm long, simple or double; flowering spikes 20–25, crowded, 5–8 cm long, 2–2.5 cm in diameter, dense; staminal clusters 10–16 mm long, the naked base of the column longer than the tip; free filament tips 0.6–1.3 mm long; the anthers 1.8–2.4 mm long, linear-lanceolate, tipped by a subulate prolongation of the connective 0.6–0.8 mm long.

HOLOTYPUS: Australia, North Queensland, Black Mountain Road, junction with Morgan Smith Lookout Road, open forest by creek, with *Casuarina litoralis, Eucalyptus tereticornis,* 1,300 ft. alt., Feb. 4, 1958, *H. St. John 26,256* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, same locality and date, fringing forest, staminate tree, *H. St. John 26,255* (BISH); Quarantine Bay, top of granite boulder beach, with *Cerbera Manghas, Calophyllum Inophyllum,* Feb. 1, 1958, *H. St. John 26,244* (BISH); and ditto, staminate, *H. St. John 26,245* (BISH);

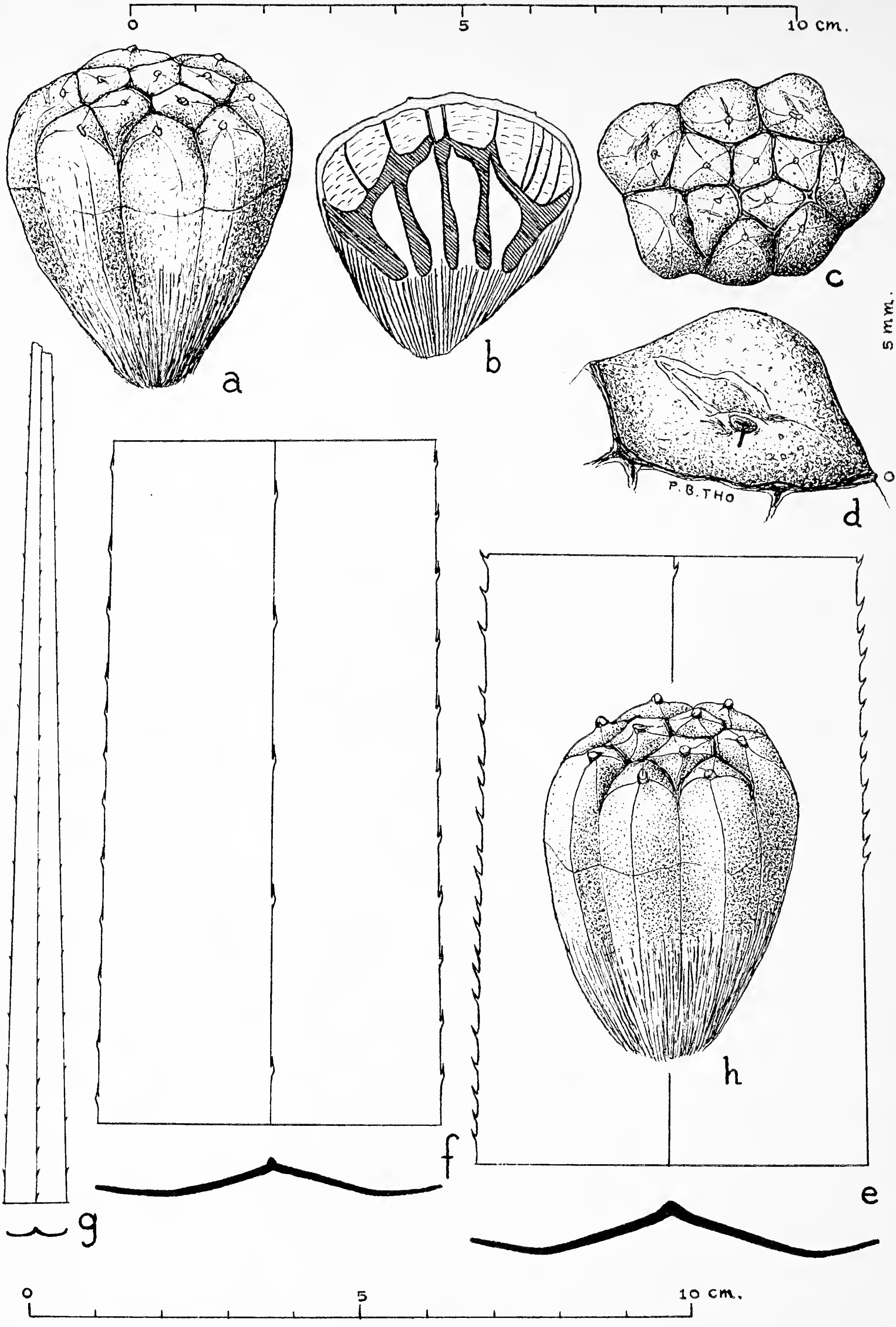

FIG. 127. *Pandanus sinuvadosus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, apical view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1; *h,* occasional phalange with low conic carpel apices, lateral view, × 1.

Archer Point, 8 miles s.e. of Cooktown, fringing forest by stream, with *Melaleuca, Eucalyptus leptophleba, E. intermedia, Tristania suaveolens,* Feb. 1, 1958, *H. St. John 26,246* (BISH).

DISCUSSION: *P. radiciferus* is a member of the section *Pandanus.* Its closest relative, *P. punctatus* St. John, of Queensland, has the leaves 2.2–2.3 m long, 8.5–12 cm wide, the lower margins with prickles 2–3 mm long, 3–15 mm apart, and the midrib below prickly at the midsection; syncarp ovoid; phalanges 5.3–6.3 cm long, 2.6–4.2 cm wide; endocarp 2.5–3.2 cm long, the lateral walls 2–4 mm thick; and the anthers 2.2–3.2 mm long. On the other hand *P. radiciferus* has the leaves 1.6–2.1 m long, 7–8 cm wide, the lower margins with prickles 1.5–2 mm long, 4–10 mm apart, the midrib below unarmed for the lower ⅔'s; syncarp globose or subglobose; phalanges 4.4–4.7 cm long, 1.6–2.9 cm wide; endocarp 1.8–2 cm long, the lateral walls 1–2 mm thick; and the anthers 1.8–2.4 mm long.

The new epithet is from the Latin *radix,* root, *fero,* to produce, because of the conspicuous production of rootlets which blanket the bark of the trunk.

Pandanus sinuvadosus sp. nov. (sect. *Pandanus*) Fig. 127

DIAGNOSIS HOLOTYPI: Arbor 8 m alta 18 cm diametro, cortice verrucoso, radicibus fulturosis 1 m longis 3 cm diametro verrucoso, foliis 1.2 m longis 6 cm latis coriaceis in sectione depresse sinuositer M-formatis in sectione mediali cum 55 nervis secundariis in quoque latere, basi amplexicauli inermi sed ex 6–11 cm marginibus cum aculeis 1.7–3 mm longis 3–8 mm distantibus subulatis adscendentibus brunneo-apicalibus, midnervo infra ex 11–15 cm cum aculeis simulantibus arcuatis adscendentibus 11–30 mm distantibus in sectione mediali marginibus cum aculeis 2–2.5 mm longis 4–10 mm distantibus proxime adpresse adscendentibus, circa apicem marginibus et midnervo infra cum serris 0.5 mm longis 3–8 mm distantibus adpressis, syncarpio inviso, phalangibus 3.7–4.6 cm longis 2.9–4.1 cm latis 2.4–3.1 cm crassis in sicco brunneis late turbinatis compressis lateribus laevibus lucidis subconvexis 5–6-angulosis parte ⅓ supera libera suturis lateralibus nullis, sinibus centralibus apicalibus 0–0.9 mm profundis plerumque olim tessellatis, carpellis 8–15 apicibus inaequalibus eis marginalibus duplo majoribus plerumque et semper in majoribus apicibus olim subconvexis et aegre distinctis, stigmatibus 1–1.5 mm longis ellipticis sulcatis obliquis centripetalibus, sinibus proximalibus ⅓–½ ad fondam extentis, endocarpio paene supramediali osseoso brunneo intra lucido lateribus lateralibus 4–5 mm crassis, seminibus 9–10 mm longis 4 mm diametro late ellipsoideis, mesocarpio supero in apice carpellae quaeque late cavernoso cum fibris longitudinalibus et membranis albis medullosis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 3–8 m tall, 18 cm in diameter; bark warty, gray; prop roots 1 m long, 3 cm in diameter, warty; leaves 1.2 m long, 6 cm wide, coriaceous, at midsection with 55 secondary veins on each side, in section depressed, sinuous M-shaped, the base amplexicaul, unarmed, but beginning at 6–11 cm the margins with prickles 1.7–3 mm long, 3–8 mm apart, subulate, ascending, brown-tipped; the midrib below beginning at 11–15 cm with similar arcuate ascending prickles 11–30 mm apart; at midsection the margins with prickles 2–2.5 mm long, 4–10 mm apart, closely appressed ascending; near the subulate apex the margins and midrib below with appressed serrae 0.5 mm long, 3–8 mm apart; peduncle short, erect; syncarp 23–30 cm long, 13–15 cm in diameter, ellipsoid-oblong; phalanges 3.7–4.6 cm long, 2.9–4.1 cm wide, 2.4–3.1 cm thick, when dried brown, broadly turbinate, compressed, yellowish above, below orange, the sides smooth, shining, gently convex, 5–6-angled, upper ⅓ free; lateral sutures none; central apical sinuses from 0–0.9 mm deep, usually merely a brown tessellate ruling but on some with low conic apices the sinuses perceptibly deep; carpels 8–15, the apices unequal, the marginal ones about twice as large as the inner ones, commonly and on all the large ones the apices only slightly convex, their profile scarcely distinguishable from that of the convex phalange apex, a few phalanges with the carpel apices depressed conic and the central sinuses almost 1 mm deep; stigmas 1–1.5 mm long, elliptic, creased, oblique, centripetal; proximal sinus

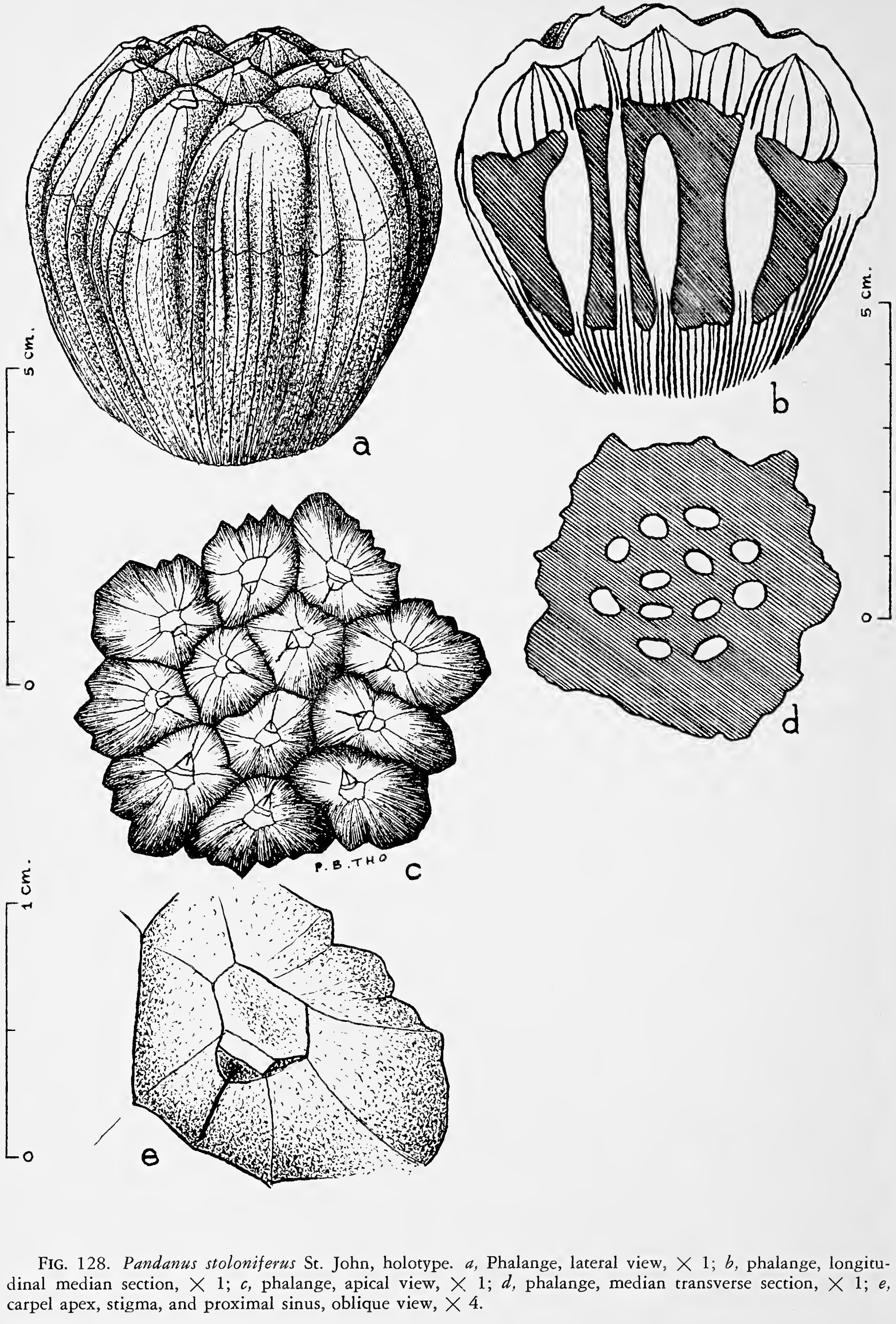

FIG. 128. *Pandanus stoloniferus* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* phalange, median transverse section, × 1; *e,* carpel apex, stigma, and proximal sinus, oblique view, × 4.

running ⅓–½ way to valley bottom; endocarp slightly supramedian, bony, brown, the inner surfaces shining, the lateral walls 4–5 mm thick; seeds 9–10 mm long, 4 mm in diameter, broad ellipsoid; upper mesocarp forming in the apex of each carpel a short, broad cavern with longitudinal fibers and white, glistening medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, Green Island, off Cairns, forest on coral sand, Feb. 9, 1958, *H. St. John 26,268* (BISH).

SPECIMENS EXAMINED: Queensland, Port Curtis Dist., Emu Park, at edge of beach, Sept. 24, 1943, *S. T. Blake 15,331* (BRI).

DISCUSSION: *P. sinuvadosus* is a member of the section *Pandanus.* In that section is its closest relative, *P. tectorius* Soland. var. *timorensis* Martelli, of Timor Island, which has the phalanges almost truncate, the central apical sinuses apparently 2 mm deep; carpel apices subequal; stigmas broad reniform; and the endocarp slightly submedian. *P. sinuvadosus* has the phalanges markedly convex at apex, the central apical sinuses too shallow to measure; carpel apices unequal, the marginal ones twice the larger; stigmas elliptic; and the endocarp slightly supramedian.

The new epithet is from the Latin *sinus,* sinus, *vadosus,* shallow, in description of the very shallow central apical sinuses of the phalanges.

Pandanus stoloniferus sp. nov. (sect. *Pandanus*)
Figs. 128, 129, 130, 126*c, d,* 132*a*

DIAGNOSIS HOLOTYPI: Arbor 7 m alta 15 cm diametro erecta gracilis in 3 m ex terra furcatus pauce ramosa, cortice pallide brunneo et cum radicillis 3–8 mm longis remotis adpresse adscendentibus, radicibus fulturosis 5 dm longis 3 cm diametro sparse muriculatis, foliis 1–1.89 m longis 5.2–6.2 cm latis coriaceis in sectione mediali cum 65 nervis secundariis in quoque latere, sensim ex basi in apice subulato diminuentibus eo in puncto 10 cm ex apice 6–7 mm lato, basi amplexicauli inermi, sed ex 12.5–14 cm marginibus cum aculeis 2.5–3.5 mm longis 7–15 mm distantibus subulatis rectis vel arcuatis adscendentibus apice rubro, midnervo toto inermi, in sectione mediali marginibus cum aculeis 2–2.5 mm longis 11–21 mm distantibus gracilibus subulatis adscendentibus adpressioribus, tertia supera et apice cum marginibus inermibus, pedunculo 15–25 cm longo terminali folioso, syncarpio solitario 20–25 cm longo 17.5–20 cm diametro ovoideo incarnato 39–50 phalangibus ferrentibus eis 5.7–6.5 cm longis 5.2–7.5 cm latis 4–6.7 cm crassis late obovoideis quadratis 4–6-angulosis, lateribus papillosis et punctatis sublucidis parte ½ supera libera, apice depresso-convexo, suturis lateralibus distinctis ½–⅔ distantia, lateribus distalibus carpellarum marginalorum cum 2–6 angulis et valleculis, sinibus centralibus apicalibus 4–6 mm profundis late V-formatis, carpellis 12–15 apicibus pyramidalibus vel marginalibus oblato-pyramidalibus, stigmatibus 2.5–4 mm longis subcircularibus ad ellipticis brunneis sulcatis obliquis centripetalibus, sinibus proximalibus ½ vel tota ad fondam extentibus, endocarpio minime submediali solido 3.5 m longo osseoso mahoganicolorato paginis interioribus lucidis marginibus lateralibus 7–10 mm crassis, seminibus 20–25 mm longis 7–8 mm diametro ellipsoideo, mesocarpio apicali in carpella quaque cavernoso cum fibris et membranis medullosis, mesocarpio basali parvo sed fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 7–12 m tall, 15–20 cm in diameter, erect, slender, first forking 3 m from the ground, few branched and the obovoid crown sparse; bark pale brown (when not blackened by the annual bush fires), with remote, appressed ascending rootlets 3–8 mm long; prop roots 5 dm long, 3 cm in diameter, sparsely muriculate; leaves 1–1.89 m long, 5.2–6.2 cm wide, coriaceous, at midsection with 65 secondary veins on each side, gradually tapering from the base to the subulate apex which 10 cm down is 6–7 mm wide, the very base amplexicaul and unarmed for 12.5–14 cm, then the margins with prickles 2.5–3.5 mm long, 7–15 mm apart, subulate, straight or arcuate, ascending, red-tipped; the midrib unarmed throughout; at midsection the margins with prickles 2–2.5 mm long, 11–21 mm apart, slender subulate, ascending, closely appressed, the upper third and apex of the leaf with the margins unarmed; peduncle 15–25 cm long, terminal, leafy; syncarp solitary, 20–25 cm long, 17.5–20 cm in diameter, ovoid, vermilion, with 39–50 phalanges, these 5.7–6.5 cm

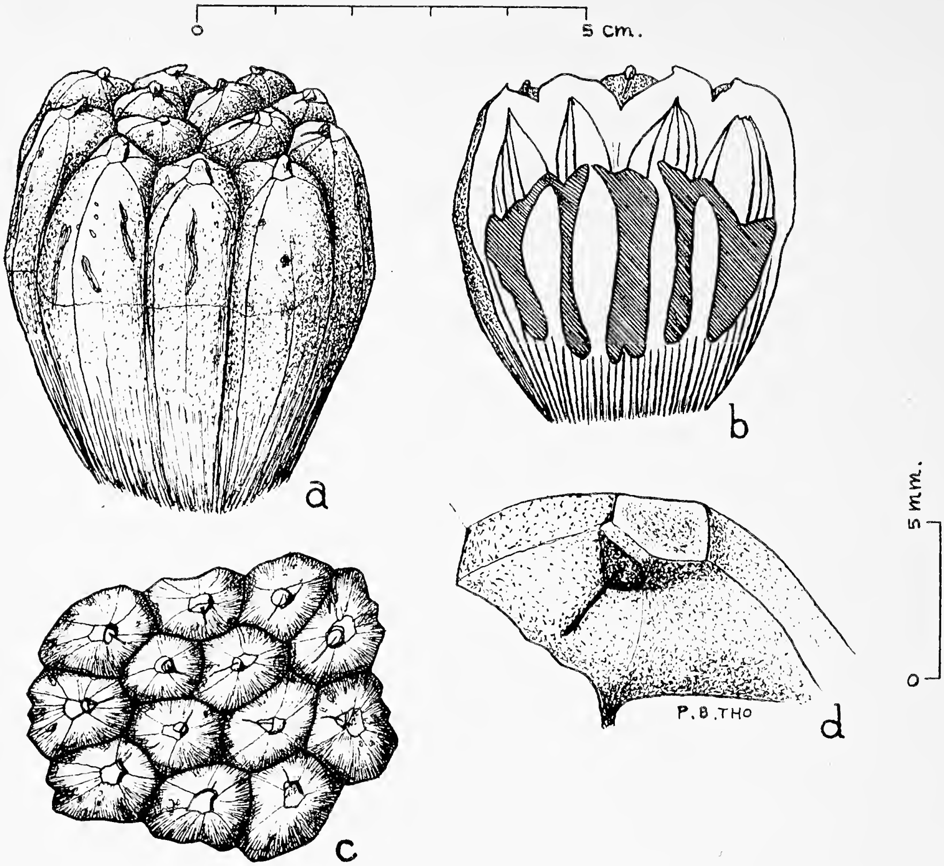

FIG. 129. *Pandanus stoloniferus* St. John, a depauperate syncarp from holotypic tree. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, with stigma, and proximal sinus, oblique view, × 4.

long, 5.2–7.5 cm wide, 4–6.7 cm thick, broadly obovoid, quadrate, 4–6-angled, with a broad median band about 2 cm wide of deep vermilion color, the rest pale vermilion, the sides papillose and punctate, a little shiny, upper ½ free, apex low convex, lateral sutures distinct ½–⅔ way, the outer side of each carpel with 2–6 prominent secondary ridges and valleys and hence mortised with the adjacent phalanges; central apical sinuses 4–6 mm deep, wide V-shaped; carpels 12–15, the apices pyramidal or the outer ones oblate pyramidal; stigmas 2.5–4 mm long, subcircular to elliptic, brown, creased, oblique, centripetal; proximal sinus running from half to all the way to the valley bottom; endocarp slightly submedian, massive, 3.5 cm long, bony, mahogany-colored, the inner surfaces polished, the lateral margins 7–10 mm thick; seeds 20–25 mm long, 7–8 mm in diameter, ellipsoid; apical mesocarp forming in each carpel a cavern with strong longitudinal fibers and white medullary membranes; basal mesocarp sparse, but fibrous and fleshy, the pulp with fruity odor, dry, mealy, the taste like that of a sweet potato then tardily slightly acrid. Staminate trees similar, but the leaves with the apex more slenderly long subulate, and 10 cm down only 2 mm wide, at the midsection the blade unarmed on one margin; in the upper third the midrib below with serrulations 0.2 mm long, 5–20 mm apart; staminate inflorescences terminal, cernuous, 70 cm long, with strong, sweet

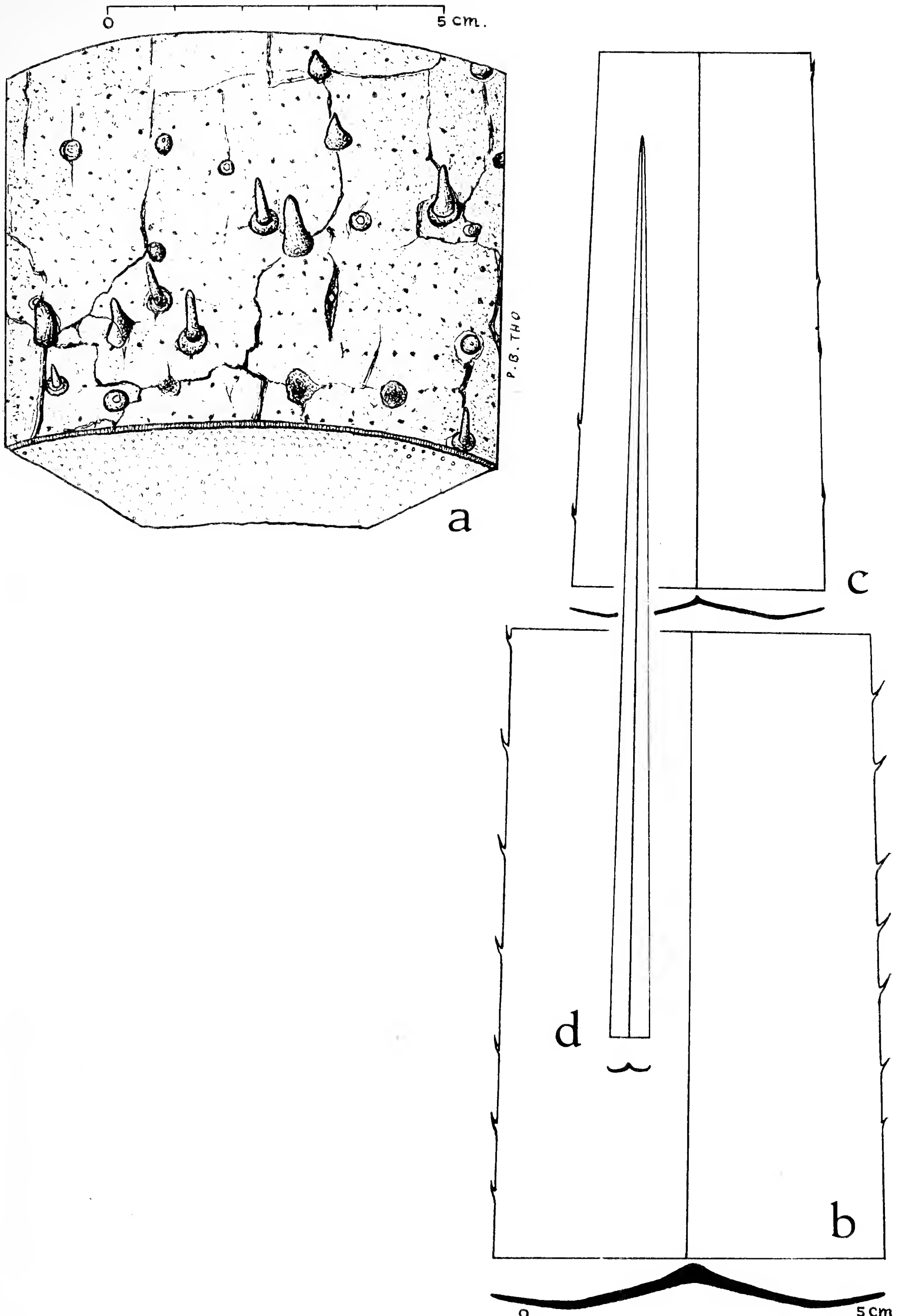

FIG. 130. *Pandanus stoloniferus* St. John, from *St. John 26,273*. *a*, Bark with adventitious ascending rootlets, and bundle scars, × 1; *b*, leaf base, lower side, × 1; *c*, leaf middle, lower side, × 1; *d*, leaf apex, lower side, × 1.

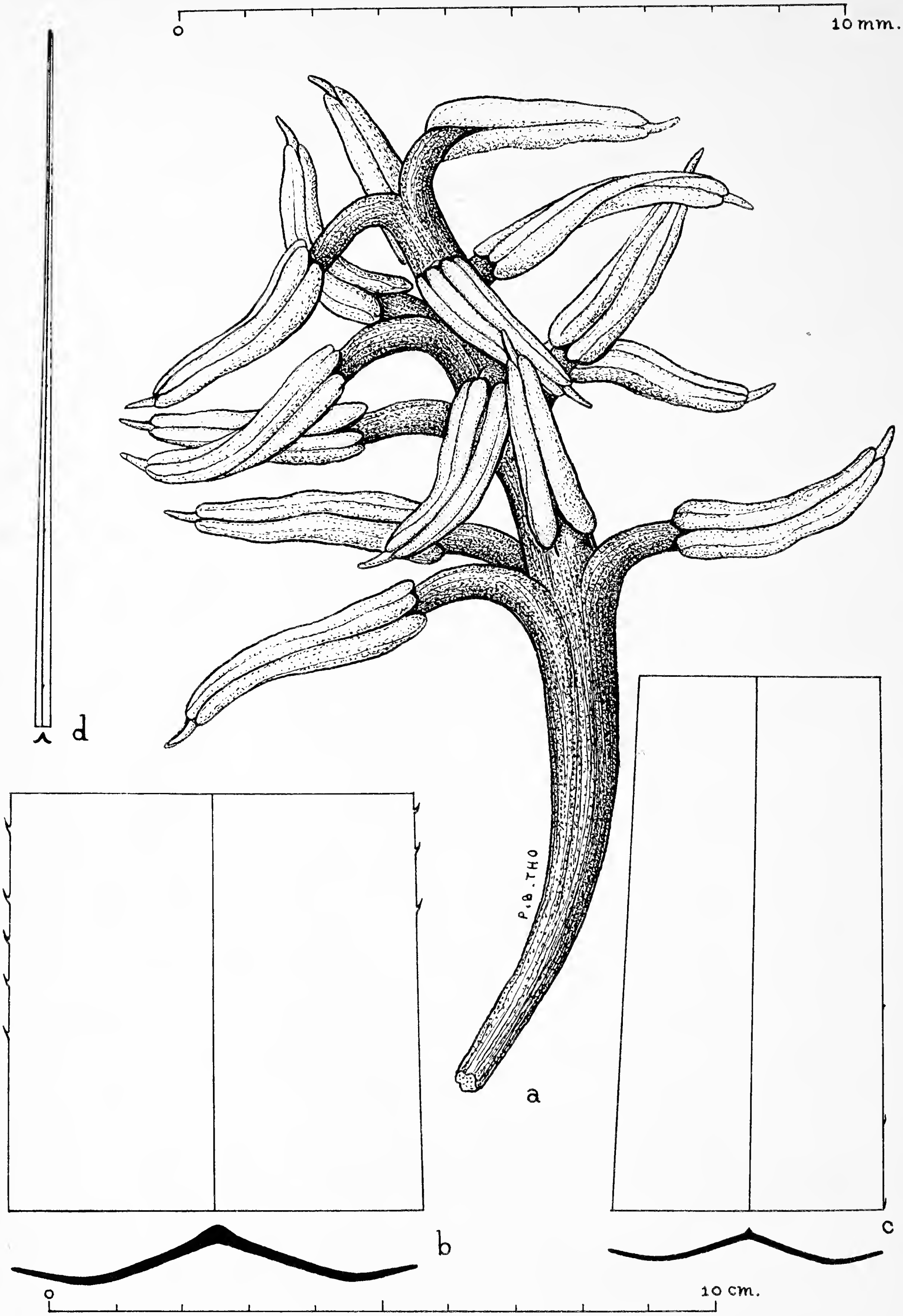

FIG. 131. *Pandanus stoloniferus* St. John, from *St. John 26,275*. *a,* Staminal column with anthers, × 10; *b,* leaf base, lower side, × 1; *c,* leaf middle, lower side, × 1; *d,* leaf apex, lower side, × 1.

Fig. 132*a. Pandanus stoloniferus* St. John, from *St. John 26,275,* showing buried stolon connecting mature staminate trees.

fragrance, and with many white bracts, the lower bracts foliaceous, the median ones 40 cm long, 3.4 cm wide, linear-lanceolate, long acuminate, the margins sparsely serrulate; the 18–20 spikes 5–7 cm long, 2 cm in diameter, dense; staminal columns 1–1.8 cm long, the lower half naked; free filament tips 1–1.5 mm long; anthers 3–4 mm long, linear-lanceoloid, beaked by the projecting, subulate apex of the connective 0.5 mm long.

HOLOTYPUS: Australia, North Queensland, 15 miles w. of Mareeba, deep sandy soil, scrubby open forest with *Eucalyptus polycarpa,* and *Melaleuca nodosa,* 1,290 ft. alt., Feb. 10, 1958, *H. St. John 26,274A* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, same locality and data, and from the type tree, but a depauperate syncarp, *H. St. John 26,274* (BISH); same locality and data, but from a different tree, *H. St. John 26,273* (BISH); same data, staminate tree, with underground stolons to other trees in the grove, *H. St. John 26,275* (BISH).

DISCUSSION: *P. stoloniferus* is a member of the section *Pandanus.* It is closely related to another Queensland species, *P. Whitei* Martelli, which has the leaves 8 cm wide, the margins in the lower third unarmed; phalanges 7–7.3 cm long, the apical central sinuses 3–5 mm deep; carpels 9–11; and the seeds 16–18 mm long, 3–5.5 mm in diameter. In contrast, *P. stoloniferus* has the leaves 5.2–6.2 cm wide, the margins near the base with prickles 2.5–3.5 mm long, 7–15 mm apart, subulate, red-tipped; phalanges 5.7–6.5 cm long, the apical central sinuses 4–6 mm deep; carpels 12–15; and the seeds 20–25 mm long, 7–8 mm in diameter.

There are evident differences between the pistillate and the staminate trees, in leaf shape, apex, and toothing. The staminate trees are stoloniferous and colony-forming. This character was not detected among the pistillate trees, and if these trees have stolons they must be at a much deeper level in the soil. None such were found.

One branch of the tree from which no. 26,274A was collected, was a lower, weak branch. From this branch was collected no. 26,274. This syncarp was only 9 cm long and 7 cm in diameter. All parts were like a smaller edition of the normal. The phalanges are 4.4–4.8 cm long, 4.3–4.9 cm wide, 3.8 cm thick. These details are not included in the description of the species, since they do not represent the normal. Though rarely so, the same type of depauperate heads with smaller phalanges has been found in a few other species. These smaller syncarps are produced on weak, lower branches, or more often as a secondary syncarp, lateral on the peduncle of the main and terminal syncarp. If collected without good data they could be the basis of a faulty classification.

The color of the ripe phalanges can be given in reference to the Royal Horticultural Society Color Chart, as follows: basal third, Saturn Red, (chart 13); middle band, Mandarin Red, (chart 17); the top, Brick Red, (chart 16).

The new epithet is formed from the Latin *stolo,* a stolon, *fero,* to bear, with reference to the stoloniferous habit of the male trees, a very unusual growth habit in the genus.

Pandanus subinermis sp. nov. (sect. *Pandanus*)

Figs. 133, 134, 135, 132*b–d,* 138*a*

DIAGNOSIS HOLOTYPI: Arbor 7–9 m alta 15 cm diametro pauciter furcata in corona aperta ellipsoidea, cortice cum radicillis adpresse adscendentibus, radicibus fulturosis nullis, foliis 1.4–1.5 m longis 6.3–6.6 cm latis coriaceis in sectione mediali cum 64 nervis secundariis in quoque latere, gladiformibus in medio 4.3–4.5 cm latis ex basi in apice longe subulato gradatim diminuentibus eo in puncto 10 cm ex apice 3.5–4 mm lato, basi amplexicauli et inermi sed ex 20 cm marginibus cum aculeis 1–2.3 mm longis

FIG. 132*b,c*. *P. subinermis* St. John, holotype. *b*, Tree habit, with S. T. Blake; *c*, fruiting branch with syncarp and phalanges.

7–14 mm distantibus arcuato-subulatis adscendentibus toto brunneis vel cum apicibus luteis, midnervo toto inermi, marginibus per parte ⅔ ultima inermibus, pedunculo 35 cm longo ad apicem 2 cm diametro incrassatem obscure trigono folioso terminali, syncarpio solitario ca. 22 cm longo et 17 cm diametro ovoideo 35–40 phalangibus ferentibus centro ellipsoideo trigono in sicco multo contracto, phalangibus 5–5.7 cm longis 4–5.3 cm latis 2.7–4.5 cm crassis late obovoideis subcompressis 5–7-angulosis in sicco brunneo lateribus subconvexis sublaevibus parte ⅓ supera libera, apice alte convexo vel semiorbiculari suturis lateralibus enim ad mediam profundis et distinctis, sinibus centralibus apicalibus 2.5–5 mm profundis in basi angustis, carpellis 9–15 plerumque 13 apicibus depresse rotundato-pyramidalibus interioribus subaequalibus vel minime minoribus, stigmatibus 1–2 mm longis suborbicularibus vel cordatis obscure brunneis papillosis obliquioribus centripetalibus sulcatis, sinu proximali tota vel fere ad fondam extento, endocarpio mediali 2.5 cm longo osseoso obscure brunneo intra brunneo et lucido lateribus lateralibus 5–6 mm crassis, seminibus 16 mm longis 6 mm diametro ellipsoideis, mesocarpio apicali in carpella quaque cum fibris longitudinalibus fortibus et membranis albis medullosis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 7–9 m tall, 15 cm in diameter, loosely few forked into an open, ellipsoid crown; bark with appressed ascending rootlets; prop roots none; leaves 1.4–1.5 m long, 6.3–6.6 cm wide, at midsection with 64 secondary veins on each side, gradually tapering from the base to the long subulate tip, this at about 10 cm down only 3.5–4 mm wide, the very base amplexicaul and unarmed, but beginning 20 cm up the margins with prickles 1–2.3 mm long, 7–14 mm apart,

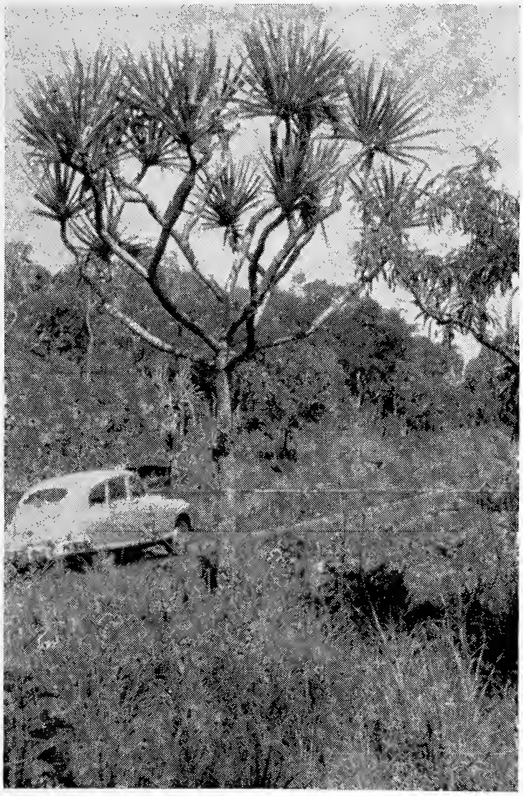

FIG. 132*d. Pandanus subinermis,* habit of staminate tree, from *St. John 26,259.*

arcuate subulate, ascending, brownish throughout or with yellow tips; the midrib unarmed throughout; the margins for the outer ⅔ unarmed; peduncle 35 cm long, increasing in width towards the apex which is 2 cm in diameter, obtusely trigonous, leafy bracted, terminal; syncarp solitary, about 22 cm long and 17 cm in diameter, ovoid with 35–40 phalanges; the core ellipsoid, trigonous, much shrunken on drying; phalanges 5–5.7 cm long, 4–5.3 cm wide, 2.7–4.5 cm thick, broadly obovoid, somewhat compressed, 5–7-angled, when dried brown, the sides gently convex, nearly smooth, upper ⅓ free, the apex high convex to semiorbicular; lateral sutures distinct and deep at least down to the middle; central apical sinuses 2.5–5 mm deep, the lower part narrow; carpels 9–15, mostly 13, the apices low rounded pyramidal, the inner ones subequal or slightly the smaller; stigmas 1–2 mm long, suborbicular to cordate, dark brown, papillose, very oblique, centripetal, creased; proximal sinus running all or nearly all the way to the valley bottom; endocarp median, 2.5 cm long, bony, dark brown, the inner surfaces brown and shining, the outer lateral walls 5–6 mm thick; seeds 16 mm long, 6 mm in diameter, ellipsoid; apical mesocarp in each carpel cavernous with strong longitudinal fibers and white medullary membranes; basal mesocarp fibrous and fleshy. Staminate tree (no. 26,259) 7 m tall, 15 cm in diameter; leaves 52–75 cm long, 5–5.5 cm wide, coriaceous, gladiate, tapering from the base into the acute tip, this 10 cm down 11–15 mm wide, in section M-shaped, at midsection with 53 secondary parallel veins in each half, appearing unarmed, but actually near the base on one margin with prickles 0.9–1.2 mm long, 4–7 mm apart, subulate, brown, appressed ascending; midrib unarmed throughout; at the midsection almost unarmed; near the tip unarmed; staminate inflorescence terminal, 40–50 cm long; peduncle 10 cm long, bracts numerous, the outer foliaceous and acuminate, blending to the reduced, whitish lanceolate ones 10–20 cm long, 2–3 cm wide, that subtend the spikes; lateral rhachises axillary, 5–7 cm long, densely flowered to the base; staminal columns numerous, crowded, 1.7–2.2 cm long, the lower half naked, the upper half bearing 25–28 racemose stamens, these with the free filament tip 1–2 mm long; anthers 4–6.5 mm long, linear, white, bipartite at base, at apex the subulate prolongation of the connective 0.7–1 mm long.

HOLOTYPUS: Australia, North Queensland, 6 miles s. of White Cliff Point, and 18 miles n. of Cairns, grove in savanna on granite boulder point, with *Eucalyptus tesselaris, Albizzia procera,* and *Heteropogon triticens,* 10–50 ft. alt., Feb. 5, 1958, *H. St. John 26,258* (BISH).

SPECIMENS EXAMINED: Australia, North Queensland, same locality and data as above, staminate tree, *H. St. John 26,259* (BISH).

DISCUSSION: *P. subinermis* is a member of the section *Pandanus.* Its close relative is *P. ferrimontanus* St. John, of Queensland, a species which has the leaves of the pistillate trees 5.8 cm wide, from the midsection to the tip the margins and midrib below prickly; phalanges 4.5–4.7 cm long, 3.4–3.5 cm wide; carpels 8–12,

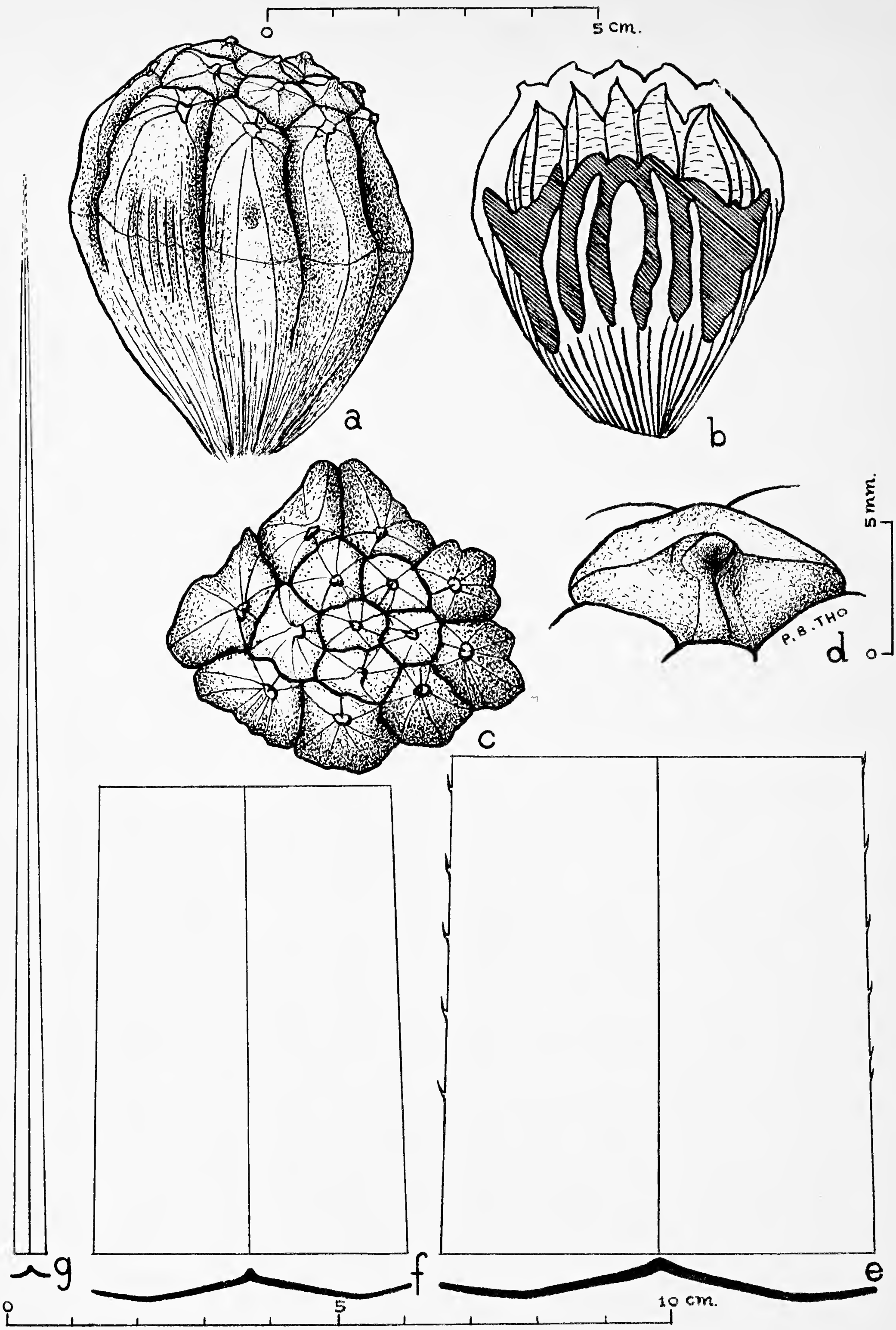

FIG. 133. *Pandanus subinermis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

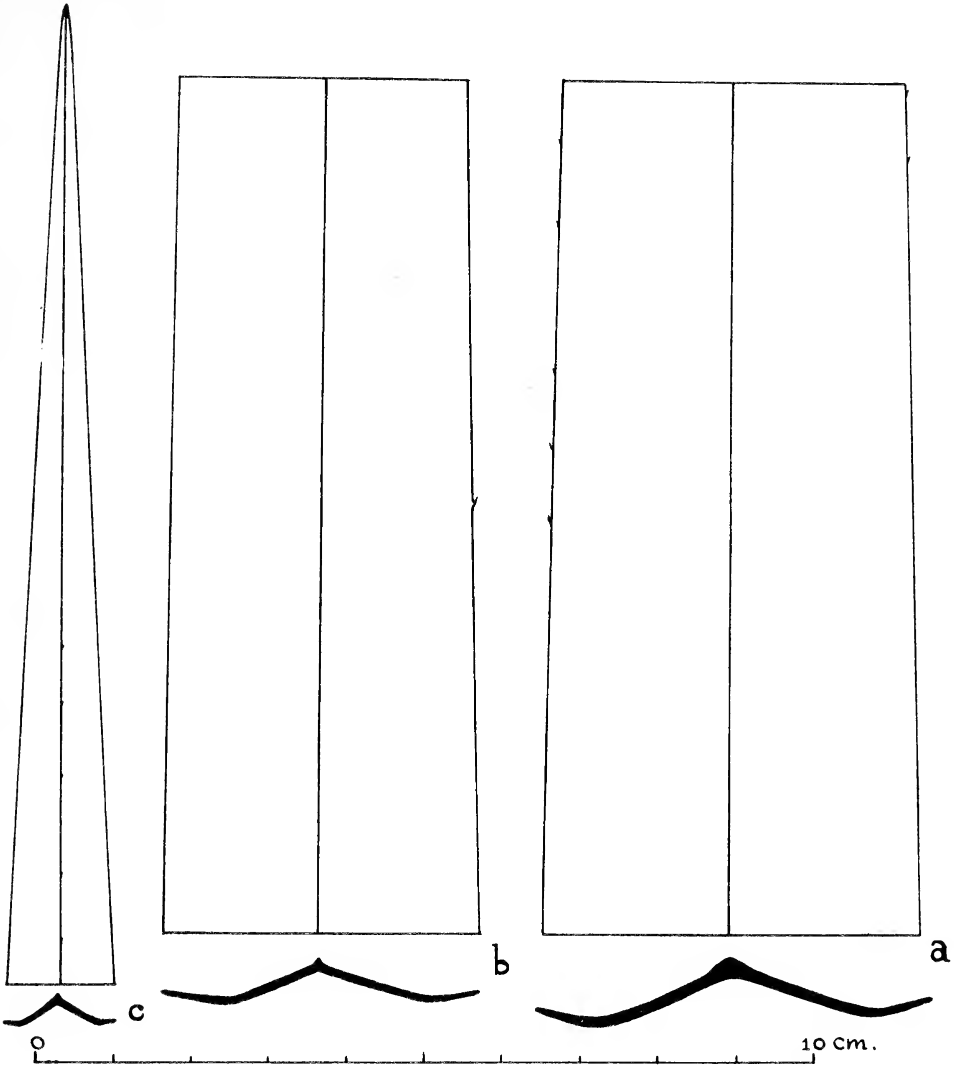

FIG. 134. *Pandanus subinermis* St. John, staminate tree, from *St. John 26,259. a,* Leaf base, lower side, × 1; *b,* leaf middle, lower side, × 1; *c,* leaf apex, lower side, × 1.

the apices with an oblique concavity distal of the stigma; endocarp stramineous; and the apical mesocarp 5–9 mm long. In contrast, *P. subinermis* has the leaves of the pistillate trees 6.3–6.6 cm wide, the midrib unarmed and the margins in the outer ⅔ unarmed; phalanges 5–5.7 cm long, 4–5.3 cm wide; carpels 9–15, mostly 13, the apices without concavity; endocarp dark brown; and the apical mesocarp 12–16 mm long.

The new epithet is the Latin adjective, *subinermis,* almost unarmed, in reference to the leaves which are almost unarmed.

Pandanus viridinsularis sp. nov. (sect. *Pandanus*)

Fig. 136

DIAGNOSIS HOLOTYPI: Arbor 8 m alta 20 cm diametro, cortice verruculoso, radicibus fulturosis 1.5 m longis 4 cm diametro, foliis 1.2–1.4 m longis 6 cm latis coriaceis in sectione depresse M-formatis gladiformatis sensim ad apicem licet

FIG. 135. *Pandanus subinermis* St. John, staminate tree, from *St. John 26,259*. Staminal column with anthers, × 10.

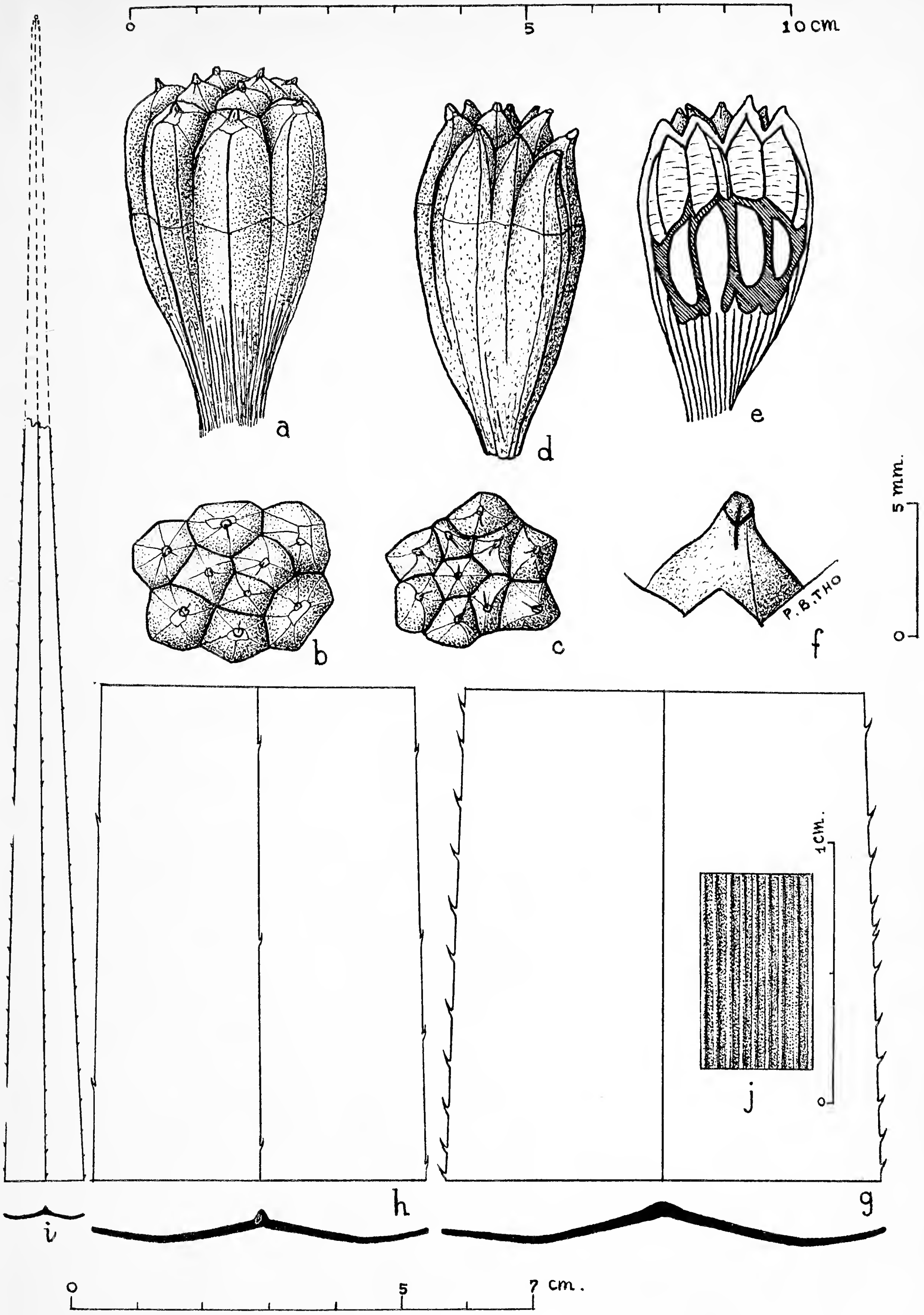

FIG. 136. *Pandanus viridinsularis* St. John, holotype. *a,* Basal phalange, lateral view, × 1; *b,* same, apical view, × 1; *c,* basal phalange, apical view, × 1; *d,* typical middle or upper phalange, lateral view, × 1; *e,* same, longitudinal median section, × 1; *f,* same, carpel apex, stigma, and proximal sinus, oblique view, × 4; *g,* leaf base, lower side, × 1; *h,* leaf middle, lower side, × 1; *i,* leaf apex, lower side, × 1; *j,* secondary veins at midsection, lower side, × 4.

subulatum diminuentibus basi amplexicauli et inermi sed ex 5–6 cm marginibus cum aculeis 2.5–4 mm longis 3–13 mm distantibus arcuato-subulatis adscendentibus apice brunneo, midnervo infra ex 17 cm cum aculeis 2 mm longis 13–28 mm distantibus arcuato-subulatis inferioribus reflexis, in regione mediali marginibus cum serrulis 1 mm longis 5–40 mm distantibus, midnervo infra cum aculeis 1.3–1.8 mm longis 16–32 mm distantibus graciliter subulatis adpresse adscendentibus, circa apicem marginibus et midnervo infra cum serrulis 0.1 mm longis 2–4 mm distantibus, syncarpio inviso, phalangibus 4.6–5.1 cm longis 2.3–3.2 cm latis 1.9–2.8 cm crassis eis medialibus et superis oblanceoloideis (aliquis basalibus brevioribus, latioribus et late oblanceoloideis) 5–6-angulosis lateribus laevibus sublucidis convexis parte ¼ supera libera apice convexo, dimidia suturis lateralibus ad mediam distinctis, sinibus centralibus apicalibus 3–5 mm profundis (in eis basalis 2–4 mm) V-formatis gradatim curvatis, carpellis 7–11 (in geminis 17, in triplo 30, et 4.3–6 cm latis) apicibus aequalibus vel subaequalibus lanceoloideis, eis centralibus symmetricalibus, eis marginalibus asymmetricalibus et apicibus divergentibus (in basalibus apicibus ovoideis acutis), stigmatibus 1.5–2 mm longis ellipticis ad subcircularis brunneis sulcatis valde obliquis proximalibus centripetalibus, sinibus proximalibus profundis ⅓–½ ad fondam extentis, endocarpio mediali 17–18 mm longo obscure brunneo intra lucido lateribus 2–2.5 mm crassis, seminibus 11–13 mm longis 3–4.5 mm diametro ellipsoideis, mesocarpio apicali in carpella quaque cavernam cum fibris paucis et membranis albis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 8 m tall, 20 cm in diameter; bark warty; prop roots 1.5 m long, 4 cm in diameter; leaves 1.2–1.4 m long, 6 cm wide, coriaceous, in section low M-shaped, swordlike, tapering gradually to the apparently subulate tip, the base amplexicaul and unarmed, but beginning 5–6 cm up the margins with prickles 2.5–4 mm long, 3–13 mm apart, arcuate subulate, ascending, brown-tipped; the midrib below beginning at 17 cm with prickles 2 mm long, 13–28 mm apart, arcuate subulate, the lower ones reflexed; at midsection the margins with serrulations 1 mm long, 5–40 mm apart; the nearby midrib below with prickles 1.3–1.8 mm long, 16–32 mm apart, slender subulate, appressed ascending; near the tip the margins and midrib below with serrulations 0.1 mm long, 2–4 mm apart; syncarp not seen; phalanges 4.6–5.1 cm long, 2.3–3.2 cm wide, 1.9–2.8 cm thick, the middle and upper ones oblanceoloid, (some of the basal ones shorter and broader, broadly oblanceoloid), 5–6-angled, the sides smooth and somewhat shiny, gently convex, upper ¼ free, the apex convex; about half of the lateral sutures perceptible half way down, but the other half invisible; central apical sinuses 3–5 mm deep (in the broad basal phalanges 2–4 mm), V-shaped, the sutures gently curving; carpels 7–11 (in a double 17, in a triple 30, and 4.3–6 cm wide), the apices equal or the central slightly smaller, lanceoloid, the central ones symmetric, the marginal ones asymmetric and the tips diverging, (in the basal phalanges the carpel apices ovoid, acute); stigmas 1.5–2 mm long, elliptic to subcircular, brown, creased, very oblique from apex down proximal side, centripetal; proximal sinus deep, running ⅓–½ way to valley bottom; endocarp median, 17–18 mm long, dark brown, bony, the inner surfaces shining, the lateral walls 2–2.5 mm thick; seeds 11–13 mm long, 3–4.5 mm in diameter, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with a few fibers and with white medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, North Queensland, Green Island, off Cairns, beach forest with *Erythrina, Cordia subcordata, Morinda citrifolia,* Feb. 10, 1958, *H. St. John 26,270* (BISH).

DISCUSSION: *P. viridinsularis* is a member of the section *Pandanus*. Its closest relative is *P. tectorius* Soland. var. *surigaensis* Martelli, which has the phalanges with the upper ½ free, the apices of the central carpels pyramidal suborbicular, and those of the marginal ones erect; stigmas of marginal carpels horizontal. On the other hand, *P. viridinsularis* has the phalanges with the upper ¼ free, the apices of the central carpels lanceoloid, but of the marginal ones

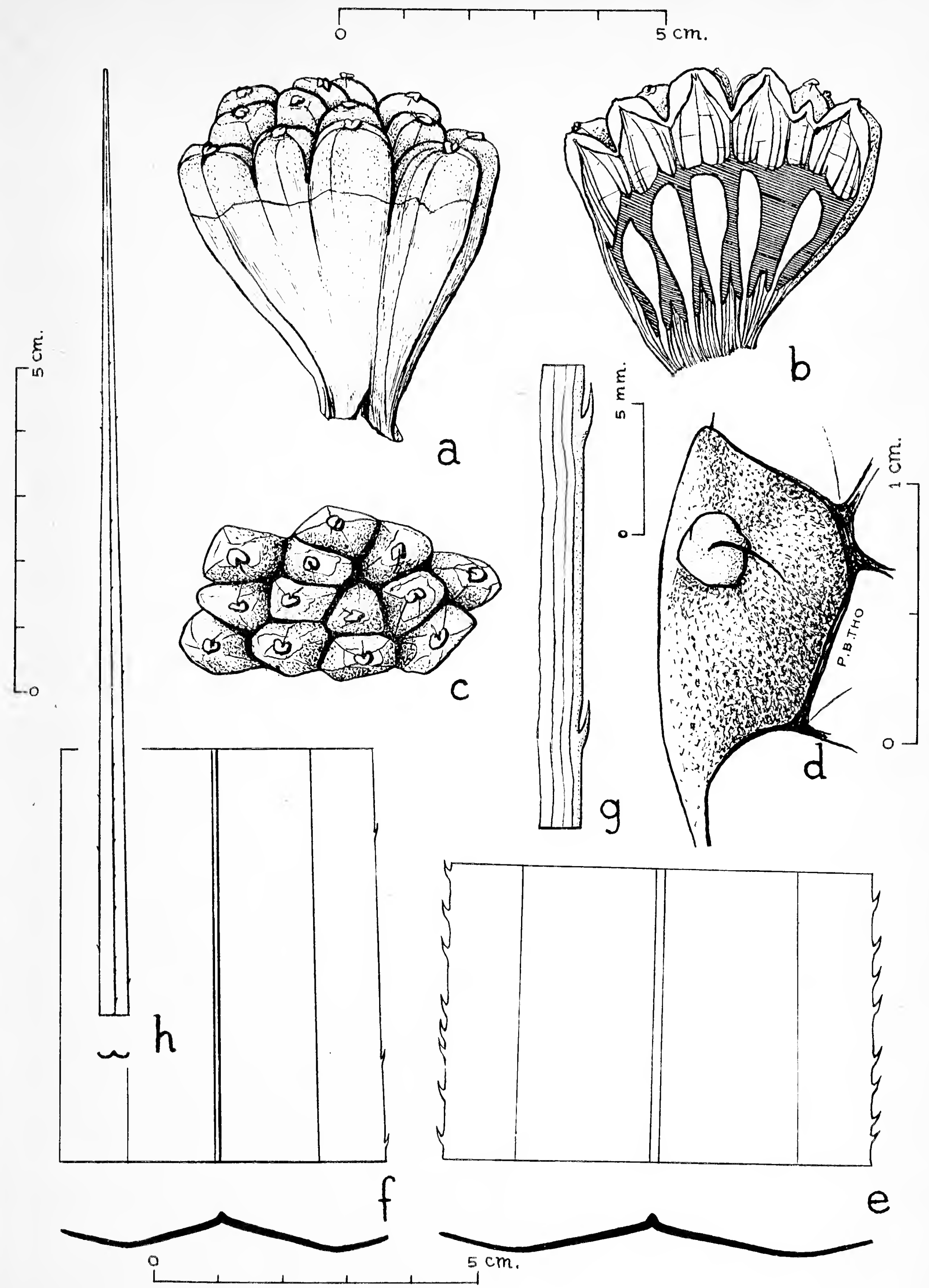

FIG. 137. *Pandanus yorkensis* St. John, holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, apical view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* margin of leaf at midsection, × 4; *h,* leaf apex, lower side, × 1.

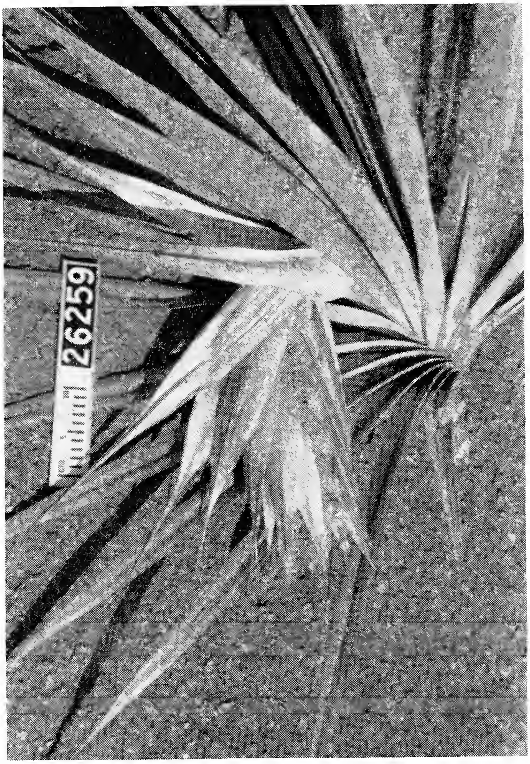

FIG. 138*a*. *Pandanus subinermis* St. John, from *St. John 26,259*, staminate inflorescence.

divergent; and the stigmas of all carpels oblique.

It is less closely related to the specimens from the Loyalty Islands illustrated by Martelli and merged by him with the Australian *P. pedunculatus* R. Br.

The new epithet is formed from the Latin words *viridis*, green, and *insularis*, of the island, in allusion to its type locality on Green Island.

Pandanus yorkensis sp. nov. (sect. *Pandanus*)
Figs. 137, 138*b*

DIAGNOSIS HOLOTYPI: Arbor 5–8 m alta valde remoteque ramosa, trunco ramisque cum umbonibus brevibus sparse armatis, foliis 117 cm longis 6.7 cm latis subcoriaceis glaucis gladiformatis ex basi in apice longiter subulata diminuentibus, in puncto 10 cm ex apice 4 mm latis, basi inermi sed ex 4.5–5.5 cm marginibus cum aculeis 1.5–3 mm longis 3–7 mm distantibus crassiter subulatis luteis adscendentibus basi arcuata, midnervo infra inermi sed in puncto 20 cm ex basi cum aculeis 1.5 mm longis paucis remotis adpressi-adscendentibus, in sectio mediali marginibus in uno latere inermi sed in altero cum aculeis 2 mm longis 11–32 mm distantibus, midnervo inermi, in parte apicale marginibus

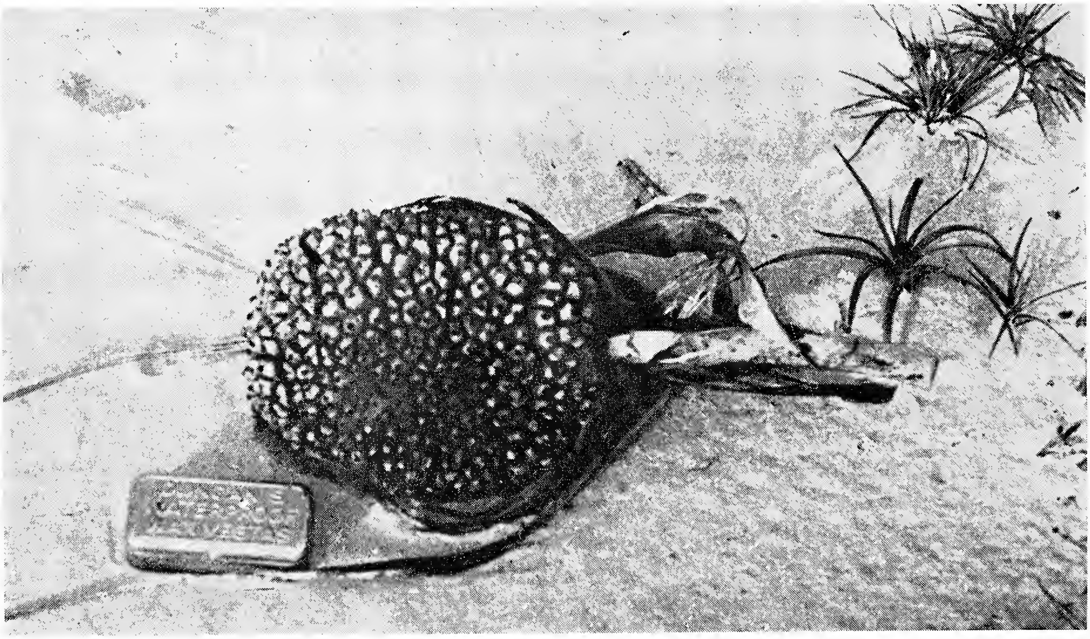

FIG. 138*b*. *Pandanus yorkensis* St. John, holotype, syncarp.

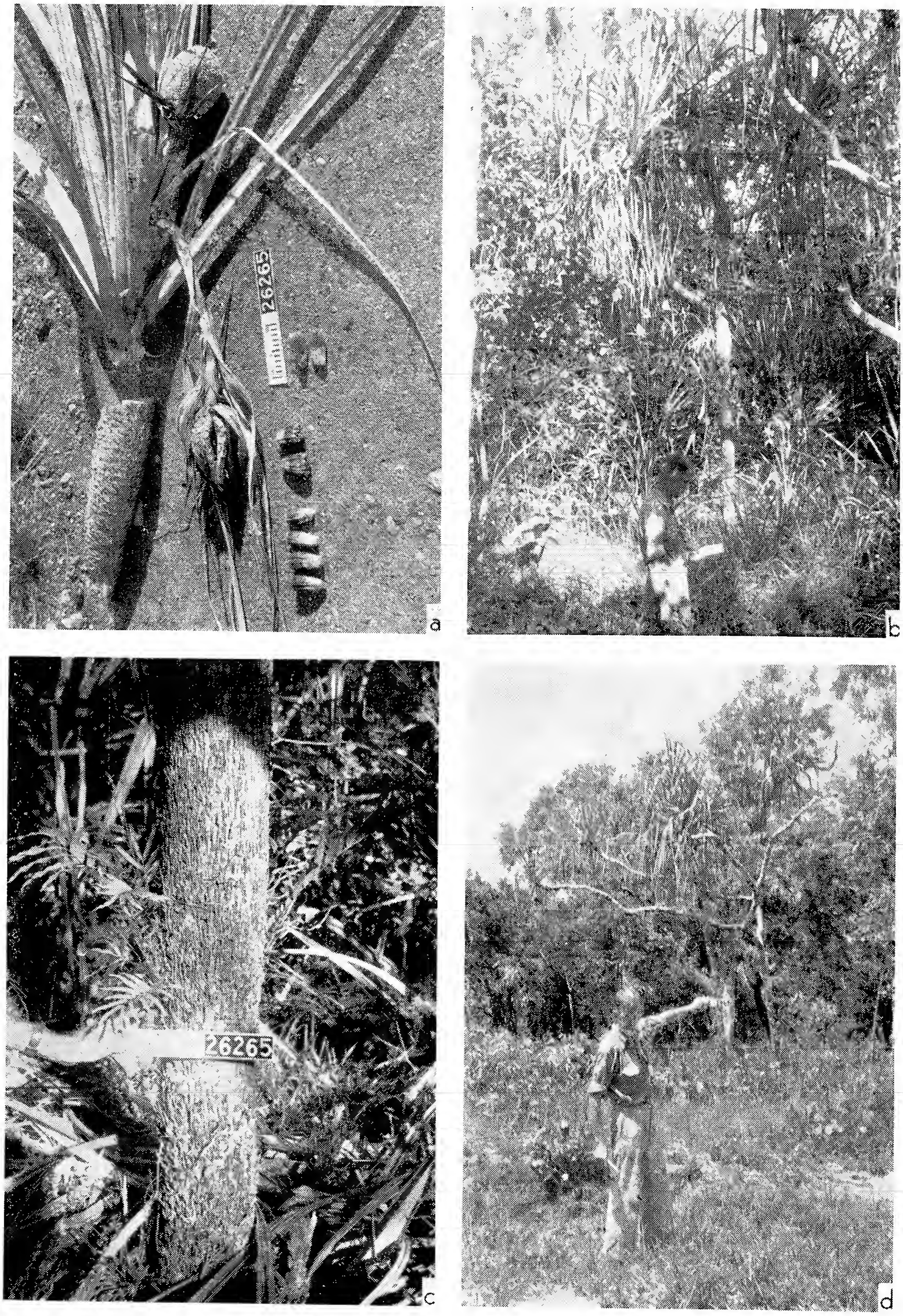

FIG. 139A. *a, Pandanus citraceus* St. John, holotype, trunk, leafy branch with syncarp in flower, and an old one with the phalanges shed from the core; *b,* tree habit, with S. T. Blake; *c,* trunk with appressed ascending adventitious rootlets. *d, P. orbicularis* St. John, holotype, tree habit, with S. T. Blake.

cum serris 0.2–0.3 mm longis 5–20 mm distantibus, midnervo inermi, pedunculo 15 cm longo sparse folioso-bracteato, syncarpio terminali solitario 15 cm longo 12 cm diametro late ovoideo triangulato cum circa 50 phalangibus eis 4.2–4.5 cm longis 3.1–4.9 cm latis 2.4–3 cm crassis late cuneiformibus 5–7-angulatis in sicco brunneis, lateribus laevibus lucidisque cum planis vel lateribus subcurvatis pluribus, in parte ¼ supera libera, apice late rotundato, suturis lateralibus angustis sed in quarto supero distinctis et rariter infra, sinibus centralibus apicalibus 6.5–8 mm profundis anguste V-formatis, carpelis 10–17 (sed in geminis 25 et phalangio 6.1 cm lato), apicibus ovoideis vel oblato-ovoideis minute papillosis, stigmatibus 2–3 mm longis suborbicularibus vel late ellipticis obscuris sulcatis centripetalibus eis interioribus obliquis, sinu proximo ¼–½ ad profundam extento, endocarpio paene submediali 2 cm longo osseoso pallido excepto partibus brunneis circum semines, lateribus exterioribus lateralibus 1–2 mm crassis, seminibus 13–17 mm longis 4–5 mm diametro ellipsoideis vel oblongo-ellipsoideis, mesocarpio supero in carpelis omnibus cavernam fibrosam et medullosam formanti.

DIAGNOSIS OF HOLOTYPE: Tree 5–8 m tall, freely and openly branched; trunk and branches "sparsely armed with short, stout bosses"; prop roots not mentioned; leaves 117 cm long, 6.7 cm wide, subcoriaceous, glaucous, swordlike, tapering from the base to the long subulate tip, this at 10 cm down only 4 mm wide, the very base unarmed, but beginning 4.5–5.5 cm up the margins with prickles 1.5–3 mm long, 3–7 mm apart, stout subulate, yellowish, ascending, the base arcuate; the nearby midrib below unarmed, but beginning 20 cm up a few remote prickles 1.5 mm long, ascending, appressed; at the midsection the margin on one side unarmed, on the other with prickles 2 mm long, 11–32 mm apart; the midrib unarmed; near the apex the margins with serrations 0.2–0.3 mm long, 5–20 mm apart; the midrib below unarmed towards the apex, but below 9 cm from the tip with similar serrations 3–4 mm apart; peduncle at least 15 cm long sparsely leafy bracted; syncarp terminal, solitary, 15 cm long, 12 cm in diameter, broadly ovoid, 3-angled, with about 50 phalanges, these 4.2–4.5 cm long, 3.1–4.9 cm wide, 2.4–3 cm thick, broad cuneiform, 5–7-angled, when dried brown, the sides smooth and shiny, of several planes or gently curving surfaces, free in upper ¼, the apex broadly rounded; lateral sutures narrow but distinct in free upper quarter, rarely further down; central apical sinuses 6.5–8 mm deep, narrow V-shaped; carpels 10–17 (but in a double 25 and the phalange 6.1 cm wide), the apices equal or somewhat unequal, fully ovoid or oblately so, dull and minutely papillose; stigmas 2–3 mm long, subcircular to broadly elliptic, dark, creased, centripetal, the inner ones oblique and slightly the smaller; proximal sinus running ¼–½ way to the valley bottom; endocarp slightly submedian, 2 cm long, bony, pale except for the brown portions near the seed cavities, the outer lateral walls 1–2 mm thick; seeds 13–17 mm long, 4–5 mm in diameter, ellipsoid to oblong-ellipsoid; upper mesocarp forming in each carpel apex a cavern crossed by numerous longitudinal fibers and with delicate, medullary membranes.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Newcastle Bay, 2½ miles s. of Somerset, May 12, 1948, *L. J. Brass 18,787* (BRI).

DISCUSSION: *P. yorkensis* is a member of the section *Pandanus*. The most similar known species is *P. duriocarpus* Martelli, of the Palau Islands. This has the phalanges 4.5–4.8 cm long, 2.5–4 cm wide; carpel apices pyramidal, lacking any concavity; and the apical central sinuses 5–7 mm deep. In contrast, *P. yorkensis* has the phalanges 4.2–4.5 cm long, 3.1–4.9 cm wide; carpel apices with an oblique, distal concavity adjacent to the stigma; and the apical, central sinuses 3.5–4.5 mm deep.

The new epithet is the geographic name York, plus *-ensis*, the Latin adjectival place ending.

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U P H

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Additional Records and Notes on *Conus* (Mollusca: Gastropoda) in Hawaii

ALAN J. KOHN[1] and CLIFTON S. WEAVER

SINCE PUBLICATION of a descriptive account of the species of *Conus* in Hawaii (Kohn, 1959) several additional species have been collected, and study of additional material has led to the discovery of a major error in the previous report. We correct this error here, discuss the recently discovered species, and provide new information on appearance of soft parts, maximum size, and vertical distribution of several species.

The Pele Expedition of May–Sep 1959 dredged from sites off Oahu and Maui much of the material reported on here.

The descriptive terminology in this paper follows Cox (1960). Names of colors of shells are those of the Inter-Society Color Council–National Bureau of Standards (ISCC–NBS) (Kelly and Judd, 1955), obtained with the standards of Ridgway (1912). Colors of soft parts in life are subjective and were not compared with standards.

Conus abbreviatus Reeve

Conus abbreviatus Reeve, 1843. Conch. Icon. 1: pl. 16, sp. 86.

C. abbreviatus has been considered (Kohn, 1959) endemic to the Hawaiian archipelago. We know of no reports in the literature of specimens from elsewhere, and none are present in the large collections of Indo–West Pacific molluscs in the major museums of Washington, Philadelphia, Cambridge, San Francisco, Honolulu, London, Cardiff, Copenhagen, Geneva, Paris, Vienna, Brussels, and Stockholm.

In April 1958, Mr. Harold G. Jewell collected a living specimen of *C. abbreviatus,* measuring 22 × 15 mm, in 1–3 m of water offshore from the cable station at Fanning Island, more than 900 miles south of Hawaii. Although stable populations do not appear to be maintained in the Line Islands, *C. abbreviatus* should no longer be regarded as endemic to the Hawaiian Islands.

Note added 16 Feb 1962: In June 1961, Mr. John H. Roberts, Jr., collected a living specimen of *C. abbreviatus,* measuring 22 × 16 mm, that was burrowing in sand in a tidal channel at a depth of 1 m at Eniwetok Island, Eniwetok Atoll, Marshall Islands, more than 2,500 miles from Hawaii.

Conus acutangulus Lamarck
Fig. 1*a–b*

Conus acutangulus Lamarck, 1810. Ann. Mus. Hist. Nat., Paris, 15: 286.

In the synonymy of this species in the earlier report (Kohn, 1959) *Conus eugrammatus* Bartsch and Rehder (1943) is listed incorrectly as a junior synonym. It is now known to be a distinct species and is discussed in detail below.

We have had the opportunity to examine living specimens of *C. acutangulus* collected by the Pele Expedition. In these the periostracum is very thin, translucent, smooth, and brown, not grayish white as indicated from long-dead specimens by Kohn (1959). The anterior portion of the sole of the foot is buff and the posterior half is light purplish brown. The siphon is buff at the tip and darker tan proximally. The rostrum is buff. Further descriptive information on the shell is given in the remarks under *C. eugrammatus* below, in which the two species are compared.

The depth range of *C. acutangulus* given previously (Kohn, 1959) erroneously included some records of *C. eugrammatus*. *C. acutangulus* has been collected alive off the south coast of Oahu (USNM 338566, 338567, 338568, Pele Expedition) and off Lahaina, Maui (USNM 338569, Pele Expedition), mainly in depths of 8–100 m, although some Pele Expedition specimens are labeled "35–75 fathoms."

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[1] Department of Zoology, University of Washington, Seattle, Washington. Manuscript received Aug 23, 1961.

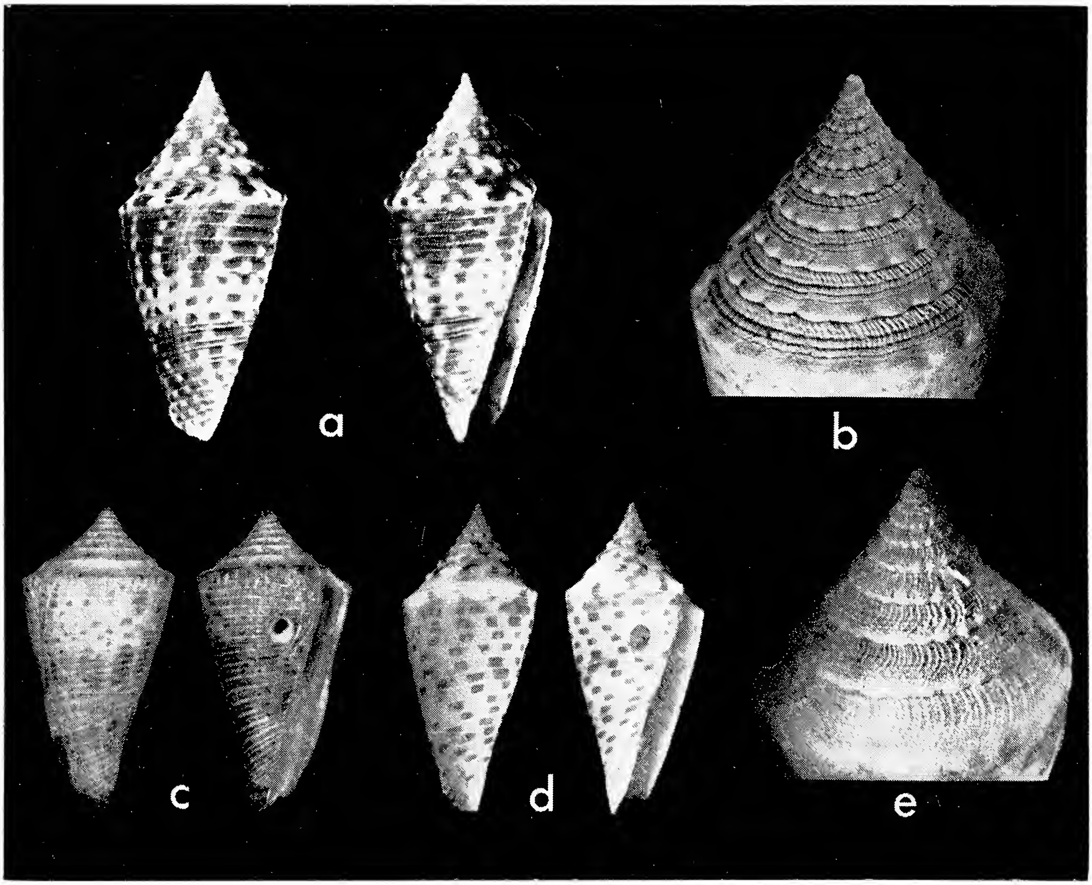

FIG. 1. *a–b, Conus acutangulus* Lamarck. *a,* Specimen collected by Pele Expedition, off Keehi Lagoon, Oahu, 70–150 m; 24 × 11.4 mm. *b,* Detail of spire; USNM 338568, off Pearl Harbor, Oahu, 25–50 m. *c–e, C. eugrammatus* Bartsch and Rehder. *c,* Holotype, USNM 173213, Molokai, 30 × 16 m; *d,* specimen collected by Pele Expedition, off Keehi Lagoon, Oahu, 150 m, 21.5 × 10 mm; *e,* detail of spire of specimen shown in *d. b, e,* Treated with NH_4Cl, after Glaessner (1947).

Conus capitaneus Linnaeus

Conus capitaneus Linnaeus, 1758. Syst. Nat., ed. 10, p. 713.

The smaller shell illustrated in figure 2 of Kohn (1959) was misidentified as a young specimen of *C. capitaneus.* This specimen is now known to be a young *C. vexillum* Gmelin, as is discussed below under that species. *C. capitaneus* is thus known in Hawaii from only one specimen, which was collected alive and is the larger shell shown in figure 2 of Kohn (1959).

Conus circumactis Iredale

Conus circumactis Iredale, 1929. Mem. Queensland Mus. 9: 281.

Visible portions of the foot of living specimens are now known to be pale lemon yellow.

Conus eugrammatus Bartsch and Rehder
Fig. 1*c–e*

Conus eugrammatus Bartsch and Rehder, 1943. Proc. Biol. Soc. Wash. 56: 85.

Conus eugrammatus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union Bull. 20: 28.

? *Asprella wakayamensis* Kuroda, 1956. Venus, Jap. Jour. Mal. 19: 9, pl. 1, fig. 2.

DESCRIPTION: Shell small, rather thin. Last whorl elongate; sides nearly straight; a few closely spaced spiral striae near the shoulder, followed abapically by spiral, punctured grooves separated by broad, flat ridges evenly spaced adapically but more closely and unequally spaced basally. Aperture narrow; outer lip protracted. Shoulder angular; spire elevated, occupying 20–33% of total shell length, turreted, slightly concave, marked by rather weak, slender, protraxially curved (opisthocyrt) axial riblets and obscure striae (Fig. 1*e*). Early (4–6) whorls weakly nodulose, later whorls smooth (Fig. 1*c–e*). Last whorl white, marked with strong yellowish-brown subquadrate spots mainly confined to the ridges and variably widely spaced (Fig. 1*d*), or condensed to form two or three interrupted spiral bands (Fig. 1*c*). Spire marked with widely spaced strong brown irregular or subquadrate spots. Periostracum very thin, yellowish-brown, translucent, smooth.

LENGTH: To 31 mm.

HOLOTYPE: USNM 173213; 30 × 16 mm; Fig. 1*c*.

TYPE LOCALITY: "Albatross" sta. 3889, off north coast of Molokai near Mokapu Islet.

REMARKS: Re-examination of the holotype and other specimens in the U.S. National Museum, as well as of material collected by the Pele Expedition, has led to the conclusion that *C. eugrammatus* and *C. acutangulus* are distinct species.

The most pronounced differences in the shells are as follows: In *C. acutangulus* the sculpture of the spire consists of >-shaped axial riblets intersected by a spiral stria at the point of the > and one or two others toward the shoulder (Fig. 1*b*). All whorls are nodulose or subcoronate, although coronation of the last whorl may be obsolete (Fig. 1*a–b*). In *C. eugrammatus* the spiral sculpture is weaker. Most prominent are slender, protraxially curved axial riblets (Fig. 1*e*). The early whorls (first 4–6) are subcoronate; the later whorls are smooth. The height of the spire of 15 specimens of *C. acutangulus* ranged from 29 to 45% of the total shell length and averaged 37%. The range in 10 specimens of *C. eugrammatus* was 20–33% and the average was 29%. The difference is significant at the .01 level of probability (Wilcoxon test; Tate and Clelland, 1957).

In both species, the last whorl is engraved with many distinct, rather broad, punctured spiral grooves. In *C. acutangulus,* the grooves and the intervening broad, flat ridges are of uniform width over the adapical half of the last whorl (Fig. 1*a*). In *C. eugrammatus,* a few closely spaced spiral striae precede the typical sculpture at the adapical part of the last whorl (Fig. 1*c–d*).

The ground color of the shells of both species is white. In *C. acutangulus,* the last whorl bears broad moderate brown axial markings, which may form two poorly defined, interrupted spiral bands at either side of the center. Rows of distantly spaced spots of the same color on the ridges mark the areas between and outside the bands (Fig. 1*a*). In *C. eugrammatus,* the markings on the body whorl consist mainly of strong yellowish-brown subquadrate spots confined to the ridges, but these may be condensed centrally and near the shoulder and base to form two or three spiral bands (Fig. 1*c*). Freshly collected specimens of *C. acutangulus* (Fig. 1*a*) in general are more darkly colored and show less of the white ground than do those of *C. eugrammatus* (Fig. 1*d*). In both species, the color pattern of the spire resembles that of the last whorl.

C. eugrammatus was described from specimens dredged by the U.S. Bureau of Fisheries steamer "Albatross" in 106–422 m. This material consists of five specimens, of which four were certainly dead when collected, from off the north coast of Molokai, off the south coast of Oahu, and in the Pailolo Channel, near Maui (USNM 173213, 190415, 205998, 335304). One specimen (USNM 190415) may well have been alive when collected, but this is not certain. The Pele Expedition obtained two empty shells at depths of 140–160 m off Keehi Lagoon, Oahu.

Although in general the records of *C. eugrammatus* are from deeper water than those of *C. acutangulus,* dead shells do not reliably indicate the habitat of the living gastropod. Unfortunately, the depth of the only "Albatross" specimen which may have been collected alive is given only as "211–53 fathoms." All other shells of *C. eugrammatus* seen by us were drilled by boring gastropods, apparently of the families Naticidae and Muricidae.

We have not thoroughly searched the vast literature to determine if an earlier name is available for *C. eugrammatus* among the more than 2,700 previously described species of *Conus*. In addition to *C. acutangulus, C. praecellens* Adams (1853; = *C. sowerbii* Reeve, 1849?) is similar in form. It differs in having no nodules on the early whorls, more pronounced spiral striae, and weaker, protraxially curved axial riblets on the spire, and a higher ratio of spire height to total length (average of 12 specimens, 41%; range, 37–46%).

Note added 16 Feb 1962: A living specimen of *C. eugrammatus* was dredged at a depth of 400 m on a mud-sand bottom 1 mile SSW of Pearl Harbor, Oahu, on 3 Jan 1962, by Mrs. Mary Eleanor King and Dr. C. M. Burgess, who have kindly permitted examination. The shell measures 36.5 × 15 mm and is thus the largest known specimen of the species. The spire bears a cheilostome ectoproct colony and a homotremid foraminiferan, suggesting that the animal does not burrow completely beneath the surface of the substrate in life. The shell and periostracum agree with the description above, but near the growing edge of the shell the periostracum bears densely spaced axial lamellae continued on the spire. The soft parts have retained little color in alcohol, but the siphon appears to have been light orange. The ungulate operculum measures 4.4 × 1.7 mm.

Conus litoglyphus Hwass *in* Bruguière

Conus litoglyphus Hwass *in* Bruguière, 1792. Enc. Méth. Vers 1: 692, pl. 338, fig. 8.

Living specimens observed by one of us (C.S.W.) have the sole and the dorsal margin of the foot olive green mottled with black; the rest of the foot is olive green. The siphon, rostrum, and tentacles are black.

Conus marmoreus Linnaeus

Conus marmoreus Linnaeus, 1758. Syst. Nat., ed. 10, p. 712.

Conus bandanus Hwass *in* Bruguière, 1792. Enc. Méth. Vers 1: 611, pl. 318, fig. 5.

Several living specimens of the Hawaiian form of this species (*C. marmoreus bandanus* Hwass *in* Bruguière, 1792) recently examined by one of us (C.S.W.) have the sole of the foot cream tinted with pale tan and the dorsum of the foot cream mottled with tan and brown. The siphon is banded proximally from the tip with white, dark brown, and white bands, and a half band of tan. The rostrum is cream mottled with brown and the tentacles cream tipped with brown.

Conus moreleti Crosse

Conus moreleti Crosse, 1858. Rev. Mag. Zool., ser. 2, 10: 122.

Living specimens of *C. moreleti* observed by us have the upper portion of the foot brownish red, mottled with brown and tipped with vermilion. The rest of the foot and the rostrum are light yellowish brown mottled with darker brown. The tip of the siphon is vermilion or yellow, followed proximally by black and yellow or vermilion bands; the rest of the siphon is yellow mottled with black. The tentacles are white or pale yellow.

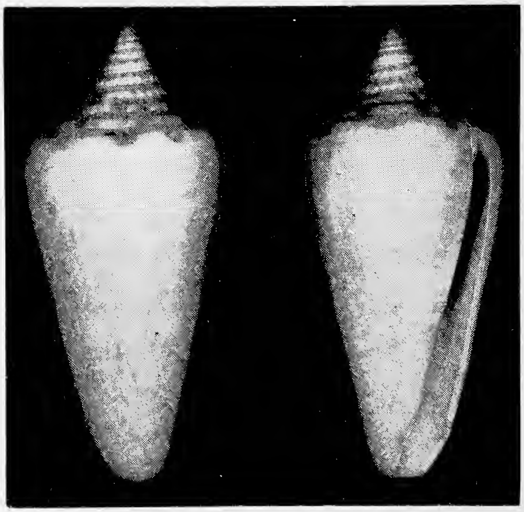

FIG. 2. *Conus suturatus* Reeve, var.? Collected by Pele Expedition, off Keehi Lagoon, Oahu, 200 m, 39 × 17 mm.

Conus obscurus Sowerby

Conus obscurus Sowerby, 1833. Conch. Illus., p. 2, pt. 29, fig. 26.

Living specimens observed by one of us (C.S.W.) have the sole of the foot flesh color tinged with pale brown. The dorsum of the foot, siphon, and rostrum are flesh color tinged with darker brown, and the tentacles are white.

Conus pertusus Hwass *in* Bruguière

Conus pertusus Hwass *in* Bruguière, 1792. Enc. Méth. Vers 1: 686, pl. 336, fig. 2.

Living specimens observed by us have the foot, siphon, rostrum, and tentacles pale golden yellow, sparsely speckled with black. The black specks are denser at the dorsal margin of the foot and the base of the siphon. The periostracum is very thin, translucent, and almost colorless. It is ornamented with widely spaced spiral ridges bearing small tufts of hairs.

Conus suturatus Reeve

Conus suturatus Reeve, 1884. Conch. Icon. 1: pl. 45, sp. 250; suppl. pl. 3, fig. 250*b*.

The Pele Expedition dredged more than 100 specimens of *C. suturatus* in depths of 40–150 m off Keehi Lagoon, Oahu, in Aug 1959.

In addition, an unusual empty shell dredged in 200 m on a mud substratum off Keehi Lagoon in Aug 1959 may be referable to this species. It measures 39 × 17 mm and is shown in Figure 2. The spire is concave, much more elevated, and at a more acute angle than in typical *C. suturatus*. The early whorls are turreted and somewhat more prominently nodulose than they are in typical specimens. The marked elevation of the spire apparently has caused a reduced diameter of the shell, which is much narrower than in typical specimens with lower, nonturreted spires (Kohn, 1959: pl. 2, figs. 24–28). The spire is deeply striate and ridged as in typical *C. suturatus*. The spiral sculpture of the last whorl is within the range of variation of *C. suturatus*.

The color pattern of the spire is identical with that of smaller typical specimens of *C. suturatus*. The color pattern of the last whorl appears somewhat faded to moderate orange yellow. It consists of interrupted spiral rows of quadrangular markings on a white ground. Some of the markings appear fused axially into larger spots. This pattern is typical of most smaller specimens of *C. suturatus* from Hawaii (Kohn, 1959: pl. 2, fig. 24), but the broad spiral bands characteristic of most larger specimens are not visible in the specimen under discussion. It is referred to *C. suturatus* with uncertainty.

In living *C. suturatus*, the siphon bears three broad bands of white, black, and tan from the tip proximally. The rostrum and tentacles are buff. The upper portion of the foot is white mottled with brown, but there is a narrow darker band near the posterior end.

Conus vexillum Gmelin
Fig. 3

Conus vexillum Gmelin, 1791. Syst. Nat., ed. 13, p. 3397.

Recent collections of many small specimens of *C. vexillum* in Hawaii have permitted an appreciation of changes in shell color pattern with increasing size and age. Figure 3 illustrates the progression from juvenile to definitive pattern. The ground color changes from dark yellow (Fig. 3*a*) through light olive (Fig. 3*b*), moderate olive (Fig. 3*c*), and light olive brown (Fig. 3*d*), to light yellowish brown (Fig. 3*e*). White spiral bands at the shoulder and centrally on the last whorl become more prominent with increasing size. The darker spots of smaller specimens (Fig. 3*a–b*) and irregular markings of larger ones (Fig. 3*c–e*) are dark brown. In life the foot of juveniles is yellow, becoming yellowish green, olive green, and greenish black with increasing size.

The smaller specimen figured for *C. capitaneus* Linnaeus in Kohn (1959: fig. 2, left) is actually *C. vexillum*. It is intermediate in size between the specimens shown here in Figure 3*a*, *b*. The spire of *C. capitaneus* of similar size is more densely and regularly tesselated with brown. The spiral striae in *C. capitaneus* number 3–4 per whorl and are widely spaced; in *C. vexillum* there are usually 6–7 fine, closely spaced striae per whorl.

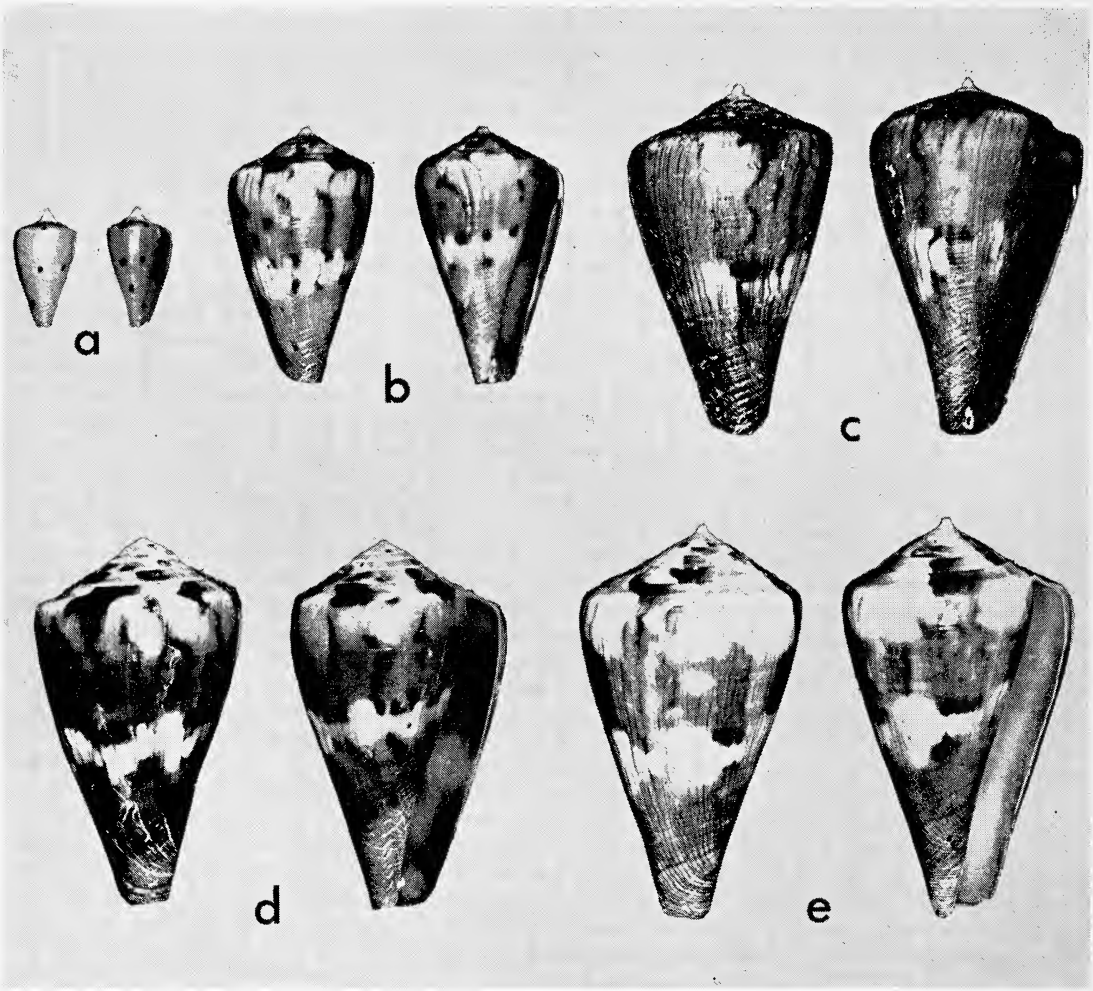

FIG. 3. *Conus vexillum* Gmelin, showing change of shell color pattern with increasing size. *a,* 9.5 × 5 mm, Kailua, Oahu, 17 m; collected by C.S.W. *b,* 21 × 12 mm, Makua, Oahu, 7 m, coll. D. Wellington. *c,* 28.5 × 17 mm, Pokai Bay, Oahu, 15 m, coll. E. Harrison. *d,* 29 × 18 mm, Rabbit Island, off Oahu, 9 m, coll. C.S.W. *e,* 32 × 19 mm, Rabbit Island, off Oahu, 9 m, coll. C.S.W.

Conus sp. cf. *C. cumingii* Reeve
Fig. 4

Conus cumingii Reeve, 1848. Conch. Icon., 4: suppl. pl. 3, sp. 282 (*non C. cumingii* Reeve, 1849. Conch. Icon., 5: suppl. pl. 8, sp. 277).

The Pele Expedition dredged about 50 living specimens of a species of *Conus* not previously known to occur in Hawaii, in 70–200 m, chiefly on coral rubble substratum off Keehi Lagoon, Oahu.

This species is extremely variable in sculpture and color pattern; some of the variation is correlated with size and, presumably, with age (Fig. 4). At the present time, we are unable to provide a specific identification of this species. It resembles very closely the little-known species *C. cumingii* Reeve (1848; described from the Philippines). The main difference is in the more elevated spire of the shell of *C. cumingii,* which was described as "smooth or obsoletely finely ridged, spire peculiarly grooved and punctured; reddish olive, with a central band, spire and upper edge of the whorls white, conspicuously painted with interrupted lineated chestnut blotches; apex pink" (Reeve, 1848).

The last whorl of some specimens of *Conus* sp. is smooth, i.e., bearing fine spiral striae and/or lirae visible only under magnification, except near the base (Fig. 4*a,d,e,h,j,k*). Other specimens are partly (Fig. 4*f,i*) or entirely (Fig. 4*b,c,g*) encircled by granular spiral lirae. The puncturing of the spire described is due, as Weinkauff (1874: 29) stated, to the intersection of axial growth lines and the ridges between spiral striae.

The ground color of the last whorl of *Conus* sp. is yellow, orange yellow, or orange. The range in lightness and saturation is indicated by the following ISCC–NBS colors of the specimens shown in Figure 4: moderate yellow (*d,h*); moderate orange yellow (*c*); dark orange yellow (*i,j*); strong orange yellow (*a,b*); moderate orange (*g,k*); deep orange (*e,f*) (Kelly and Judd, 1955).

Conus sp. agrees in other shell characteristics, except spire elevation, with the diagnosis and holotype of *C. cumingii* (in British Museum, Natural History). The periostracum of *Conus* sp. is thin, yellowish-brown, and may bear projecting hairs on ridges corresponding to the

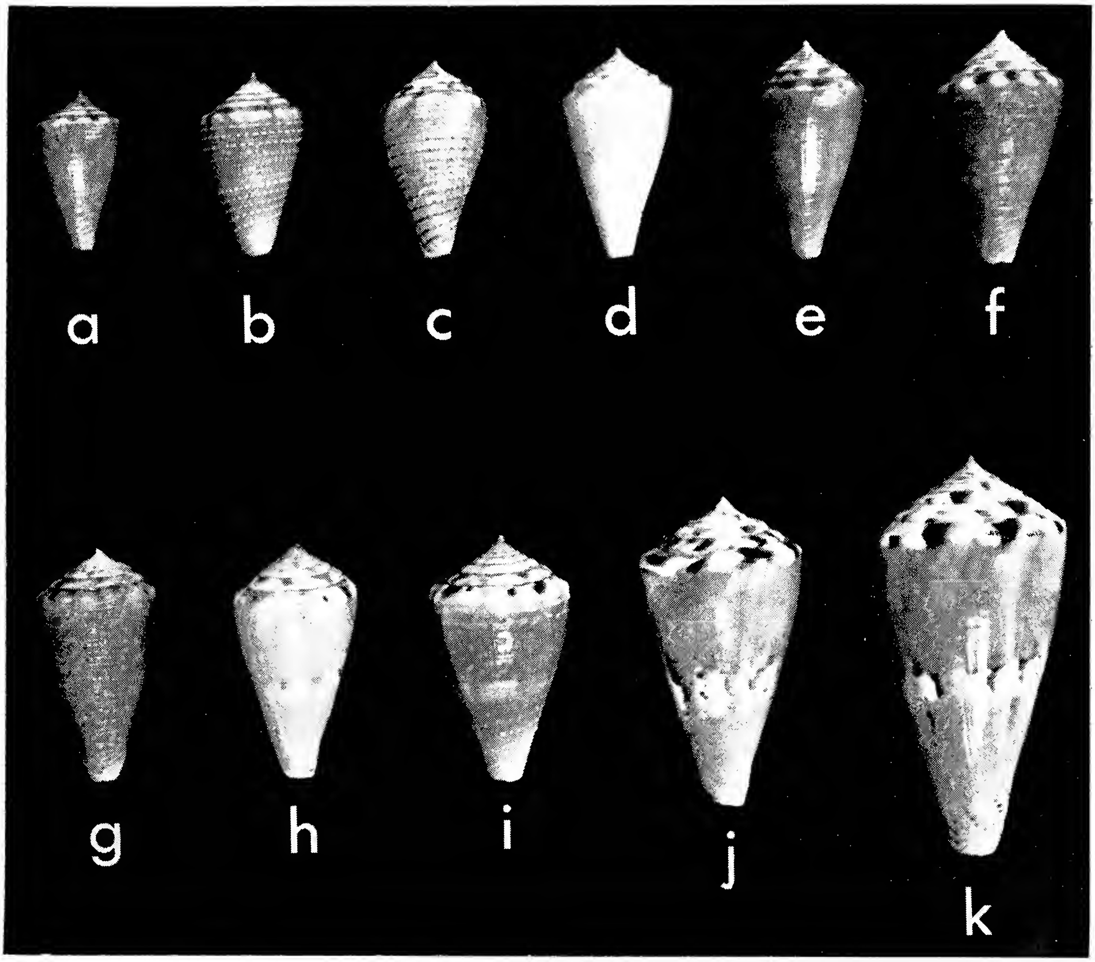

FIG. 4. *Conus* sp. cf. *C. cumingii* Reeve. Collected by Pele Expedition, off Keehi Lagoon, Oahu, 70–200 m. *a,* 16.5 × 9 mm; *b,* 19 × 11 mm; *c,* 20 × 11 mm; *d,* 21 × 12 mm; *e,* 22 × 12 mm; *f,* 24 × 13 mm; *g,* 24 × 13 mm; *h,* 24 × 13 mm; *i,* 25 × 15 mm; *j,* 31 × 17 mm; *k,* 40 × 19.5 mm.

spiral lines. In life, the foot of *Conus* sp. is buff mottled with light tan, and the anterior and posterior extremities are tinged with light vermilion. The siphon is light vermilion, mottled with small darker blotches. The rostrum and tentacles are pale buff. The periostracum and color of the soft parts of *C. cumingii* are unknown.

We do not assign *Conus* sp. (Fig. 4) with certainty to *C. cumingii.* It approaches the diagnosis and holotype of that species more closely than to that of any other known to us. It would be inadvisable to describe *Conus* sp. as new, since we have not been able to study in detail the more than 2,700 nominal species of *Conus* to ensure that it has not previously been described. To help solve problems of this type, one of us (A.J.K.) has begun a study of the type specimens and identity of the described species of *Conus,* in chronological order.

ADDITIONAL SPECIES KNOWN IN HAWAII ONLY FROM COLLECTION OF EMPTY SHELLS

Conus aurisiacus Linnaeus

Conus aurisiacus Linnaeus, 1758. Syst. Nat., ed. 10, p. 716.

The Pele Expedition dredged three fragments of shells of *C. aurisiacus* in Aug 1959. Two pieces were obtained on mud and coral rubble substratum in 110 m between Maui and Lanai. The other was obtained on sand and coral rubble in 100 m off Keehi Lagoon, Oahu.

Conus sp. cf. *C. granifer* Reeve
Fig. 5

Conus granifer Reeve, 1849. Conch. Icon. 5: suppl. pl. 7, sp. 272.

The Pele Expedition dredged three fresh but empty shells, agreeing in several respects with the diagnosis and holotype of *C. granifer,* in 150–210 m off Keehi Lagoon, Oahu, in Aug and Sep 1959. In addition, two similar specimens from off Kauai (USNM 190416) and Oahu (USNM 338572) are in the U.S. National Museum.

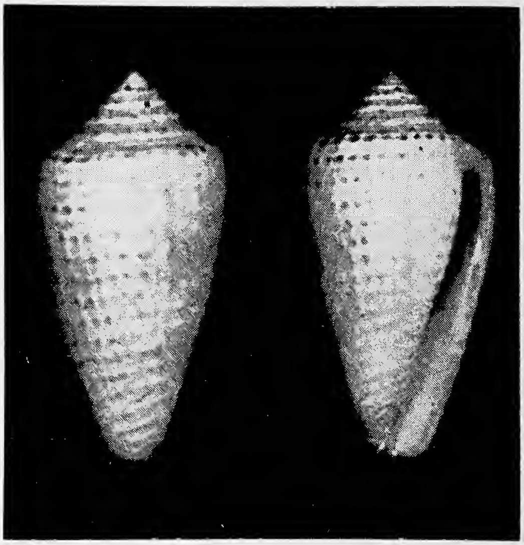

FIG. 5. *Conus* sp. cf. *C. granifer* Reeve. Collected by Pele Expedition, off Keehi Lagoon, Oahu, 150–200 m; 23 × 11.5 mm.

The Hawaiian specimens (Fig. 5) agree with the diagnosis and holotype of *C. granifer* (in British Museum, Natural History) in size, shape of last whorl and spire, granose ornamentation of last whorl, and white ground color. They differ in color pattern, *C. granifer* being tinged with light brown at the base and apex, and the Hawaiian specimens having distantly spaced moderate yellow markings on the spire and two faint, broad, spiral bands of the same color on the last whorl. The color pattern thus resembles that of *C. suturatus,* and it is just possible that the specimens under discussion are unusually shaped and ornamented individuals of that species.

Conus luteus Sowerby

Conus luteus Sowerby, 1833, Conch. Illus., pt. 25, figs. 8, 8*.

The Pele Expedition dredged one intact but empty shell and one fragment of a recently dead specimen of *C. luteus* on a mud and coral rubble substratum in 110 m off Lahaina, Maui, in Aug 1959. The intact specimen measures 27 × 11.5 mm.

TABLE 1

MAXIMUM SIZE OF SPECIES OF *Conus* IN HAWAII

SPECIES	PREVIOUS LENGTH × WIDTH (mm)*	PREVIOUS LENGTH × WIDTH (mm)*	REFERENCE
C. acutangulus Lamarck	30	32 × 15.5	fossil; Honolulu Harbor dredging, 1960; Children's Museum of Honolulu
C. catus Hwass *in* Bruguière	40	48 × 29.5	Kauai; Muséum National d'Histoire Naturelle, Paris
C. chaldaeus (Röding)	44	49 × 27	Kahuku, Oahu; coll. C.S.W.
C. marmoreus Linnaeus	139	142	Maalaea Bay, Maui; coll. Mrs. J. Kern
C. pennaceus Born	82	86 × 46	Waikiki, Oahu; 1 m; Children's Museum of Honolulu
C. retifer Menke	50	69 × 40	off Rabbit I., near Oahu; 8 m; coll. C.S.W., 1961
C. spiceri Bartsch and Rehder	110	139 × 74	Lahaina, Maui; coll. H. Hall, Jr.
C. striatus Linnaeus	120 × 53	125 × 61	Waimanalo, Oahu; 8 m; coll. C.S.W., 1959
C. textile Linnaeus	100	128 × 66	subfossil; Kapaa, Kauai; coll. W. R. Haas, 1959

* Data from Kohn, 1959.

TABLE 2

MAXIMUM DEPTH OF SPECIES OF *Conus* IN HAWAII

SPECIES	PREVIOUS DEPTH (m)*	NEW DEPTH (m)	NEW REFERENCE
C. abbreviatus Reeve	—	50–100	off Keehi Lagoon, Oahu; Pele Exped., May 1959
C. marmoreus Linnaeus	16	50–90	off Keehi Lagoon, Oahu; Pele Exped., Aug 1959
C. moreleti Crosse	"several"	30–50	off Keehi Lagoon, Oahu; Pele Exped., Aug 1959
C. obscurus Sowerby	"several"	15–25	off Keehi Lagoon, Oahu; Pele Exped., Aug 1959
C. pertusus Hwass *in* Bruguière	50	90	off Keehi Lagoon, Oahu; Pele Exped., May 1959
C. sponsalis Hwass *in* Bruguière	—	40–100	off Keehi Lagoon, Oahu; Pele Exped., May 1959
C. vexillum Gmelin	50	70	off Ewa, Oahu; Pele Exped., June 1959

* Data from Kohn, 1959.

SUMMARY

The number of species of the gastropod genus *Conus* known from more than one individual collected alive in the Hawaiian archipelago remains 33.

C. eugrammatus Bartsch and Rehder, erroneously placed in synonymy under *C. acutangulus* Lamarck by Kohn (1959), is now considered to be a valid species but is not known with certainty to have been collected alive in Hawaii.

One of two specimens identified as *C. capitaneus* Linnaeus by Kohn (1959) is actually *C. vexillum* Gmelin. *C. capitaneus* is thus known in Hawaii from only one specimen. The progressive changes from juvenile to definitive color pattern in *C. vexillum* are described.

Living specimens of *Conus* sp. cf. *C. cumingii* Reeve have been collected by the Pele Expedition since publication of the earlier paper.

The Pele Expedition also collected empty shells or fragments of three additional species not previously known from Hawaii, *C. aurisiacus* Linnaeus, *C.* sp. cf. *C. granifer* Reeve, and *C. luteus* Sowerby.

Conus abbreviatus Reeve, formerly considered endemic to the Hawaiian Islands, has been collected alive on Fanning Island, Line Islands.

New information on the appearance of soft parts, often useful in field identification, is reported for 10 species.

Recent collections have established larger sizes of nine species (Table 1) and occurrence in greater depths of seven species (Table 2) than previously reported.

ACKNOWLEDGMENTS

A National Science Foundation grant (G-8859) supported this work. We are grateful to Dr. Harald A. Rehder and to Dr. Yoshio Kondo for providing working facilities and access to specimens in the U.S. National Museum and in the Bernice P. Bishop Museum, respectively. The Pele Expedition, under the auspices of the Bishop Museum, was made possible by the generosity of Mrs. Mary Eleanor King. Mr. Harold G. Jewell kindly permitted examination of his extensive collection from the Line Islands.

ERRATA IN KOHN, 1959

P. 381, col. 2, line 11, *add* Fig. 15 in Plate 1.

P. 382, col. 1, line 1, *for* obsolutely, *read* obsoletely.

P. 397, col. 2, line 18: quite possibly the specimens of *C. aureus* referred to were not collected in the Hawaiian Islands.

P. 399, col. 2, line 31, *for* 586–787, *read* 586–757.

P. 399, col. 2, line 35, *for* 1778, *read* 1788.

REFERENCES

ADAMS, A. 1853. Descriptions of new species of the genus *Conus,* from the collection of Hugh Cuming, Esq. Proc. Zool. Soc. Lond. 1853 (pt. 21): 116–119.

BARTSCH, P., and H. A. REHDER. 1943. New cones from the Hawaiian Islands. Proc. Biol. Soc. Wash. 56:85–88.

COX, L. R. 1960. Gastropoda. General characteristics of Gastropoda. Treatise on Invertebrate Paleontology, Part I: 84–169.

GLAESSNER, M. F. 1947. Principles of Micropaleontology. Wiley, New York. 296 pp.

KELLY, K. L., and D. B. JUDD. 1955. The ISCC–NBS Method of Designating Colors and a Dictionary of Color Names. Nat. Bur. Standards Circ. 553. 158 pp.

KOHN, A. J. 1959. The Hawaiian species of *Conus* (Mollusca: Gastropoda). Pacific Sci. 13 (4): 368–401.

REEVE, L. A. 1843–49. Conchologia Iconica. Vol. 1. Monograph of the Genus *Conus.* Vols. 4, 5. Supplementary plates. Reeve, London. Unpaginated.

RIDGWAY, R. 1912. Color Standards and Color Nomenclature. Ridgway, Washington. 44 pp., 53 pls.

TATE, M. W., and R. C. CLELLAND. 1957. Nonparametric and Shortcut Statistics. Interstate, Danville, Ill. 171 pp.

WEINKAUFF, H. C. 1873–75. Die Familie der Coneae oder Conidae. In: Küster, H. C., ed., Systematisches Conchylien-Cabinet von Martini und Chemnitz. Bd. 4, Abt. 2: 125–413.

On a New Species of *Lepeophtheirus* (Copepoda parasitica) from *Pseudopleuronectis americanus* Walbaum

JU-SHEY HO[1]

IN EARLY APRIL 1961 while I was looking for parasitic copepods in fish specimens preserved in our specimen gallery, I discovered two different kinds of parasite coexisting on a single flat-fish, *Pseudopleuronectis americanus* Walbaum (26.5 cm long). Some of them, 19 in number, were found on the inner margin of the operculum, and have been identified as the present new species. The other 22 individuals, restricted to the gill filaments, were identified as belonging to the Lernaeopodidae. Because I do not have complete references at hand, I shall leave them to be studied later. It is interesting to find two kinds of parasites belonging to two different families on the same fish.

It is regrettable that the locality and collecting date of the host of these parasites are unknown, but it is believed that this fish was not collected from near the Island of Formosa, since, up to the present, *Pseudopleuronectis americanus* is reported only from American waters. Moreover, this flat-fish was not collected recently, but has been preserved for at least 17 years. Fortunately, however, the parasites in its branchial chambers have remained unchanged.

I am indebted to Dr. Yu-hsi Moltze Wang, chairman of the Department of Zoology, National Taiwan University, for reading the preliminary draft of my manuscript, and to Mr. Tchaw-Ren Chen for identifying the host fish for me.

Lepeophtheirus hidekoi n. sp.

OCCURRENCE: Eighteen mature and 1 immature females were taken from the inner margin of the operculum of *Pseudopleuronectis americanus* Walbaum, 10 of them from the "colored side" and others from the "white side."

MEASUREMENTS: Body length without egg string 6.24–7.02 mm; length of carapace 2.47–2.56, width of the same 2.15–2.20; length of free thoracic segment 0.20–0.26, width of the same 0.55–0.58; length of genital segment 1.92–1.98, width of the same 1.45–1.52; length of abdomen 1.56–2.28, width of the same 0.42–0.59; length of egg string 3.14–3.28.

DESCRIPTION OF ADULT FEMALE: One of the parasites taken from the "color side" is selected as holotype.

Carapace ovate, 2.40 × 2.08 mm, with marginal semitransparent membrane; frontal plate well defined, broadly incised at center; posterior sinus moderately deep; posterior median lobe rounded, with posterior margin projecting slightly beyond lateral lobes, its width about half as broad as carapace; dorsal rib nearly H-shaped, with two rather wide lateral arms curved nearly at middle where fine transverse suture arises; another pair of transverse ribs situate laterally at this sinus. Free thoracic segment short, 0.20 × 0.48 mm, lateral margin round, not projected.

Genital segment large and swollen, nearly triangular, truncate posteriorly, 1.92 × 1.48 mm, with conical lobe at each posterior corner. Segmentation between this and the following segment indistinct, merely indicated by two lateral notches.

Abdomen elongate, cylindrical and unsegmented, 2.16 × 0.56 mm, a little longer than the genital segment, slightly tapering both forwards and backwards.

Caudal ramus (Fig. 4) small, furnished with four plumose setae and two spines, inner side

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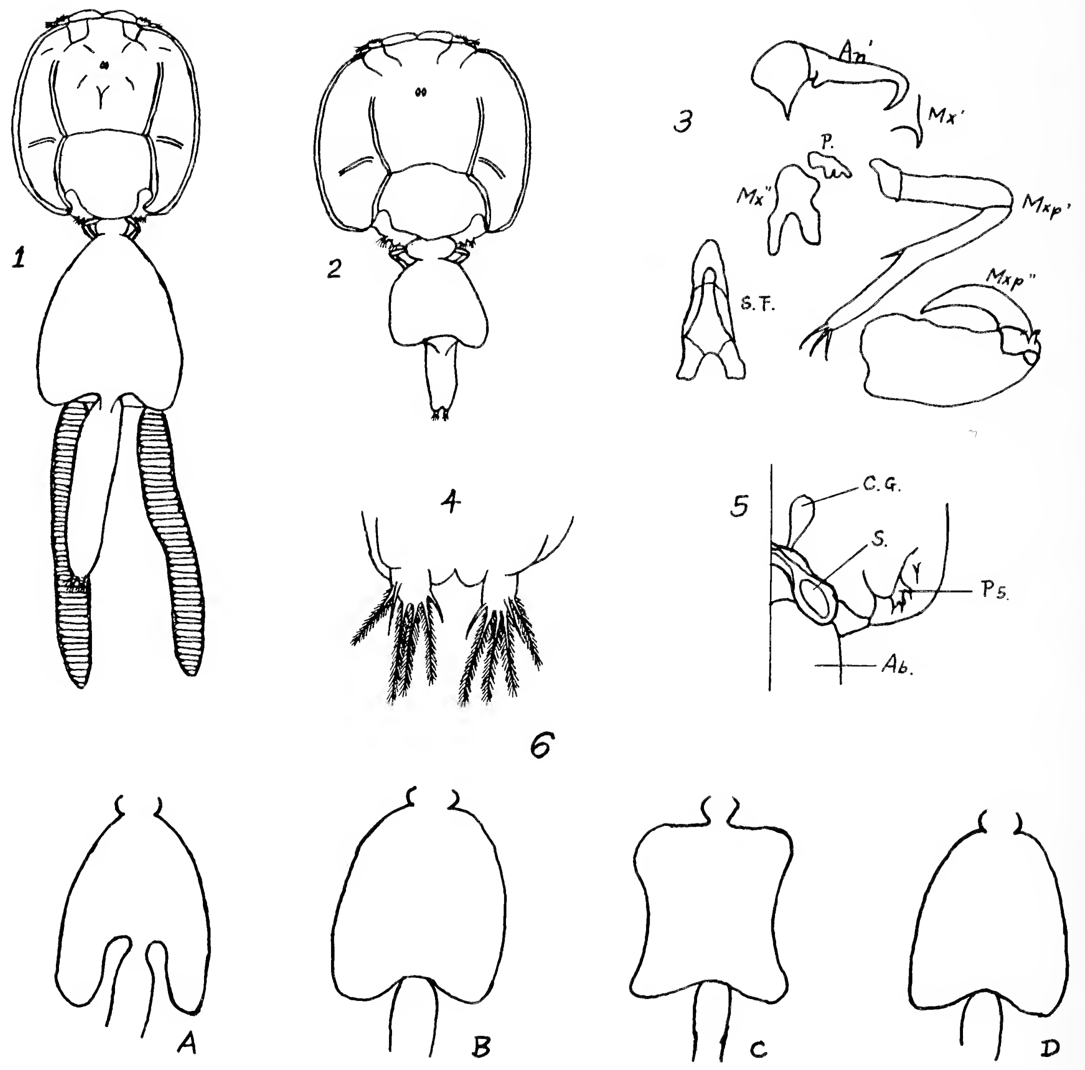

FIGS. 1–6. *Lepeophtheirus hidekoi* n. sp. female. 1, Dorsal view of adult female; 2, dorsal view of young female; 3, appendages on mouth part (for explanation, see description); 4, ventral view of caudal rami; 5, ventral view of posterior left half of young female. 6, Configuration of genital segments of: *A, longiventralis; B, salmonis; C, pollachius; D, longipalpus.*

armed with one spine, tip with three plumose setae, and outer side with one spine ventrally and one plumose seta dorsally.

Egg strings narrower than the abdomen, 3.28 mm long, containing one series of discoid eggs, commences just above 5th pereiopod.

First antenna about ¾ of the frontal plate, two-jointed, with terminal joint shorter than the basal joint, the latter with numerous pointed teeth at distal end of posterior margin; terminal joint rod-shaped with eight setae at tip.

Second antenna (Fig. 3 *An′*) curved at the apex, with a large basal joint associating with an accessory piece armed with a stout spine on the posterior border; the hooked terminal joint having a spine protruding backward at its base.

First maxilla (Fig. 3 *Mx′*) stout spiniform, situated rather towards the border of carapace than the median line, its apex not much curved.

Second maxilla (Fig. 3 *Mx″*) biramose, with the outer ramus stronger and shorter than the inner ramus.

Palp (oral tube) (Fig. 3 *P*) short, situated between the bases of second antenna and second maxilla, and inside to the first maxilliped; its terminal end trifurcate.

Sternal fork (furca or forcula) (Fig. 3 *F*) not a well U-shaped, longer than wide, its anterior part much longer than the posterior branches which are short, stout but not pointed at tip, as are those of common species of *Lepeophtheirus.*

First maxillipede (Fig. 3 *Mxp′*) long and slender, two-jointed, with the terminal joint much longer than the proximal joint, armed with three terminal spines and a small spine at middle of inner border.

Second maxilliped (Fig. 3 *Mxp″*) having an enlarged basal joint and a sharply curved distal joint which is hook-like and used for prehension while attaching on its host; a blunt spine situated at laterobasal margin of the distal joint, other parts bared.

First, second, third, and fourth pereiopod. Armation of all of these is much like that of *L. salmonis.*

Fifth pereiopod (Fig. 5 *P5*). Rudimentary, projecting from a small lobe on the ventral surface of genital segment; this lobe bears a trifurcate protuberance, each branch of it armed with one seta; another seta arises from ventral surface of genital segment, close to anterior border of fifth pereiopod.

YOUNG FEMALE: One immature specimen, obtained from "white side" of *Pseudopleuronectis americanus.* Compared with the adult female, the juvenile form is shorter in the abdomen, and has a rounder and larger carapace, and a smaller genital segment. On the posteroventral surface of the genital segment, two pairs of sacs are seen (Fig. 5); the anterior pair, being smaller, is the cement gland, and the oval-shaped posterior pair is the spermatophore which is not found in the adult female. Other characteristics are similar to those of the adult female.

MALE: Unknown.

DIAGNOSIS: The new species closely resembles *L. salmonis* (Kroyer), *longiventralis* Yu & Wu, *pollachius* Bassett-Smith, and *longipalpus* Bassett-Smith in the presence of the elongated abdomen and configuration of the carapace, but the following dissimilarities make the present new species easily recognized:

1. Presence of fifth pereiopod. This character distinguishes the new species, for *L. salmonis, longiventralis,* and *longipalpus* are lacking for this appendage. Because of the poor original description made by Bassett-Smith in 1896 for *pollachius,* I am unable to compare this character in his species and mine.

2. Trifurcate palp. This character is also present in *salmonis,* but *longipalpus* and *pollachius* have merely a spiniform palp. The palp of *longiventralis* was not described by Yu and Wu.

3. Two posterior branches of sternal fork truncate at tip. Usually, in the species of genus *Lepeophtheirus,* the divergent branches of the sternal fork are blunt or conical, but this new species has its own peculiarity.

4. A genital segment with narrower anterior portion and wider posterior portion. As shown in Figs. 1 and 6, the genital segment of *hidekoi* is nearly triangular, but differs from that of *longiventralis* in lacking two large lateral lobes; while the genital segments of *salmonis, pollachius,* and *longipalpus* are rather trapezoid.

Specimens of this new caligoid copepod have been deposited in the U. S. National Museum. The numbers are: holotype, 107281; paratype, 107282.

REFERENCES

BASSETT-SMITH, P. W. 1896. Notes on the parasitic Copepoda of fish obtained at Plymouth, with description of new species. Ann. Mag. Nat. Hist., ser. 6 8: 12, pl. 4, fig. 2.

——— 1898. Further new parasitic Copepods found on fish in the Indo-Tropical Region. Ann. Mag. Nat. Hist., ser. 7, 2: 88–89, pl. 5, fig. 2.

——— 1899. A systematic description of parasitic copepoda found on fishes, with an enumeration of the known species. Proc. Zool. Soc. London, pp. 455, 457.

HEEGAARD, P. E. 1943. Parasitic copepods mainly from tropical and Antarctic seas. Ark. f. Zool. 34A(16): 20.

SCOTT, A. 1901. *Lepeophtheirus* and *Lernaea.* Liverpool Mar. Biol. Mem. 6: 1–32, pls. 1–3.

——— 1929. The copepoda parasites of Irish Sea fishes. Proc. Trans. Liverpool Biol. Soc. 37: 92, 94.

SHIINO, S. M. 1952. Copepods parasitic on Japanese fishes, I. On the species of *Caligus* and *Lepeophtheirus.* Rep. Fac. Fish., Mie Univ. 1 (2): 100–105, figs. 10–11.

——— 1959. Sammlung der parasitisschen copepoden in der Präfekturuniversität von Mie. Rep. Fac. Fish., Mie Univ. 3(2): 348.

YAMAGUTI, S. 1939. Parasitic copepods from fishes of Japan, Part 5. Caligoida, III. Vol. Jub. Prof. S. Yoshida, vol. 2: 451–453, pls. 16–17.

YU, S. C., and H. W. HU. 1932. Parasitic copepods of the flat-fishes from China. Bull. Fan Mem. Inst. Biol. 3(4): 55–57, pl. 1.

Geographical Relationships of New Zealand Fern Flora

G. BROWNLIE[1]

THEORETICAL DISCUSSIONS on the relationships of the New Zealand flora have been confined mainly to the classical works of Hooker (1853), Oliver (1925), and Skottsberg (1915), and in these little reference was made to the nonflowering plants. Cockayne (1928) included fern species in his various lists of elements and associations, but did not deal with the fern flora as a unit. Cheeseman (1925) and the revised edition of Dobbie (1951) listed distributions outside New Zealand for the individual fern species.

When looking at fern relationships the admittedly ancient groups, the Eusporangiatae, Osmundaceae, Schizaeaceae, and Gleicheniaceae, are of little use, partly because of their widespread distributions and partly because of their long geological history. In addition to this it is now felt that the existing genera in these groups represent isolated remnants of successive fern floras each as diverse as the modern fern groups. In other words, the units we look on as genera may be as distinct from one another as the various families or subsections of what has been known as the Polypodiaceae *sens. lat.*

Even within those groups of ferns which seem to have developed most recently, the genus is an unsuitable unit to use in relationship patterns because few fern genera are of restricted distribution. An extreme example of this is shown by the genus *Asplenium* which, although apparently still undergoing specific evolution almost everywhere, is cosmopolitan. It is best then to study distribution patterns of species or of obviously closely related groups of species.

In analysing the New Zealand ferns it is necessary only to consider the nearest land areas—Australia, the islands to the north, and to a lesser extent the subantarctic part of South America. In the single example of extremely discontinuous distribution, that of the local variety of *Thelypteris palustris* Schott., which is said to occur elsewhere only in parts of tropical Africa, the accuracy of the identification is immediately open to doubt. It is a fact that the genus *Thelypteris* is very much in need of revision in the whole Pacific area.

The revised edition of Dobbie admits 153 species of ferns, but for the purposes of this paper I have reduced the number to 143 by omitting the ones confined to the Kermadecs and also a few species of doubtful occurrence in New Zealand. When compared with neighbouring areas we find the following distributions:

	SPECIES
Found in New Zealand, Australia, and widespread	16
Found in New Zealand, Australia, and one or more of the islands to the north of New Zealand	19
Found in New Zealand, Australia, and South America	6
Found in New Zealand, Australia, and widely distributed around the subantarctic	2
Found in New Zealand and Australia only	32
Total species in common between New Zealand and Australia	75
Found in New Zealand and one or more of the islands to the north	9
Found in New Zealand and SE Polynesia	2
Found in New Zealand and subantarctic South America	3
Found in New Zealand and tropical Africa	1
Endemic in the main islands	53

It will be seen from these figures that somewhat more than 50% of the species of ferns

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found in New Zealand occur also in Australia, particularly in the southeastern region and in Tasmania. In addition to this total a number listed as endemics, such as *Hymenophyllum revolutum* Col. and *Dicksonia fibrosa* Col., are so close to the Australian species *Hymenophyllum cupressiforme* Lab. and *Dicksonia antarctica* Lab. as to be doubtfully distinct. A comparable situation is seen in the fact that of the 67 fern species listed by Wakefield (1957) for Tasmania, 47 are also found in New Zealand. In the light of the prevailing wind direction, it seems probable that a large percentage of the New Zealand fern flora has been distributed by wind from Australia. This parallels the situation already noted in the Orchidaceae. It should be observed, however, that the picture as seen by van Steenis (1934–36) in the temperate mountain floras of Malaya could not be explained by wind dispersal, even in the case of plant groups with minute diaspores.

The bulk of the ferns common to the two regions appears to be derived from the Malaysian area. In the South Pacific the general picture is a gradual decrease in fern species from New Guinea southwards and eastwards, but the whole forming a closely related assemblage.

When looking at New Zealand as a possible source of distribution, the only close association to the east is with the Kermadecs and the Chathams. In the former, 24 of the 31 species are identical with those on the main islands, while all the species of the Chathams are found in New Zealand. However, a small element in the fern flora of SE Polynesia (Rapa and the Australs) may be derived from this country. Examples are *Asplenium obtusatus* Forst., *Trichomanes endlicherianum* Pr., and a fern identical with or very much similar to *Polystichum richardi* (Hk.) J. Sm.

Although only two species are confined to New Zealand and South America (*Hymenophyllum ferrugineum* Colla and *Grammitis crassa* Fee), there appears to be an element in the flora with a wider distribution around the Antarctic. This includes those species common to New Zealand–Australia and South America, and those found around the subantarctic islands. These appear to be maritime ferns, such as *Asplenium obtusatum,* or those found most abundantly in the southern beech forests—*Polystichum vestitum* (Sw.) Pr. and *Grammitis billardieri* Willd.

There is a small number of ferns found in the northern parts of North Island and otherwise only in the rather unusual ecological situation of warm ground in the thermal area. As all the species in this group, one each of *Dicranopteris* and *Nephrolepis* and two of *Cyclosorus,* are widespread throughout the Pacific islands, it is possible that they may be accidental Polynesian introductions. Also, the two areas where they occur were both centres of Maori settlement. To this group may also belong the local representative of *Marattia,* which had as one variant Maori name *para-tawhiti* (Best, 1942). This can be taken to mean the "*para* from abroad" or, more definitely, the "*para* from Tahiti."

Lovis (1959) agrees with the relationships described above but prefers to lean heavily on the Continental Drift hypothesis to explain them. However, the scale of geological time seems ample to allow for chance dispersal from Australia to New Zealand and to account for the very marked likeness between the ferns of the two regions. The Orchidaceae, which can be dispersed in a similar manner, show an even greater degree of similarity. Taylor (1954) in his study of Macquarie Island believes that long-distance dispersal is the only method by which plants could have recolonised that completely glaciated island, and presumably this applies to a large extent to all the subantarctic islands.

Endemism is most apparent in the Hymenophyllaceae with 17 species, and in the Aspleniaceae, a group which everywhere appears to be undergoing speciation. Most of the older groups, such as *Leptopteris* and *Lygodium,* are represented by endemic species, and *Loxsoma* appears to be a relic of another old group. The heterogeneous older group with marginal sori which was distinguished by Manton (1958) is represented by *Leptolepia novae-zealandiae* and *Sphenomeris viridis.* Of the remaining endemics most are closely related to other local species or to species in neighbouring areas.

From all this it seems that the fern flora of New Zealand shows a much closer relationship with that of southeastern Australia and Tasmania than with that of any other region, and that endemism is most apparent in those groups which diversified earliest and those which diversified most recently.

SUMMARY

At the specific level slightly more than 50% of the fern flora of New Zealand is found also in SE Australia, suggesting dispersal in the manner postulated for many of the orchids. A small group of species is widespread around the cool parts of the Southern Hemisphere, with extensions into eastern Polynesia. A few species with unique distribution within New Zealand, but widespread in Polynesia, may be Maori introductions.

The greatest degree of endemism is exhibited in the Hymenophyllaceae.

REFERENCES

BEST, ELSDON. 1942. Forest Lore of the Maori. Dom. Mus. Bull. 14.

CHEESEMAN, T. F. 1925. Manual of the New Zealand Flora. 2nd ed. Govt. printer, Wellington.

COCKAYNE, L. 1928. The vegetation of New Zealand. In: Engler and Drude, Die Vegetation der Erde. Leipzig.

DOBBIE, H. B. 1951. New Zealand Ferns. 4th ed., rev. and ed. by Marguerite Crookes. Whitcombe and Tombs, Ltd.

HOOKER, J. D. 1853. Introductory Essay to the Flora Novae-Zealandiae, London.

LOVIS, J. D. 1959. The geographical affinities of the New Zealand pteridophyte flora. Brit. F. Gaz., Dec. 1–8.

MANTON, I. 1958. Chromosomes and fern phylogeny with special reference to "Pteridaceae." J. Linn. Soc. Bot. 56: 73.

OLIVER, W. R. B. 1925. Biogeographical relations of the New Zealand region. J. Linn. Soc. Bot. 47: 99.

SKOTTSBERG, C. 1915. Relationships of floras of sub-antarctic America and New Zealand. The Plant World 18: 129.

TAYLOR, B. W. 1954. An example of long-distance dispersal. Ecol. 35: 569.

VAN STEENIS, C. G. G. J. 1934–36. On the origin of the Malaysian flora. Buit. Jard. Bot. Bul. ser. 3, 13: 135, 289; 14: 56.

WAKEFIELD, N. A. 1957. The Tasmanian representatives of the Pteridophyta. Pap. Proc. Roy. Soc. Tas. 91: 157.

Studies in Hawaiian Rutaceae, II
Identity of *Pelea sandwicensis*

BENJAMIN C. STONE[1]

THE HAWAIIAN RUTACEAE, comprising the three indigenous genera *Pelea, Platydesma,* and *Fagara,* include some 70 or 80 species all of which are trees or shrubs. Individuals of various species of *Pelea,* in particular, constitute an important element in much of the Hawaiian vegetation. The genus *Pelea* (commemorating Pele, goddess of Hawaiian volcanoes) was established by Asa Gray, who described several species. Gray's student Horace Mann botanized in the Hawaiian Islands with William Brigham, collected on several islands, and published several important works on the taxonomy of Hawaiian plants. One of Mann's special interests was the Hawaiian Rutaceae, and in a revision of these plants (in 1866) he described several new species and established the endemic genus *Platydesma.* Later, in his incomplete *Flora of the Hawaiian Islands,* Mann presented a detailed treatment of *Pelea.* It is from the original description of *Pelea sandwicensis* according to Gray, and from Mann's writings, that a long-held misconception of the identity of this perplexing species stemmed.

The species which originally was named *Pelea sandwicensis* has been misinterpreted for about a century. During the period 1832–1944 several other species of *Pelea* have passed under the name *Pelea sandwicensis,* in default of their nomenclatorially correct names. The purpose of the present discussion is to trace the confusing history of the name *Pelea sandwicensis,* to identify the various other species to which this name has been applied, and to bring into order the nomenclature and taxonomy of all these taxa.

For the sake of clarity, there follows a concise summary of the appropriate synonymy, and a newly prepared description of the holotype of *Pelea sandwicensis,* which was kindly loaned to me by the Royal Gardens, Kew.

I wish to thank the curators of the herbaria listed below for their aid. Thanks are due also to Harold St. John, whose long-standing interest in *Pelea* inspired the monographic work now in progress, and to Otto Degener, whose numerous collections were placed at my disposal.

Herbaria are indicated by the following abbreviations: BISH (Bishop Museum, Honolulu), BM (British Museum, Natural History), GOTH (Botanic Garden, Gothenburg, Sweden), CORN (Cornell University Herbarium), GH (Gray Herbarium), EDINB (Royal Botanic Gardens, Edinburgh), K (Kew), US (U. S. National Herbarium).

Pelea A. GRAY SECT. *Apocarpa* B. C. STONE in Deg. Fl. Haw. fam. 179. 1961

Pelea sandwicensis (Hook. f. & Arn.) A. Gray in Bot. U. S. Explor. Exped. 15(1): 345. 1854 (Excluding specimens cited)
Fig. 1.

Brunellia sandwicensis W. J. Hooker & Walker-Arnott in Bot. Capt. Beechey's Voy. 80. 1832.

Trees (to 8 ft high, according to Degener), with innovations, petioles, young branchlets, and dorsal leaf surfaces puberulent with minute closely appressed to slightly spreading olivaceous or buff simple trichomes 0.05–0.15 (rarely to 0.2) mm long, those of the leaves and innovations closely appressed, those of the branchlets somewhat spreading. Branchlets subterete, slightly compressed at the nodes. Leaves opposite, petiolate, the petioles 0.7–1.5 cm long, puberulent on all sides; blades oblong-elliptic, 3–8.5 cm long, 2–4.5 cm broad, entire, rounded or emarginate at apex, rounded or subtruncate at base, the costa sulcate ventrally along almost its entire length, dorsally raised and rounded; lateral nerves 6 to 10 on each side of the costa,

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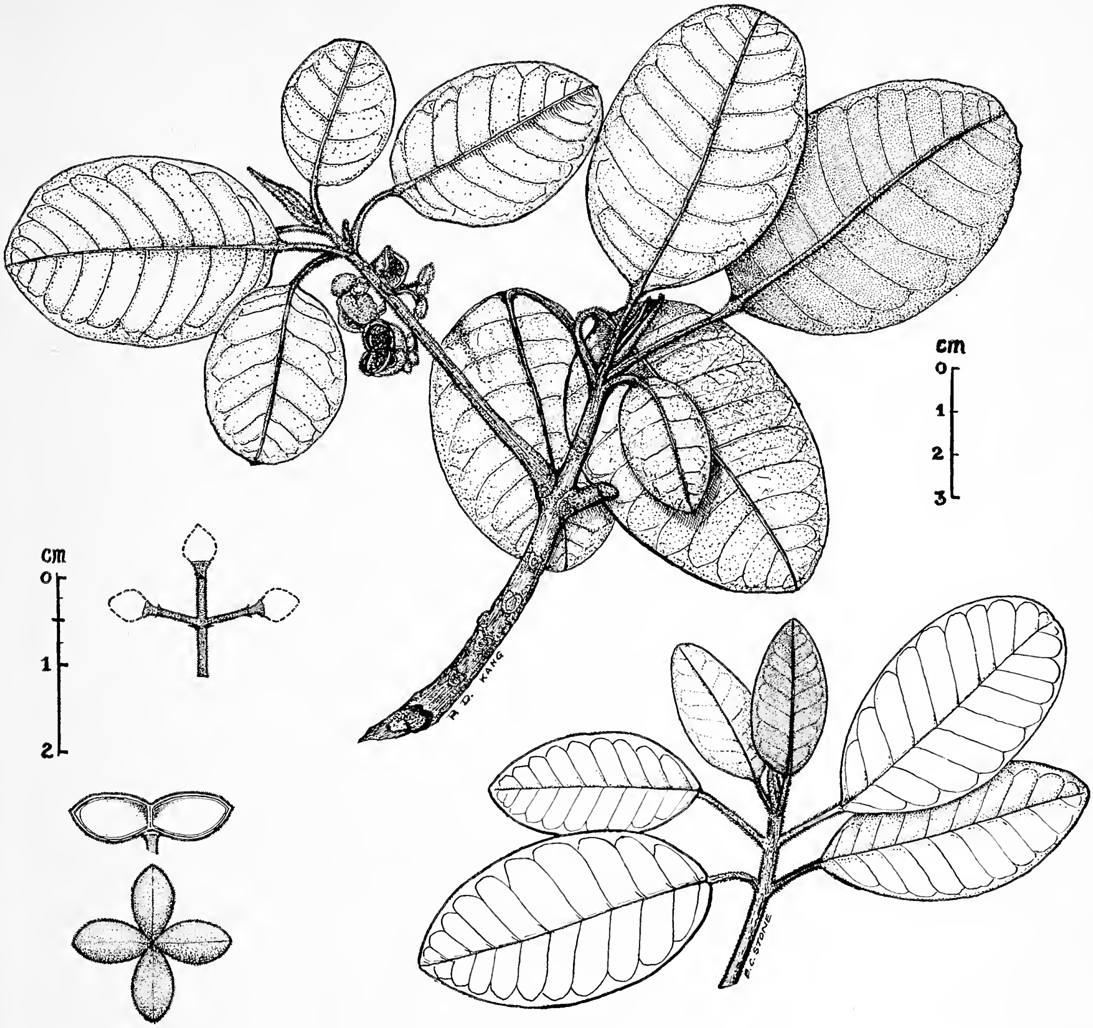

FIG. 1. *Pelea sandwicensis* (Hook. f. & Arn.) A. Gray. *1,* Habit (from holotype); *2,* cyme; *3,* capsule in top view and cross-section (from holotype; diagrammatic); *4,* habit (from *Degener 8575*).

slightly raised both ventrally and dorsally, ascending subparallel and distally upcurved, united near the margin by a slightly sinuate-arcuate nerve; minor venation slightly raised dorsally. Inflorescence axillary, cymose, 3-flowered, the peduncle ca. 6 mm long, the pedicels ca. 5–7 mm long, all minutely and closely puberulent. Flowers unknown. Fruit capsular, apocarpous, of four discrete follicles, dry, dehiscing along the upper and the distal end of the lower sutures, externally puberulent with pale erect trichomes ca. 0.1 mm long (very densely crowded on juvenile fruit), very slightly glabrate in age; endocarp smooth, glabrous, semitranslucent, glossy, yellowish brown; seeds two per follicle, irregularly ovoid (one or more flattened surfaces present), with thin glossy crustaceous black testa; capsule about 20 mm in diameter over-all.

HOLOTYPE: Oahu; Without definite locality; collected by Mssrs. Lay and Collie, on Capt. Beechey's voyage (H.M.S. "Blossom"), in May or Feb, 1826 (K).

SPECIMEN EXAMINED: Molokai; Kahua'awi gulch, near field of pigeon-peas, in moderately dry area, 12 May 1928, *O. Degener 8575* (BISH, NY).

Examination of many hundreds of herbarium sheets and of hundreds of undistributed collections, and considerable time spent in personal exploration on various Hawaiian Islands, has failed to reveal another collection or individual of this species. Thus little can be said of the natural distribution of the species. However, with a certain amount of extrapolation, based on the known distributions of other Hawaiian species, I would suggest that *Pelea sandwicensis* was characteristic of dry lowland forests on Oahu, Molokai, and possibly on Maui. Such forests on Oahu have long since been seriously disturbed and often eradicated by the inroads of civilization, and those on Molokai scarcely less so. Introduced plants (whether weeds or crops), the grazing of stock, and the growth of metropolitan and suburban Honolulu and other towns all have been inimical to the survival of the lowland forest. Since well over a century elapsed between the original discovery of the species, and its subsequent rediscovery by Degener in 1928, it would seem plausible that the species has succumbed to the disturbances mentioned. There is yet the possibility, however, that the species persists on Molokai. Much of the low-level area of Molokai has been planted with pineapple or other crops; and recent plans have been suggested for the planting of quick-growing species of *Pinus* to be used for pulp and boxwood. Such activity will almost certainly be inimical to the survival of this very rare species, and if not yet extinct, it will probably soon go the way of such species as *Kokia Cookei* (*"Gossypium drynarioides"*)[2] and other members of the peculiar lowland forests of the Hawaiian Islands which are of great scientific interest.

Nomenclatorial History of Pelea sandwicensis

Although not valid under our present nomenclatural rules, the name *brunelia sandwicensis* (sic) must be mentioned because of its role in the history of this species of *Pelea.* The name first appeared in a commentary on Hawaiian vegetation by Gaudichaud (in Voy. Uranie et Physicienne . . . Capt. Freycinet. Bot. 93. 1826) as a *nomen nudum.* Since Gaudichaud never provided a description (or illustration) of this plant, the name is not validly published. However, it seems probable that the validly published *Brunellia sandwicensis* Hook. f. & Arn. was meant to be a validation of Gaudichaud's species. Gaudichaud had collected a specimen (as will be seen further on, almost certainly on the island of Hawaii) which is extant and labelled in his script. It is not known whether Hooker and Arnott saw the specimen, which is now preserved at Paris (and a fragment also at Geneva). At any rate, they based their brief description on a specimen collected by the naturalists of the HMS "Blossom," Lay and Collie, which is labelled "Oahu." This collection represents a species distinct from that represented by the Gaudichaud specimen; and of course the Lay and Collie specimen is thus the holotype of *Pelea sandwicensis* (Hook. f. & Arn.) A. Gray.

The species represented by Gaudichaud's collection is relatively well known, and was (at last) named *Pelea Gaudichaudii* St. John in 1944. It is a close relative of *Pelea hawaiensis* Wawra, thus also a member of Section *Apocarpa.*

It is with the establishment of the genus *Pelea* by Gray that the years of confusion truly begin, however. The naturalists of the U. S. Exploring Expedition had collected several species of *Pelea* in the Hawaiian Islands which allowed Gray to distinguish the genus as new. However, Gray placed the apocarpous species of *Pelea* (i.e., species of Section *Apocarpa*) in the genus *Melicope* Forst., an unnatural position later corrected by Hillebrand. Gray did not see the Lay and Collie specimen; if he had he would have placed it in *Melicope.* He selected some U.S.E.E. specimens and, most importantly, a specimen from Oahu collected by Macrae (at Kew), to represent his concept of *Pelea sandwicensis.* It is this concept—*Pelea sandwicensis* sensu Gray—which until recently has passed as the original of this name. This concept, based on specimens representing a valid species endemic in Oahu, was finally named *Pelea honoluluensis* St. John in 1944. It is a member of Section *Megacarpa.*

Hillebrand, author of the classic *Flora of the Hawaiian Islands,* introduced still another species which he considered to be *Pelea sandwicen-*

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[2] A few trees of this *Kokia* are said to exist in cultivation. Rock (Hawaii Bd. Agr. For. Bull. 6: 11, 1919) has vividly described the melancholy aspect of the last decadent members of this highly interesting species which once inhabited the arid western end of Molokai.

sis. He attempted to follow Gray, but apparently did not consult either the Macrae or the Lay and Collie specimens. That Hillebrand was aware, however, of an inconsistency is shown by his description which states explicitly that the puberulent endocarp, mentioned by Gray, was not a feature of his own specimens. The species which Hillebrand characterized under the name *Pelea sandwicensis* was named *Pelea Wawraeana* Rock in 1913. None of the several varieties which Hillebrand appends to the species is referable to it, but constitute two or three distinct species (discussed below).

The complex relationships of these species and their names may be elucidated as follows.

Descriptions of the Taxa Involved

Although the species mentioned which have become confused with *Pelea sandwicensis* are for the most part clearly distinct, and are grouped in different sections of the genus, it seems necessary to add brief descriptions of them.

1. *Pelea sandwicensis* (Hook. f. & Arn.) A. Gray. (Sect. *Apocarpa.*)

Brunellia sandwicensis Hook. f. & Arn.
Not *brunelia sandwicensis* Gaud. nom. nud.

TYPE: Oahu; Lay and Collie (K).

This is the original and long neglected *Pelea sandwicensis,* as described above. The fact that Gray erred in describing the species does not invalidate the purely mechanical nomenclatorial action of transferring the specific epithet coined by Hooker and Arnott to the genus *Pelea.* Nor does Gray's earlier mention of the name (in Proc. Amer. Acad. Arts Sci. 3: 5. 1853, repr.) matter, since the publication mentioned only "Gaud. Bot. Freyc." as the reference, and, as mentioned, his use of the name *brunelia sandwicensis* does not constitute a valid publication.

2. ***Pelea hawaiensis*** Wawra var. ***Gaudichaudii*** (St. John) B. C. Stone, comb. and stat. nov. (Sect. *Apocarpa.*) Fig. 2.

Pelea Gaudichaudii St. John in Lloydia 7: 272. 1944 .
brunelia sandwicensis Gaud. nom. nud. in Bot. Freyc. Voy. 1826.

TYPE: Hawaii; Gaudichaud (PARIS; GENEVA).

A tree with opposite leaves, the petioles 7–15 mm long, appressed-hirsutulous with pale tawny trichomes, the blades 2.5–5.1 cm long and 1.4–2.5 cm broad, subcoriaceous, ovate, dorsally somewhat reticulate, the minor venation prominulent, the costa sparsely appressed-hirsutulous, the laminar surface glabrate, ventrally at last glabrous; marginal nerve remote from the edge, sinuous-arcuate. Flowers borne in a compound cymose 15–25-flowered dichasium, the axes and minute lanceolate bracts densely puberulent. Calyx and corolla externally finely appressed-puberulent. Ovary and style puberulent, the style with spreading trichomes; stigma rotate, 4-lobed, the lobes minutely papillose, reddish; stamens (in pistillate flowers) rudimentary. Capsules mostly 16–22 mm in diameter, the carpels discrete, follicular, externally densely tawny-hirsutulous, the exocarp firm; endocarp pale, villous, thin cartilaginous; seeds 3–4 mm long, ovoid, the thin papery testa glossy black, the putamen minutely warty.

HOLOTYPE: 'Sandwich Islands' (Hawaii), Gaudichaud (PARIS). Duplicate fragment at Geneva.

SPECIMENS EXAMINED: Hawaii: Hawaii National Park, Kilauea, Kipuka Puaulu ("Bird Park"), *L. H. McDaniels 212* (BISH); *Fagerlund & Mitchell 573* (BISH, HAWAII NAT. PARK HERB.); *Cranwell, Selling & Skottsberg H.B.S. 3257* (GOTH).

The type specimen was mentioned by Adrien de Jussieu in 1825 (Mém. Rutacées, p. 119):

> Obs.—Species 6 ex America australi; inter tropicos. Praeteria quaedam ex Insulis Sandwich et Rawak inedita (a Gaudichaud communicata) genere aut confunditus aut certe proxime accedit, fructibus et seminibus suppetentibus, floribus ignotis . . . endocarpium . . . in species Sandwichiana intus pube molli vestitum.

This is the earliest mention of the pubescent endocarp found in many species of the genus.

St. John quite correctly segregated the Gaudichaud specimen as a distinct taxon; however, in its significant features it corresponds so closely to *Pelea hawaiensis* Wawra (in Flora 56: 110. 1873) that I believe it is best regarded as one of several clear-cut varieties of that species. From the typical variety of *Pelea hawaiensis,*

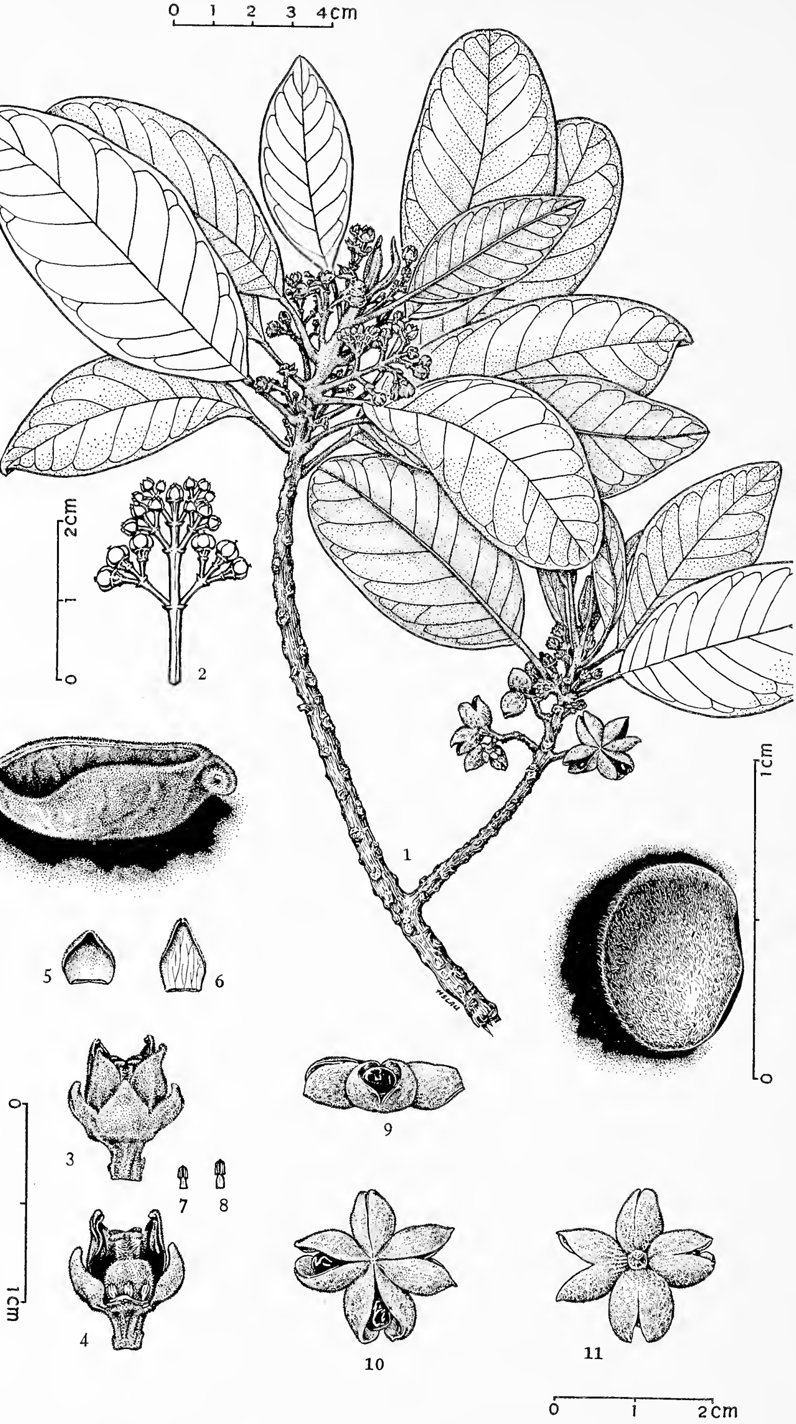

FIG. 2. *Pelea hawaiensis* Wawra var. *Gaudichaudii* (St. John) B. C. Stone. *1,* Habit; *2,* cyme (pubescence not drawn); *3–8,* pistillate flower; *9–13,* capsule: *9,* in side view; *10,* in top view; *11,* from beneath; *12,* a single follicle; *13,* endocarp. All from *L. H. McDaniels 212* (Kipuka Puaulu, Hawaii).

the var. *Gaudichaudii* differs only in the conspicuously smaller capsules, the perhaps more multiflorous cymes, and the somewhat glabrate leaves. From *Pelea sandwicensis,* it differs in the more ample compound dichasia, more ovate leaves, capsules with a much denser pubescence, and the villous rather than glabrous endocarp.

3. *Pelea honoluluensis* St. John in Lloydia 7: 268. 1944. (Sect. *Megacarpa.*)

P. sandwicensis sensu A. Gray in Bot. U. S. Explor. Exped. 15(1): 345. 1854; Atlas, pl. 37.B. 1856; sensu H. Mann in Proc. Boston Soc. Nat. Hist. 10: 315. 1866; Proc. Essex Inst. 5: 167. 1868; Rock in Indig. Trees Haw. Is. 224. pl. 85. 1913.

TYPE: Oahu; *Rock 10215* (BISH).

This species is well described and illustrated in the sources listed. It is restricted to Oahu, where it may be found chiefly in the Koolau Mountains, in wet forests generally between 2,000 and 3,000 ft elevation. It may be recognized by the following characters: rather large broad leaves, pubescent beneath on the costa; tomentose new leaves; finely puberulent small 4-lobed capsules about 20–24 mm in diameter; distinctly pubescent endocarp. Several very similar species have been described, some of doubtful validity; the following key is an attempt to elucidate their differences.

Other species similar to those keyed above are known from other islands which do not occur on Oahu. Some of these also are of dubious status. A detailed consideration of them will be presented in the monograph in progress.

4(a). *Pelea Wawraeana* Rock, Indig. Trees Haw. Is. 231. 1913. (Sect. *Megacarpa.*)

P. sandwicensis sensu Hillebrand (as to alpha var. only) in Fl. Haw. Is. 66. 1888.

TYPE: Oahu; *Rock 10220* (GH).

This species is described by Rock as new, but it is quite probable that one of the many species so carelessly described by Léveillé two years earlier (in Fedde, Rep. Sp. Nov.) is in fact the same. It is unmistakably a member of Section *Megacarpa,* endemic to Oahu.

KEY TO OAHU SPECIES OF *Pelea* SECT. *Megacarpa,* GROUP OF *P. honoluluensis*

1. Leaves glabrous.
    2. Inflorescence 7–15-flowered; endocarp at least slightly puberulent.
        3. Capsule glabrous; endocarp minutely sparsely puberulent near the sutures; capsule 11–17 mm diam. .... *P. waipioensis* St. John
        3. Capsule puberulent; endocarp finely puberulent throughout; capsule 25–32 mm diam. .... *P. Christophersenii* St. John
    2. Inflorescence 1–5-flowered; endocarp glabrous; capsule glabrous, 13–17 mm diam. .... *P. descendens* St. John
1. Leaves pubescent at least on the costa dorsally.
    4. Capsule 30–38 mm diam.
        5. Capsule deeply parted (¾); cyme 3–5-flowered; capsule and endocarp pubescent .... *P. kauaensis* St. John
        5. Capsule moderately (½–⅔) parted; cyme 9–20-flowered; capsule and endocarp pubescent .... *P. kaalaensis* St. John
    4. Capsule 9–28 mm diam.
        6. Capsule villous throughout externally .... *P. Storeyana* St. J. & Hume
        6. Capsule finely puberulent or somewhat glabrate.
            7. Capsule 9–18 mm diam.; innovations cinereous-puberulent; endocarp velutinous .... *P. Hosakae* St. John
            7. Capsule 20–28 mm diam.; innovations tawny-tomentose; endocarp densely pilosulous .... *P. honoluluensis* St. John

Hillebrand united as mostly unnamed varieties under his concept of *Pelea sandwicensis* two or possibly three distinct species.

4(b). ***Pelea Wawraeana*** var. ***ternifolia*** var. nov.

P. sandwicensis γ var. Hillebrand, op. cit. 67. ("leaves 3 in a whorl, otherwise as in β. Oahu: Halemano"); Rock in Bot. Gaz. 65: 265. 1918.

P. Wawraeana var. *tenuifolia* (Hbd. ex Rock) St. John & Hume in Lloydia 7: 273. 1944. (Nom. illegit.)

TYPE: Oahu; Hillebrand (BERLIN; now destroyed).

In taking up the varietal epithet *tenuifolia,* St. John and Hume relied on Rock's mention of this name in 1918. However, Rock had no intention of validating the name, and stated merely: "In the HILLEBRAND collection this var. β of *Pelea sandwicensis* is marked as var. *macrocarpa* Hbd., and his var. γ of the same species var. *tenuifolia* Hbd."

On page 266, Rock states:

> HILLEBRAND'S var. γ *tenuifolia* of *P. sandwicensis* has also a cuboid capsule, but leaves are three in a whorl. . . . He says: "otherwise the same as β." This is not so, for *P. sandwicensis macrocarpa* has larger capsules and the carpels are divided to the middle.

Rock was correct here taxonomically; but this passing mention of varietal names from Hillebrand's manuscript is not a formal nomenclatural action. In any event, the name of the β var. is the only one used in ternary combination. Further, it is believed that Rock misread Hillebrand's script ("tenuifolia" instead of "ternifolia"). The chief character singled out by Hillebrand is the fact that the leaves are 3 in a whorl. This immediately brings to mind the epithet *ternifolia,* which I have applied here. There is some doubt however that this variety is really a form of *Pelea Wawraeana.* The locality suggests that perhaps it is not distinct from *Pelea semiternata* St. John.

5. *Pelea peduncularis* Léveillé in Fedde, Rep. Sp. Nov. 10: 443. 1912. (Sect. *Megacarpa.*)

P. sandwicensis sensu Hillebrand β var. Hillebrand in Fl. Haw. Is. 66. 1888.

P. sandwicensis macrocarpa Hbd. ex Rock in Bot. Gaz. 65: 265. 1918.

P. Rockii St. John in Lloydia 7: 271. 1944.

TYPE: Oahu; Faurie 189 (EDINB).

Arborescent; innovations finely scurfy and somewhat sparsely cinereous-puberulent, the trichomes soon caducous; the mature branchlets and leaves glabrous or the petioles sometimes with a sparse persistent minute puberulence, later glabrate. Petioles 13–35 (–40) mm long, lenticellate in age (especially at the ends); blades coriaceous, elliptic, rounded to slightly emarginate at the apex and at the base, 3–15 (–18) cm long, 2–9 (–11) cm broad, darker green above, the margin especially near the base tightly revolute (thus the leaf appearing somewhat obovate), midrib above sulcate, beneath prominent, often reddish purple; major lateral nerves mostly about 7–10 in opposed pairs, united distally by a lightly sinuate marginal nerve only 1–5 mm from the edge. Inflorescence a pedunculate usually 5–21-flowered minutely cinereous glabrate cyme often exceeding the petiolar length of the subtending leaf, the peduncle rarely up to 4 cm long (to the first node), and with 8 nodes, commonly shorter and with 2–4 nodes, stout (1–2 mm thick in fruit), the pedicels usually short, stout, 3–4 mm long; bracts lanceolate; bractlets deltoid; both minutely ciliate and sparsely puberulent, 1–3 mm long. Female flowers with sparsely scurfy-puberulent deltoid-ovate sepals about 2 × 1.8 mm, with glabrous punctate lanceovate petals about 5 mm long, reduced sterile stamens just exceeding the glabrous 4-lobed ovary, glabrous disk, reddish filiform style ca. 2 mm long with stigmatic branches 0.5 mm long, these slightly clavate and reddish, papillose, rotate. Male flowers similar but slightly larger, the petals about 7 mm long, the gynoecium much reduced, the stamens ca. 8 mm long in two subequal quartets, the longer quartet of barely exserted stamens. Capsule glabrous, about 20 mm broad and 10 mm high, lobed halfway or less; endocarp glabrous; seeds two per lobe.

HOLOTYPE: Oahu: Koolau Mountains, Kalihi, Oct. 1909, *Faurie 189* (EDINB; duplicate at PARIS).

SPECIMENS EXAMINED: Oahu: Koolau Mountains; Konahuanui, 1000 m alt., May 1910, *Faurie 194* (PARIS). Pupukea summit trail, Feb 1960, *Pearsall 480* (BISH). No definite locality, *Rémy 621* (male, PARIS).

This species is thoroughly distinct from *Pelea sandwicensis* and from *P. honoluluensis*. It is reminiscent of *P. Wawraeana*, but in general easily distinguished. However, it is characterized by capsules which may sometimes be mistaken for those of the latter species; they are larger and not cuboid, but sometimes are nearly square in top view. The reddish flowers and rather elongate inflorescences serve to distinguish the species.

Léveillé did not mention any of Hillebrand's specimens, and his usual cryptic description, though longer than customary, is quite inadequate to distinguish the species. A study of the isotypes (*Faurie 189*) and of a considerable number of recent collections convinces me that the name must be taken up. There are a number of problematic entities and names associated with this species which may merit recognition which will be treated later. Also there is the problem of delimiting Section *Cubicarpa*, which in turn is based on the constancy of the degree of carpel separation in fruits of several species.

The revolute basal leaf margins in plants of this species provide a conspicuous but overlooked character. It is also found in specimens of *Pelea Zahlbruckneri* Rock, *P. paniculata* St. John, and sometimes in other species.

6. *Pelea lucens* (Hillebrand) St. John in Lloydia 7: 269. 1944. (Sect. *Cubicarpa?*)

P. sandwicensis δ var. *lucens* Hillebrand op. cit. 67.

TYPE: Oahu; Mt. Kaala, Hillebrand (BERLIN; the type destroyed).

LECTOTYPE: Oahu; Mann & Brigham 208 (CORN; duplicate at BISH). Cited by Hillebrand.

This tentatively accepted species appears to be a relative of *Pelea Wawraeana*.

Variable Factors Affecting the Apparent Range and Estimated Concentration of Euphausiids in the North Pacific

EDWARD BRINTON[1]

THE QUANTITATIVE and qualitative contents of a zooplankton sample are influenced by two kinds of variables: (1) natural variables such as temperature of the water, currents, latitudinal and seasonal variations in sunlight intensity, water transparency, amount of food or nutrients, oxygen content of the water, which may modify or maintain the horizontal and vertical distribution of species and condition their breeding and growth cycles; (2) artificial variables associated with (a) the method used to present the data, (b) the method used to take aliquots and count the plankton, and (c) the collecting method—type of net, depth of tow, hour of day of sampling.

This discussion deals with the artificial variables in the study of euphausiid distribution. Before ecological relationships can be considered, apparent variability in number and kind of organisms due to artificial circumstances must be distinguished where possible.

The standard net, 1 m in mouth diameter, used by the California Cooperative Oceanic Fisheries Investigations, or CCOFI (Ahlstrom, 1948), and the Pacific Oceanic Fisheries Investigations, or POFI (King and Demond, 1953), is now widely used in the Pacific area. This paper examines the hypothesis that the net is a reliable sampler of euphausiids and considers density estimates in relation to other variables in sampling and data processing procedures.

This paper represents one of the results of research conducted under the Marine Life Research Program, the Scripps Institution's component of CCOFI. The suggestions of Professor M. W. Johnson are gratefully acknowledged. I want to thank Dr. E. W. Fager for planning the test of the counting method and for many important suggestions. I am grateful to Professor C. L. Hubbs for critical review of much of the original manuscript.

METHODS OF COLLECTION AND ANALYSIS

The euphausiids here considered were taken from plankton collected during oceanographic surveys carried out by the Scripps Institution of Oceanography, 1950–57, and from surveys in the region of the California Current by CCOFI, 1949–59. Data from seven cruises are considered (Table 1).

The standard 1-m net is conical, 5 m long, and made of heavy-duty grit gauze, 0.65 mm between threads.

Quantitative estimates of flow through the net were obtained by means of an Atlas Flow Meter. An analysis of the performance and calibration of the flow meter is given by Ahlstrom (1948). Readings were made of meters placed at the center and at the periphery of the mouth of the net. The standard deviation of the paired readings was 6.5%.

The counts of euphausiids are standardized on the basis of 1000 m^3 of water strained. Most samples were obtained by oblique hauls, while the ship moved at a speed of 1–2 knots. In such hauls the net strained 400–1000 m^3 of water. Individual samples consisted of elements of plankton populations integrated across a horizontal distance of 0.3–2.0 miles and depths of 0–70, 0–140, or 0–280 m. (Tows made by the "E. W. Scripps" off Monterey, Oct 1950, were vertical. The ship was anchored during the 7-day period.)

Subsurface layers were sampled by nets which were opened and closed at desired depths, using a device described by Leavitt (1938).

During the 1956 cruise to the mid-Equatorial Pacific ("Equapac"), a smaller net, 45-cm mouth diameter and 0.33-mm mesh width, was used in conjunction with the standard 1-m net. Both nets, the smaller attached to the wire above the

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TABLE 1

CRUISES ON WHICH PLANKTON WAS COLLECTED

CRUISE	AREA SAMPLED	NET USED	DEPTHS SAMPLED
1939 "E. W. Scripps" Cruise VIII	California Current; Cascade Head, Ore., to Viscaino Bay, Baja California	1.0 m, #24XXX grit gauze; open and opening-closing nets	0–40, 40–80, 80–120 m; oblique hauls
Oct 1950 CCOFI Cruise 19	sta. 72.60: 35° 35.5′ N, 122° 07.5′ W	1.0 m, #30XXX grit gauze; open net	0–140 m, vert.
	sta. 70.90: 34° 51′ N, 124° 33′ W	1.0 m, #30XXX grit gauze; open net	0–140 m, oblique
	sta. 70.130: 33° 33′ N, 127° 16.5′ W	1.0 m, #30XXX grit gauze; open net	0–140 m, oblique
Apr 1952 CCOFI Cruise 36	California Current; San Francisco to Magdalena Bay; grid-buoy survey off Punta Eugenia	1.0 m, #30XXX grit gauze; open net	0–140 m, oblique
Aug–Dec 1953 "Transpacific" Exped.	San Diego–Bering Sea, Japan, Hawaii	1.0 m, #30XXX grit gauze; open and opening-closing nets	0–150 m, oblique 150–300 m, oblique 300–450 m, oblique 450–600 m, oblique 0–700 m, oblique
Apr–May 1954 Pelagic Area Cruise	Offshore Baja California	1.0 m, #30XXX grit gauze; open and opening-closing nets	surface net 0–25 m, oblique 25–50 m, oblique 50–75 m, oblique 75–100 m, oblique 100–300 m, oblique 300–500 m, oblique 500–700 m, oblique
Aug–Sep 1955 Norpac Survey (CCOFI Cruise 5508)	North Pacific east of 150° W, 20–48° N	1.0 m, #30XXX grit gauze; open and opening-closing nets	0–140 m, oblique 140–280 m, oblique 0–700 m, oblique
Aug–Sep 1956 Equapac Survey; sta. occupied by "Stranger"	mid-Equatorial Pacific	1.0 m, #30XXX grit gauze; 45 cm, 0.33 mm between meshes	0–140 m, oblique

other, were towed obliquely. Standardized counts of samples obtained from the two nets are compared.

PRESENTATION OF ZOOGEOGRAPHICAL DATA

Estimated concentration and geographical distribution of zooplankton are usually plotted by indicating the volume, weight, or number of organisms on a map of the collecting pattern of the survey. The quantity at a given locality may be indicated as (1) a number, often used when numbers of organisms at the localities are small; (2) a symbol (Glover, 1952; Johnson, 1956; Bary, 1959; Baker, 1959), the size or shape of which is related to the observed concentration; (3) a straight line bearing a linear relationship to the concentration, drawn through the position of the station (Johnson, 1953); (4) a numerical range which is an interval between selected sequences of contour levels (Thrailkill, 1957; Glover, 1957; David, 1958; Bieri, 1959).

The contour method may best be used to describe a distribution when the local patchiness is less than the geographical variation in concentration shown by the contours. Use of this method implies that the plankton net has strained enough water to average out the local patchiness.

Charts using contour levels to show species concentration combine presentation and interpretation of the data. The contoured distribution of a species visually relates the similar concentrations sampled. The resulting geographical patterns of presence and absence, abundance and scarcity, become discrete with respect to the sampling pattern. Intervals must be wide enough to minimize sampling and counting variables, but small enough to reflect significant geographical variations in population size.

Intervals between contour levels might have been selected according to a graphical method described by Cushing (1953). This method, not used in the present analysis, has the advantage that confidence limits can be attached to single observations. Confidence limits of some values will, of course, overlap two contour intervals.

Levels derived by Cushing for *Calanus* differed from one another by a factor of 7. Those used here differ by a factor of 10, arrived at by trial after the ranges of concentration were determined for all species in the several surveys.

The effects of artificial variables, such as diurnal discrepancies in the availability of euphausiids to the nets, and sampling and counting errors, are reduced when the contour intervals have a wider range than the variables. It will be seen that some details of the distributions would be altered if the hour of day of sampling and depth of tow were standardized. In most zoogeographical studies attention focuses on the general character of the distribution, or on features of boundary and concentration based upon a number of records. Less reliability can be attached to details, which may be influenced locally by transient hydrographic anomalies, cloudiness, or the swarming habits of certain nearshore or cold-water species.

REPLICATE COUNT ANALYSIS

In our treatment of the many plankton samples it was necessary to use aliquots, while retaining as far as possible the quantitative and qualitative worth of the large sample. The procedure included (1) counting and measuring all specimens in an aliquot of the sample, and (2) scanning the remainder of the sample under the microscope for species that appeared not to have been represented properly in the aliquot, or that were entirely lacking in it. In general, the fraction served for counts of the dominant species, while for the rarer species all individuals were counted.

When the sample was seen to contain few euphausiids, an aliquot of ¼ or ⅕ the sample was taken. One-tenth of the sample was usually counted when the sample was rich, that is, when it contained more than 700–1,000 euphausiids. Two methods have been used for taking aliquots. The Folsom plankton sample splitter has been shown to be statistically reliable for fractioning and for the euphausiid component of the plankton (McEwen, Johnson, and Folsom, 1954), but a quicker method proved adequate. The sample was gently agitated. When the plankton was in suspension it was poured into a 500-ml graduate cylinder. The combined volume of plankton and fluid, usually about 400 ml, was measured, and all but the intended aliquot (approximately the lower 1/10 or 1/5) was quickly poured back into the original container. Since the larger euphausiids settle to the bottom of the cylinder in 20–40 sec, it was important to keep the material in a state of agitation while fractionating except when the volumetric readings were made. The majority of the euphausiid specimens in the samples were larvae or immature individuals. These remained longer in suspension than did the adults.

The reliability of the aliquot and counting procedure was examined in a test in which replicate counts were made of 1/10 aliquots of three samples. Quantities of plankton containing up to three test species were, one at a time, provided the author, who was not informed of the number of samples prepared, or of the number of specimens of the test species, if any, added to them. This plankton contained many euphausiid species, but had previously lacked those which were added for the purpose of the test counts. The three samples were then presented, one at a time, in random sequence until a total of five counts had been made of each. Two "nuisance samples," not counted in replicate, were inserted in the sequence.

Counts of the 1/10 aliquots are given in Table 2.

Analysis of the counts for each of the densities (15 counts each) indicated that in this range of densities the present fractionating method yields effectively random aliquots of the plankton samples (agreement with Poisson, all probabilities over 0.10). The square root of the count on a single sample may, therefore, be considered an estimate of the variation due to sampling, and, for counts over 10, 95% confidence intervals may be estimated by the count ± two times its square root. Although the three test species differed considerably in size, there was no evidence that this factor influenced the counts. The greatest apparent difference, *P. latifrons* vs. *N. simplex* at density 19, was not significant ($p = 0.40$). Mean estimates of density based on 15 aliquots each were 15.27, 2.00, and 1.13; true values were 19.00, 2.60, and 0.90. The distributions of observed counts above and below the true mean values were not significantly different from the expected 7.5/7.5 for the two lower densities; for density 19.00, there were 12.5 below and only 2.5 above ($p =$ about .01). This suggests that higher densities may be consistently somewhat underestimated. No reason for this is apparent.

The importance of scanning the entire sample for the rarer species is indicated by the fact that in random aliquots, a species with a mean density of one individual per aliquot would be absent in about 37% of all aliquots, and a species with a mean density of 0.5 individual per aliquot would be absent in about 61% of all aliquots.

DEPTH OF TOW

Sampling at more than one depth using opening-closing nets, carried out on "E. W. Scripps" Cruise VIII, 1939, the "Transpacific" expedition, and the "Norpac" survey, has made it possible to consider the extent to which change in depth of tow can alter the apparent range and estimated density of a species.

"E. W. Scripps" Cruise VIII surveyed an area off Oregon, California, and Baja California. At 50 stations between the latitude of San Diego (32° N) and the Columbia River, Oregon (46° N), samples were collected from three strata of water. Only two of these strata were sampled on station lines off Baja California (Fig. 1).

The upper net sampled obliquely between the surface and a depth of approximately 40 m; the intermediate net sampled the layer between

TABLE 2

REPLICATE COUNTS OF $\frac{1}{10}$ ALIQUOTS OF THREE SAMPLES
(Number in parenthesis is $\frac{1}{10}$ of actual number present in sample)

REPLICATE COUNT NO.	SAMPLE I			
	E. pacifica (19)	*N. simplex* (2.6)	*P. latifrons* (0.9)	Total (22.5)
1	19	3	1	23
2	13	2	1	16
3	11	3	0	14
4	15	2	0	17
5	9	1	2	12
	SAMPLE II			
	P. latifrons (19)	*E. pacifica* (2.6)	*N. simplex* (0.9)	Total (22.5)
1	24	4	1	29
2	10	1	0	11
3	22	1	3	26
4	18	3	3	24
5	15	1	1	17
	SAMPLE III			
	N. simplex (19)	*P. latifrons* (2.6)	*E. pacifica* (0.9)	Total (22.5)
1	12	3	0	15
2	16	3	1	20
3	16	1	1	18
4	17	2	0	19
5	12	0	3	15

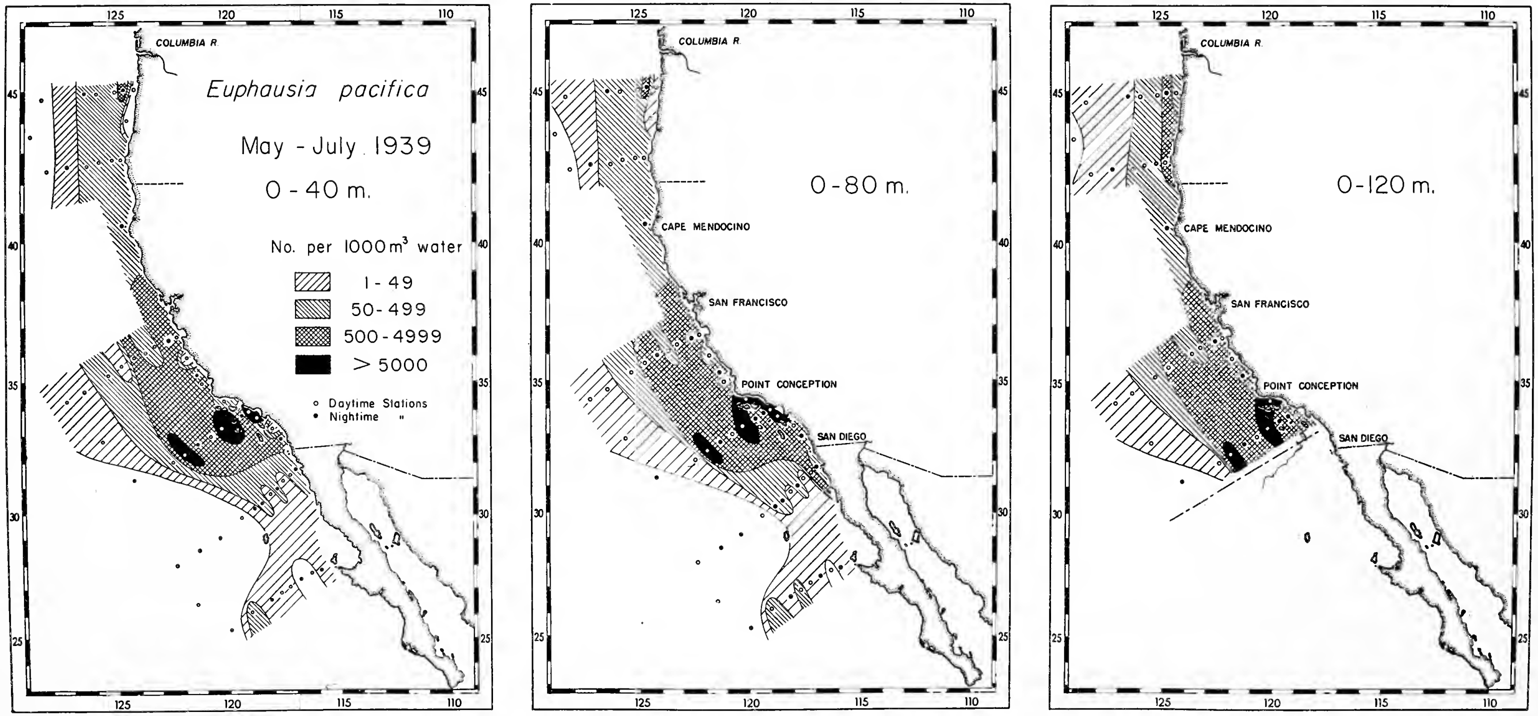


FIG. 1. Distribution of *Euphausia pacifica*, based upon sampling to 0–40 m, 0–80 m, and 0–120 m. "E. W. Scripps" Cruise VIII, May 10–July 10, 1939. Stations off Baja California, south of 32° N, were sampled only to 40 m and 80 m.

TABLE 3

"E. W. SCRIPPS" CRUISE VIII, 1939:
EFFECT OF ALTERING DEPTH OF TOW ON ABUNDANCE INTERVAL (CONTOUR)
(Intervals: 0, 1–49, 50–499, 500–4,999, > 5,000, per 1000 m^3; only those stations are considered at which tows were made to three depths)

SPECIES	CHANGE OF DEPTH OF TOW (m)	NO. STATIONS WHERE ABUNDANCE INTERVAL WAS UNCHANGED BY INCREASING DEPTH OF TOW	NO. STATIONS WHERE ABUNDANCE INTERVAL WAS CHANGED BY INCREASING DEPTH OF TOW			NO. NEGATIVE STATIONS MADE POSITIVE BY INCREASING DEPTH OF TOW
				To Higher Interval	To Lower Interval	
Euphausia pacifica	0–40 to 0–80	27	10	6	4	2
	0–40 to 0–120	27	10	6	4	3
	0–80 to 0–120	33	4	2	2	1
Thysanoessa gregaria	0–40 to 0–80	15	7	7	0	6
	0–40 to 0–120	9	13	12	1	11
	0–80 to 0–120	14	8	6	2	6
T. spinifera	0–40 to 0–80	9	9	7	2	5
	0–40 to 0–120	11	7	5	2	5
	0–80 to 0–120	16	2	0	2	0
Nematoscelis difficilis	0–40 to 0–80	20	10	8	2	5
	0–40 to 0–120	14	16	12	4	8
	0–80 to 0–120	24	6	4	2	3
Tessarabrachion oculatus	0–40 to 0–80	5	7	7	0	7
	0–40 to 0–120	4	8	8	0	7
	0–80 to 0–120	11	1	1	0	0
Thysanopoda aequalis	0–40 to 0–80	3	1	0	1	0
	0–40 to 0–120	3	1	0	1	0
	0–80 to 0–120	4	0	0	0	0
Stylocheiron carinatum	0–40 to 0–80	2	2	1	1	1
	0–40 to 0–120	2	2	1	1	1
	0–80 to 0–120	4	0	0	0	0
Nyctiphanes simplex	0–40 to 0–80	1	3	2	1	1
	0–40 to 0–120	0	4	2	2	2
	0–80 to 0–120	1	3	1	2	1

40 and 80 m; the lowest net sampled the layer between 80 and 120 m. The summed catch of the two upper tows (0–80 m) is thus comparable to samples taken during the 1949–50 cruises of CCOFI, which made single oblique hauls from depths of 0 to ca. 70 m. After 1950, the depth of sampling on CCOFI cruises was changed from 0–70 m to 0–140 m. Using data from the 1939 "E. W. Scripps" cruise it is possible to compare the numbers of euphausiids caught in the 0–80-m stratum with those collected in the 0–120-m layer.

The question arises: Are the qualitative or quantitative determinations of the distribution of euphausiid species significantly changed by changing the depth of tow? If a map is plotted (on the basis of 0–40-m tows) showing the qualitative aspects of the distribution of a species in the region of the California Current, the character of the distribution is somewhat altered if a different depth of tow (0–80 m or 0–120 m) is used.

Species of four faunal groups are considered (Table 3). They are: *Euphausia pacifica* and *Thysanoessa spinifera,* which have an affinity with cold northern waters; *Nyctiphanes simplex,* with upwelled areas marginal to the equatorial zone; *Thysanoessa gregaria,* with a transitional belt which lies at 35–45° N in mid-ocean; and *Stylocheiron carinatum* and *Thysanopoda aequalis,* with offshore central waters. All occur in part of the California Current. The apparent concentration of each species was most changed if the depth of tow was altered from 0–40 m to 0–120 m; it was not changed at all for *Thysanopoda aequalis* and *Stylocheiron carinatum,* and only at one station for *Thysanoessa spinifera* when the depth of tow was changed from 0–80 to 0–120 m—the same order of change in depth of tow that was made in the CCOFI sampling program in 1950. *Nyctiphanes* was little affected by altering the depth from 0–40 m to 0–80 m but, where *Nyctiphanes* was present, the concentration interval was changed at each of the four stations when the depth of tow was increased from 40 m to 120 m.

Changes in depth of tow had comparable effects on records of the presence of species: increasing the depth from 40 m to 80 m considerably increased the number of positive stations; the increase from 80 m to 120 m had less effect.

Inasmuch as oceanwide distribution charts of

TABLE 4

"NORPAC" CRUISE, 1955:
EFFECT OF ALTERING DEPTH OF TOW ON ABUNDANCE INTERVAL (CONTOUR)
(Intervals: 0, 1–49, 50–499, 500–4,999, > 5,000, per 1000 m^3; only those stations are considered at which tows were made to three depths)

SPECIES	CHANGE OF DEPTH OF TOW (m)	NO. STATIONS WHERE ABUNDANCE INTERVAL WAS UNCHANGED BY INCREASING DEPTH OF TOW	NO. STATIONS WHERE ABUNDANCE INTERVAL WAS CHANGED BY INCREASING DEPTH OF TOW			NO. NEGATIVE STATIONS MADE POSITIVE BY INCREASING DEPTH OF TOW
				To Higher Interval	To Lower Interval	
Euphausia pacifica	0–140 to 0–280	9	6	5	1	2
	0–140 to 0–700	4	11	9	2	6
	0–280 to 0–700	9	6	5	1	4
Thysanoessa gregaria	0–140 to 0–280	10	3	0	3	0
	0–140 to 0–700	6	7	0	7	0
	0–280 to 0–700	9	4	0	4	0
T. spinifera	0–140 to 0–280	4	0	0	0	0
	0–140 to 0–700	2	2	1	1	1
	0–280 to 0–700	2	2	1	1	1
Nematoscelis difficilis	0–140 to 0–280	9	5	1	4	1
	0–140 to 0–700	2	12	3	9	2
	0–280 to 0–700	6	8	2	6	2
Tessarabrachion oculatus	0–140 to 0–280	2	3	3	0	3
	0–140 to 0–700	1	4	4	4	4
	0–280 to 0–700	4	1	1	1	1
Thysanopoda aequalis	0–140 to 0–280	16	4	1	3	1
	0–140 to 0–700	7	13	4	9	3
	0–280 to 0–700	11	9	3	6	2
Stylocheiron carinatum	0–140 to 0–280	17	1	0	1	0
	0–140 to 0–700	11	7	3	4	3
	0–280 to 0–700	12	6	3	3	3
Euphausia brevis	0–140 to 0–280	7	8	7	1	5
	0–140 to 0–700	3	12	7	5	5
	0–280 to 0–700	11	4	0	4	0
E. tenera	0–140 to 0–280	8	0	0	0	0
	0–140 to 0–700	5	3	3	0	2
	0–280 to 0–700	5	3	3	0	2

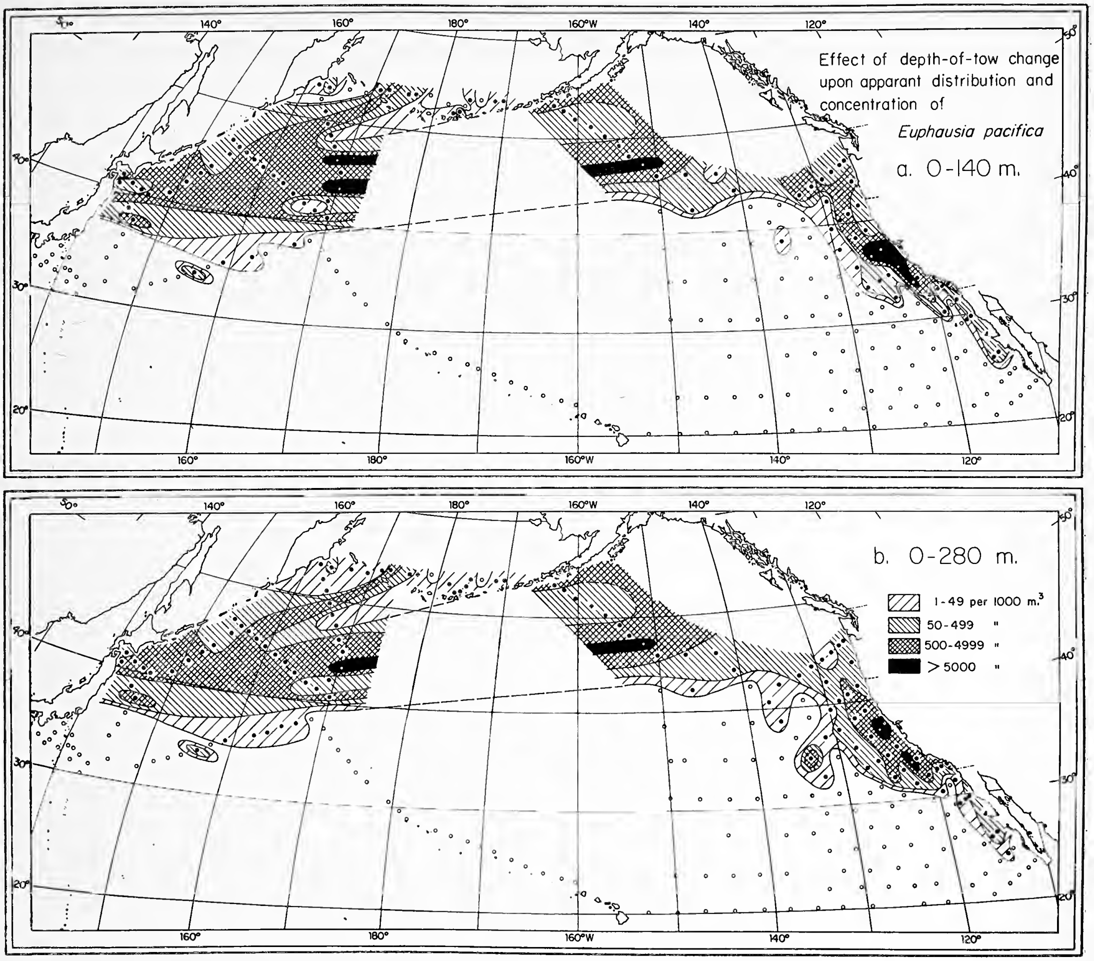


FIG. 2. Distribution of *Euphausia pacifica* during "Transpacific" expedition and "Norpac" cruise, based on sampling to, *a,* 0–140 m, *b,* 0–280 m. Only those stations are plotted at which sampling was carried out at both depths. Positive stations for *E. pacifica* are blackened.

species may be based on collections made at different depths, it is important to consider the relationship of depth of tow to species distribution outside of the region of the California Current. The multiple-depth sampling carried out by the "Transpacific" expedition, 1953, and the "Norpac" cruise, 1955, makes it possible to consider the effect over a much larger area on apparent euphausiid distribution. Table 4 shows the extent to which concentration intervals were altered in the area of the "Norpac" cruise in the eastern North Pacific when the depth of tow was increased from 0–140 m to 0–280 m or to 0–700 m.

As in the "E. W. Scripps" Cruise VIII, fewer concentration intervals were changed at "Norpac" stations when the depth attained by the net was least changed: 0–140 m to 0–280 m. The concentrations of *Euphausia pacifica* and *E. brevis* were altered at about 50% of the "Norpac" stations by sampling to 280 m instead of to 140 m, but the general features of the distributions of these two species were little changed (Figs. 2, 3). This was true despite the fact that *E. pacifica* occurred at only 44 "Norpac" stations, based on sampling to a depth of 140 m, but at 53 stations when sampling reached a depth of 280 m. The number of positive records of *E. brevis* was similarly increased from 32 to 45 by this change in the depth of sampling. The other species listed in Table 4 were only slightly affected by it. The increase to 700 m frequently altered the apparent concentrations of species, but few negative stations were made positive, even by this largest increase in depth of tow.

HOUR OF DAY OF SAMPLING

The diurnal vertical migrations performed by euphausiids bring certain species and stages of development near to the surface of the sea at night, where they can be taken by plankton nets sampling the upper 200–300 m. In many species, the adults descend to depths in excess of 300 m during the daylight hours, and consequently become unavailable to the nets sampling above that depth. The vertical ranges of the larvae and immature individuals of many species do not extend to depths beneath the stratum sampled. Thus, certain categories of size are more effectively sampled by the routine techniques than others.

The patterns of survey grids do not permit emphasis upon nighttime sampling to the exclusion of daytime sampling. The stations, situated 20–60 miles apart, are ordinarily occupied in sequence without regard for the time of day. It is therefore necessary to consider the diurnal changes in numbers in the sampled layers, as

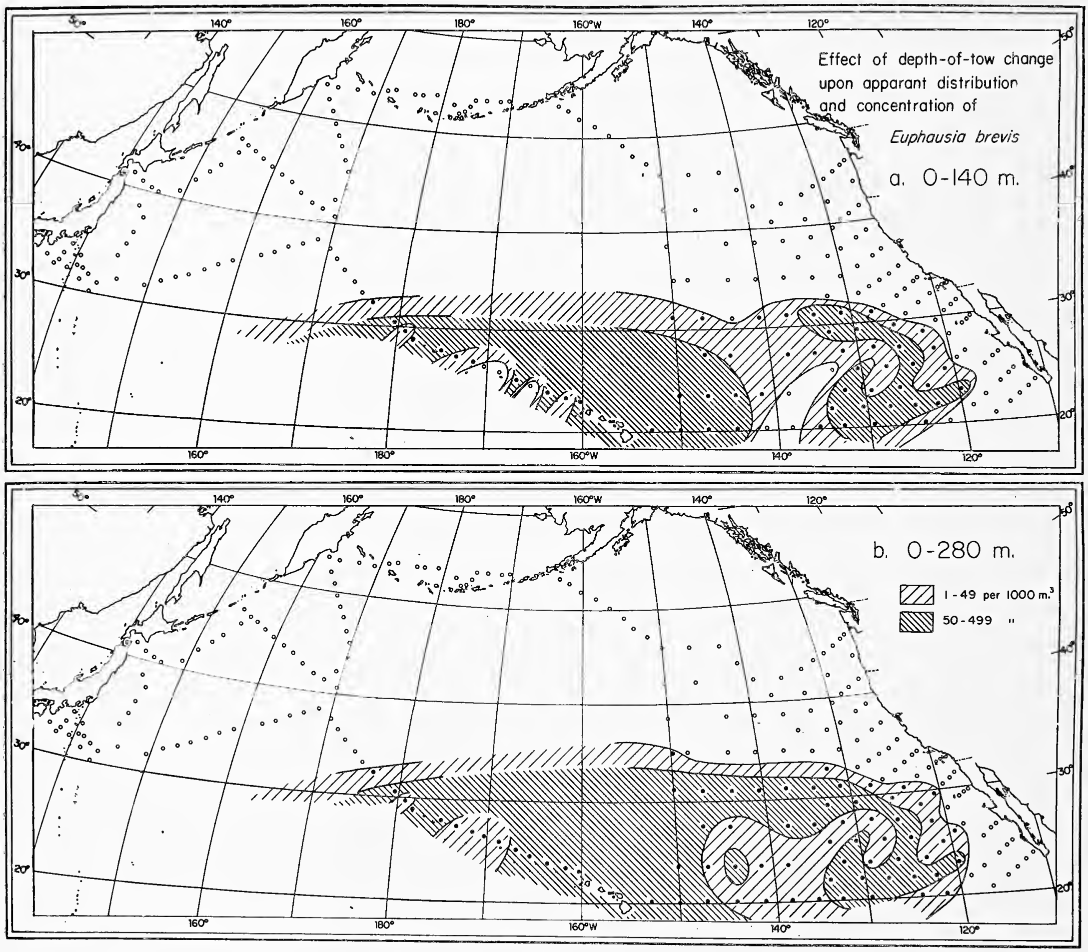


FIG. 3. Distribution of *Euphausia brevis* during "Transpacific" expedition and "Norpac" cruise, based on sampling to, *a,* 0–140 m, *b,* 0–280 m. Only those stations are plotted at which sampling was carried out at both depths. Positive stations for *E. brevis* are blackened.

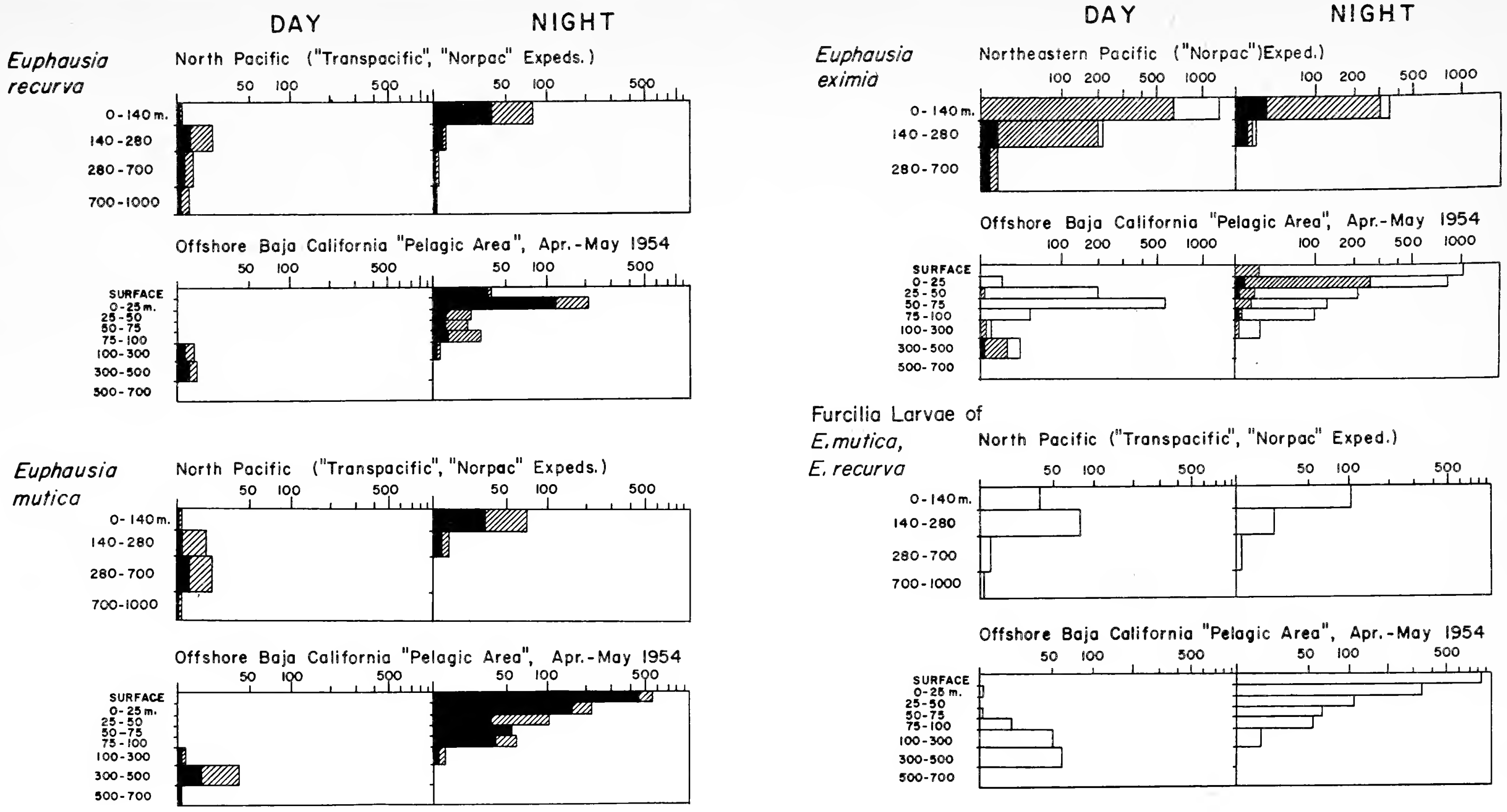


FIG. 4. Vertical distributions of certain euphausiid species in the North Pacific, from cruises listed in Table 1. Positions of stations are plotted in Figs. 2, 3, and 5. In each histogram, adults are indicated by the solid black bars, juvenile specimens by the cross-hatched bars, and furcilia larvae by the open bars. The number of specimens at each depth is the average collected at all stations within the ranges of the species, determined for each of the survey cruises.

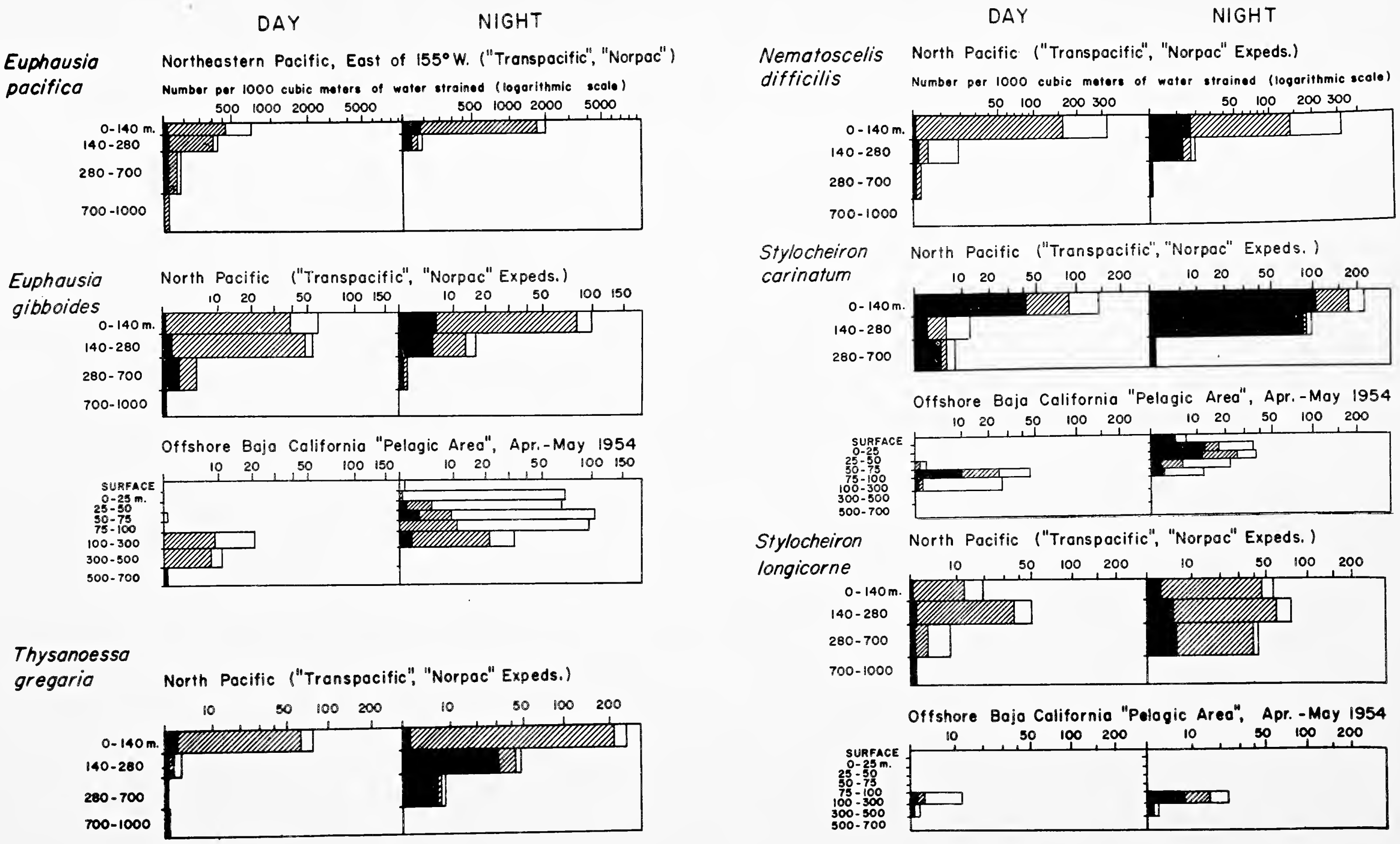


FIG. 5. Vertical distributions of certain euphausiid species in the North Pacific. (See caption for Fig. 4.)

these relate to coastal regions, mixed waters, and the open sea.

Daytime levels of occurrence of nine California Current species are compared with nighttime levels (Figs. 4, 5). These euphausiids, with the exception of *Stylocheiron longicorne,* are more abundant in the upper (0–140 m) layer by night than by day. The histograms indicate average day and night values for the indicated depths, based upon those stations of "Transpacific," "Norpac," and "Pelagic Area" surveys located within the known distributional ranges of the particular species.

Diurnal changes in the concentration of several euphausiid species were observed during an 8-day period at three stations (Fig. 6) off central California, Oct 11–19, 1950, on CCOFI "Anchor Station" Cruise 5010. The near-shore locality, station 72.60, was 75 miles south of Monterey and 50 miles offshore. Station 70.90 was 200 miles offshore, while station 70.130 was 400 miles west of Point Conception. The near-shore ship was at anchor during the 8-day period of observations. The two offshore ships maintained fairly constant positions by steaming to compensate for drift.

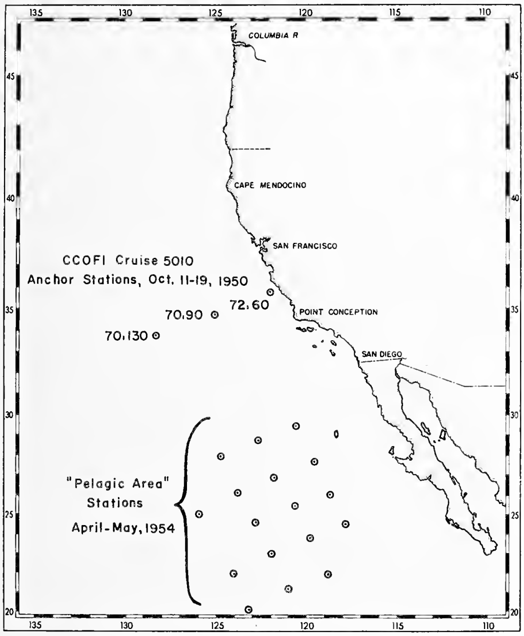


FIG. 6. Region of the California Current, showing positions of anchor stations (CCOFI Cruise 5010), and stations of the "Pelagic Area" survey at which vertical distributions (Figs. 4, 5) were determined.

The three stations were situated across the California Current. They were midway between the northern region, where this current arises in the southeastward flow of the Aleutian Current and the North Pacific Drift, and the region off the northern part of Baja California, where the current bends offshore and Equatorial water appears. The stations provided an opportunity to observe time changes in local populations, including day-night changes in the available euphausiid component of the plankton in the 0–140-m layer.

Anchor Station 72.60. The biological and physical changes which occurred at station 72.60 illustrate the manner in which the coastal environment may change. The numbers of the several euphausiid species occurring at this station are plotted in Figure 7, as a function of time. Vertical net hauls were made from the anchored "E. W. Scripps" at 3-hr intervals during the 8-day period.

No flow meter was used in the mouth of the vertically hauled net; 500 m^3 of water strained per net-haul was estimated for the hauls, based upon their elapsed time compared with a mean value for water strained by quantitative hauls of the same duration. This value is probably significantly in error for some hauls, owing to changes in current velocity. Nevertheless, the repetitive nature of the sampling provided a general picture of variability in the numbers of plankton organisms in the near-shore environment.

The sampling carried out at station 72.60 may be separated into three periods:

1) From Oct 11 (haul K-2) to 14 (haul K-21) *Thysanoessa gregaria* and *Stylocheiron longicorne* were relatively abundant, *Euphausia pacifica* larvae were few, and *Nyctiphanes simplex* was present in 6 of the 19 hauls. This indicated the presence of plankton with southern (*N. simplex*) and non-coastal (*T. gregaria* and *S. longicorne*) affinities. Haul K-15, within this period, had more northern characteristics. *T. gregaria, S. longicorne,* and *N. simplex* dropped off sharply at the time of this haul; while a characteristic subarctic species, *Tessarabrachion oculatus,* was present in small numbers, its only recorded appearance during the 8-day period.

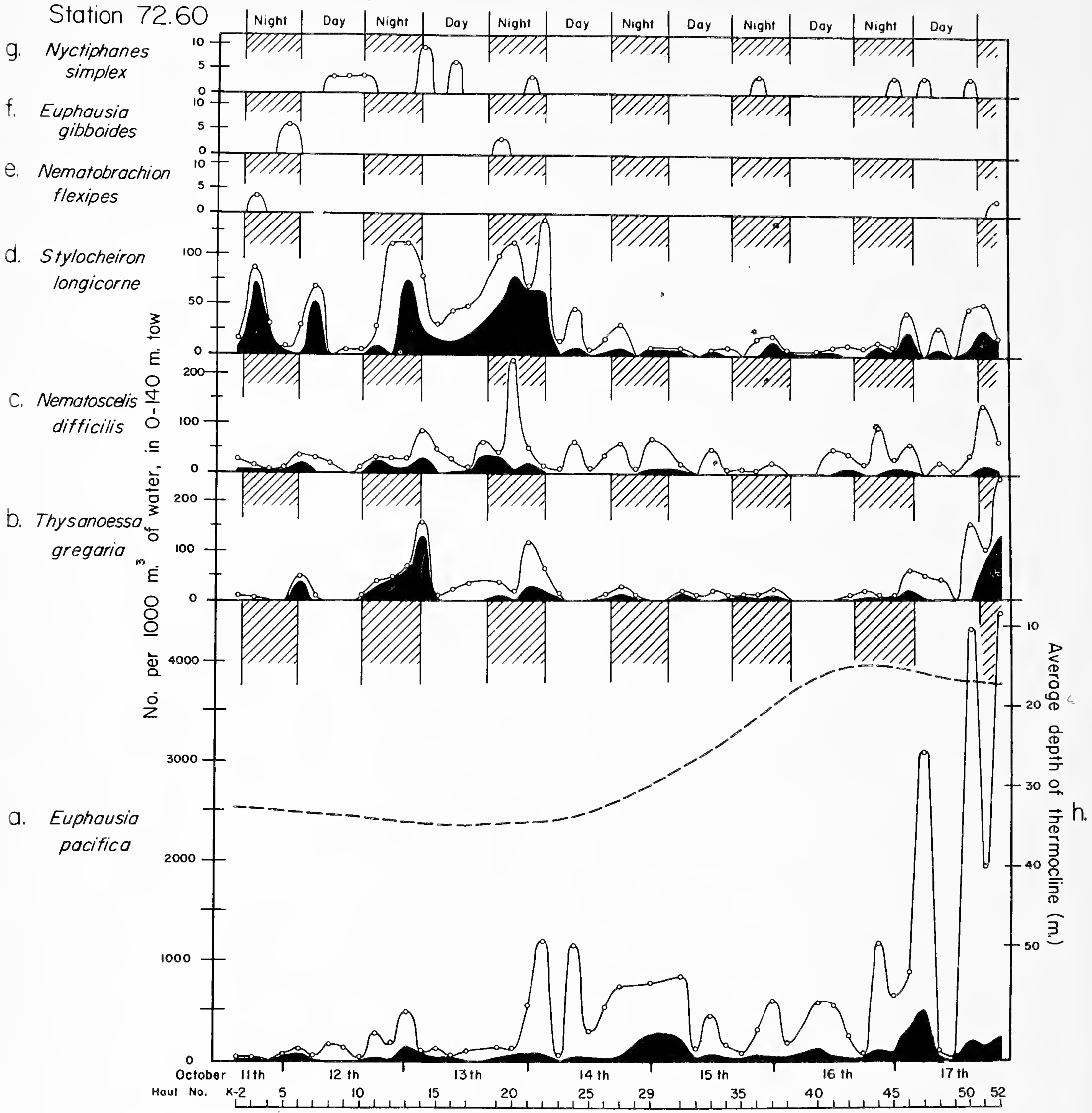


FIG. 7. Time variation in concentration of euphausiids at anchor station 72.60. Sampling was by vertical hauls to 140 m, at 3-hr intervals over an 8-day period. Blackened areas indicate concentrations of adults. Upper curves indicate total concentration of each species, including furcilia and juvenile individuals.

The adjacent hauls, K-14 and K-16, were characteristic of this first 3-day period, Oct 11–14.

2) From Oct 14 (haul K-22) to 16 (haul K-45) *Euphausia pacifica* larvae were more consistently abundant, while *Thysanoessa gregaria, Stylocheiron longicorne,* and *Nyctiphanes simplex* were few. This suggests a nearer-shore, coastal plankton, coincident with a shoaling thermocline and cooling surface temperatures.

3) From midnight Oct 16 (haul K-45) to the end of observations at midnight Oct 17, *Euphausia pacifica* larvae were numerous, *Thysanoessa gregaria* and *Stylocheiron longicorne* were more numerous than during Oct 14–16, and *Nyctiphanes simplex* was present in 3 of 8 hauls. These populations differed from the first group in the greater numbers of *E. pacifica,* but they clearly have southern, possibly more offshore

affinities as presumed from the prevalence of *T. gregaria.*

The species composition of the euphausiids at station 72.60 was nearly constant, and the subsurface physical characteristics of the water (Fig. 8), were rather uniform. Changes in the numbers of individuals of the species appear to be caused by changes occurring within the upper 100 m of the sea. These are apparently related to inconstant direction of surface flow, more characteristic of the near-shore region than of the open ocean. Day-night changes in the surface plankton due to the vertical migrations of euphausiids seem here to be limited to maximum concentrations of *Thysanoessa gregaria, Nematoscelis difficilis,* and *Stylocheiron longicorne* met with during hours of darkness. The numerically dominant species, *E. pacifica,* showed no significant day-night periodicity.

Anchor Station 70.90. The species present at the inshore anchor station 72.60 also occurred at station 70.90, occupied midway across the California Current.

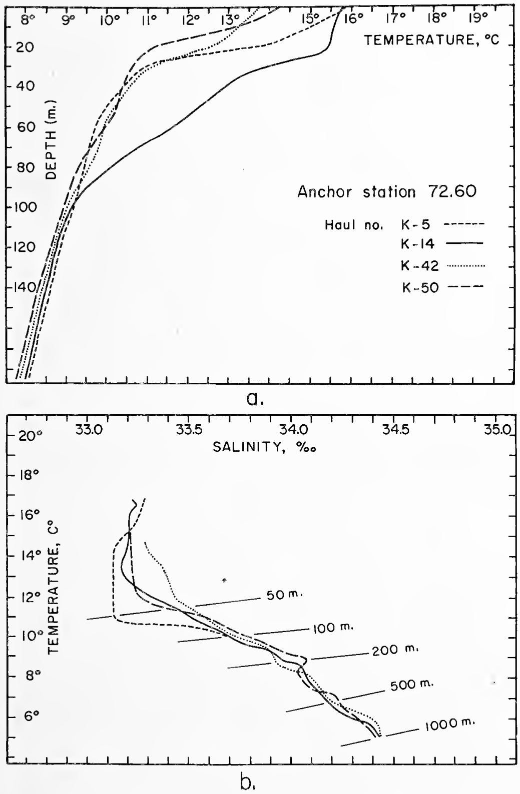


FIG. 8. *a,* Temperature and, *b,* temperature-salinity characteristics at selected times during occupancy of anchor station 72.60.

A warm-water species, *Euphausia recurva* (Fig. 9*f*), was found in one to three samples during each of the 8 nights. Nearly all individuals of this species were fully grown; one furcilia larva was present in haul K-19. The average depth of daytime occurrence of the adult *E. recurva* is below 140 m, though the larvae may be present at lesser depths (Fig. 4). Thus, in this region located near the eastern margin of the range of the species where few larvae and immature individuals are present, the population of *E. recurva* was not sampled by 0–140-m daytime hauls. It was sampled elsewhere, however, by the 0–280-m daytime hauls made by the Scripps oceanic expeditions. This is true also of the cold-water species, *Euphausia pacifica,* at this station and at anchor station 70.130, both situated near the western limit of the range of the species (Figs. 2, 6). Here, young individuals are few, and in the daytime the bulk of the adult population migrates deeper than the 140-m sampling depth.

Nighttime sampling of *Euphausia pacifica* indicated consistent concentrations in the range of 500–4,999 per 1000 m^3, except on the final night of sampling, Oct 18, when numbers fell off sharply.

Of the daytime samples, 13 were negative for *Euphausia pacifica,* 13 fell in the 1–49 per 1000 m^3 interval, while 3 were in the 50–499 range.

An unusually high concentration (3,110 per 1000 m^3) of half-grown specimens of *Euphausia pacifica* was recorded during daylight hours (1330 PST) on Oct 15, haul K-33. No other species occurred in unusual numbers at that time. It was partially overcast throughout the day. The peculiar near-surface appearance of these euphausiids cannot be attributed, then, to a sudden change in the intensity of light. It may be remarked, however, that the thermocline was relatively shoal, near 25–30 m of depth, during the first 12 hr of Oct 15 (hauls K-29 to K-33, Figs. 9*h,* 10).

A second factor possibly related to the large catch of *Euphausia pacifica* in haul K-33, is that few individuals of this species were in the sampled layer during the previous night, Oct 14–15. If migration toward the surface was in-

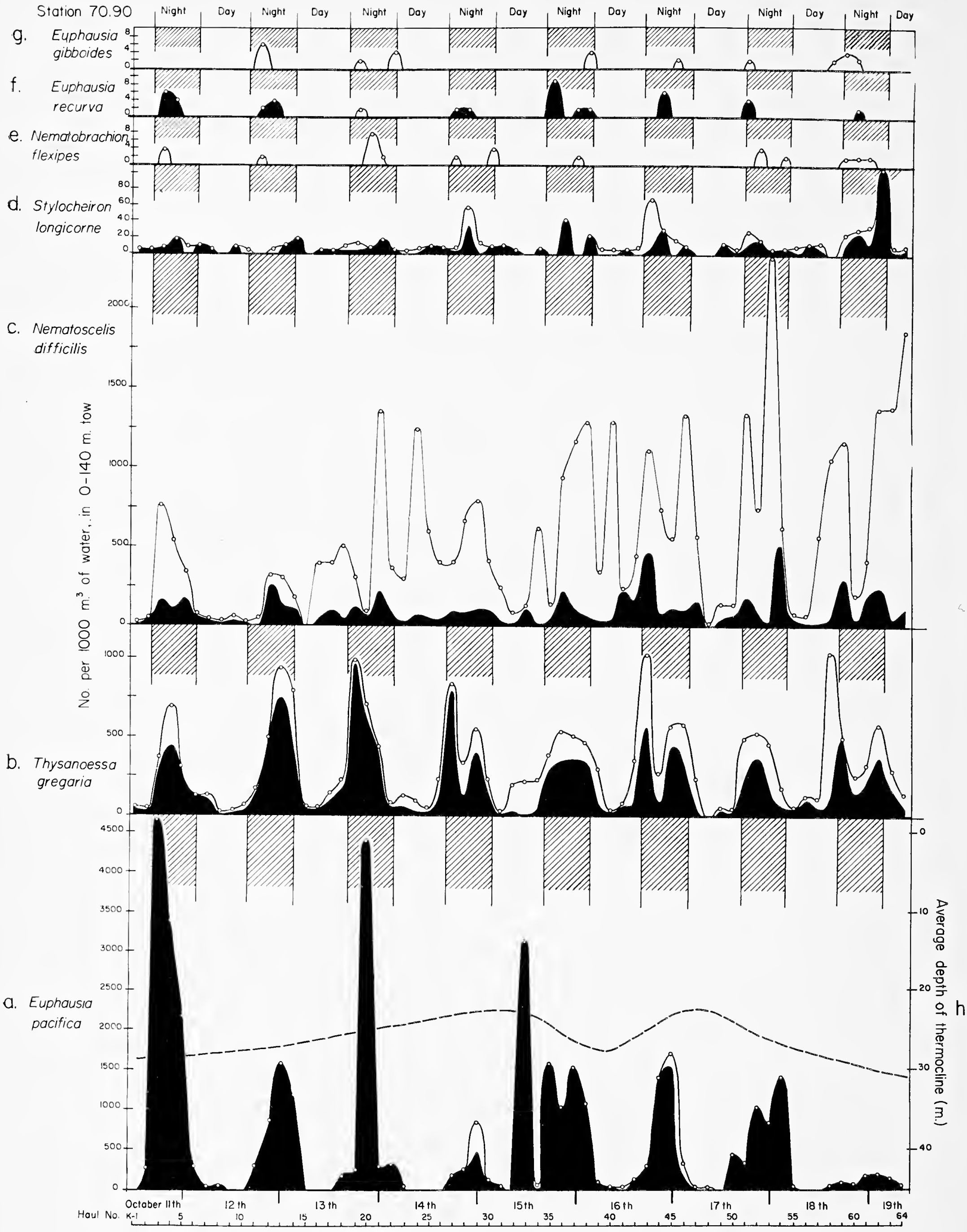


FIG. 9. Time variation in concentration of euphausiids at anchor station 70.90. Sampling was by standard oblique hauls to 140 m at 3-hr intervals over an 8-day period. Blackened areas under curves indicate concentrations of adults. Upper curves indicate total concentrations of each species, including furcilia and juvenile individuals.

hibited during the night of Oct 14–15, interruption of the diurnal periodicity of migration during the succeeding day-night interval may have resulted.

Thysanoessa gregaria also showed a constant day-night periodicity. Its population was made up largely of strongly migrating juvenile and adult euphausiids.

The combined juvenile-adult size group of the third prevalent species at station 70.90, *Nematoscelis difficilis,* showed less conspicuous nighttime peaks in numbers. Data for this species included in Figure 5 indicates that it is a less active vertical migrant than the species discussed above. The larvae, which made up the bulk of this species, were present in the 0–140-m layer without regard to time of day. Daytime populations of *Euphausia gibboides* (Fig. 9*g*) and *Nematobrachion flexipes* (Fig. 9*e*) were not sampled by the 0–140-m tows at station 70.90. Remarkable consistency in the catch of these two species is evident in the repeated presence of one, two, or three specimens of each species in nighttime samples: two nights were negative for *E. gibboides* and one night was negative for *N. flexipes.* Concentrations of *Stylocheiron longicorne* (Fig. 8*d*) exceeded 50 per 1000 m^3 on only three occasions. Otherwise numbers were within the 1–49 interval, with 7 negative samples in the series of 64.

Anchor Station 70.130. This station was situated far out at sea, in an environment which showed little variation in temperature during the period of observations (Fig. 13). The numbers of individuals of the colder-water species (Fig. 11) showed marked night-day maxima and minima. The offshore warm-water species (Fig. 12), allied to the central pelagic province, were less regular in this respect, being consistently within the 1–49 per 1000 m^3 numerical range during night and day.

The water layer above 150 m was warmer than at station 70.90 (by 2.5° at the surface, by 4° at 100 m). The thermocline at station 70.130 was close to 50 m, as compared with an average depth of about 30 m at station 70.90, and was less abrupt.

At station 70.130, *Euphausia pacifica* (Fig. 11*a*) was found in the 0–140-m stratum at night, usually in the 1–49 per 1000 m^3 range of density. At station 70.90, where it was caught during the day as well as at night, *E. pacifica* was most often in the 50–499 interval. On the other hand, the environment at station 70.130 was somewhat more favorable for *Thysanoessa gregaria* (Fig. 11*b*) than the environment at station 70.90 (Fig. 9*b*). Both species showed two nocturnal peaks of abundance, the first after sunset and the second after midnight on all eight nights. Similar twin peaks were observed for these species on only two to three of the eight nights at station 70.90.

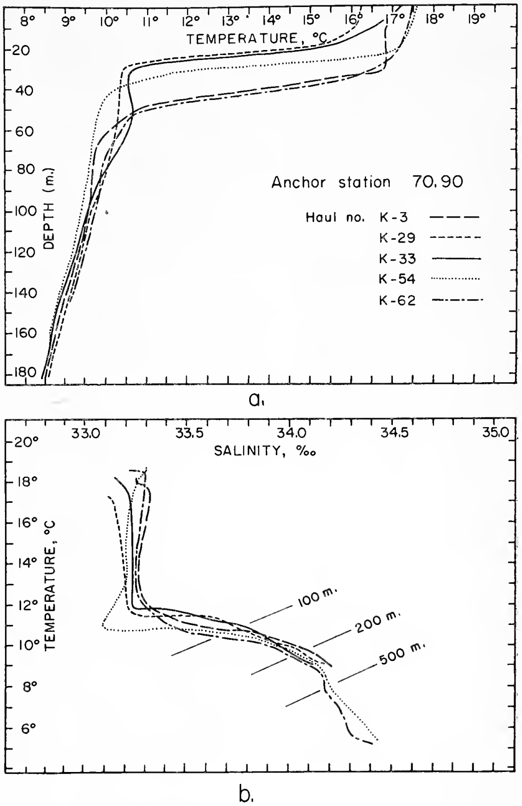


FIG. 10. *a,* Temperature and, *b,* temperature-salinity characteristics at selected times during occupancy of anchor station 70.90.

Nematoscelis difficilis (Fig. 11*d*), a species allied in distribution to *Thysanoessa gregaria,* appeared in all samples. Compared with station 70.90, few larvae were present, and there was a nocturnal maximum in the numbers of adults. The concentration of this species was 50–499 per 1000 m^3 until dawn, Oct 14. (One count was greater than 500, and one was less than 50.) After haul K-22, 23 of the 39 hauls sampled

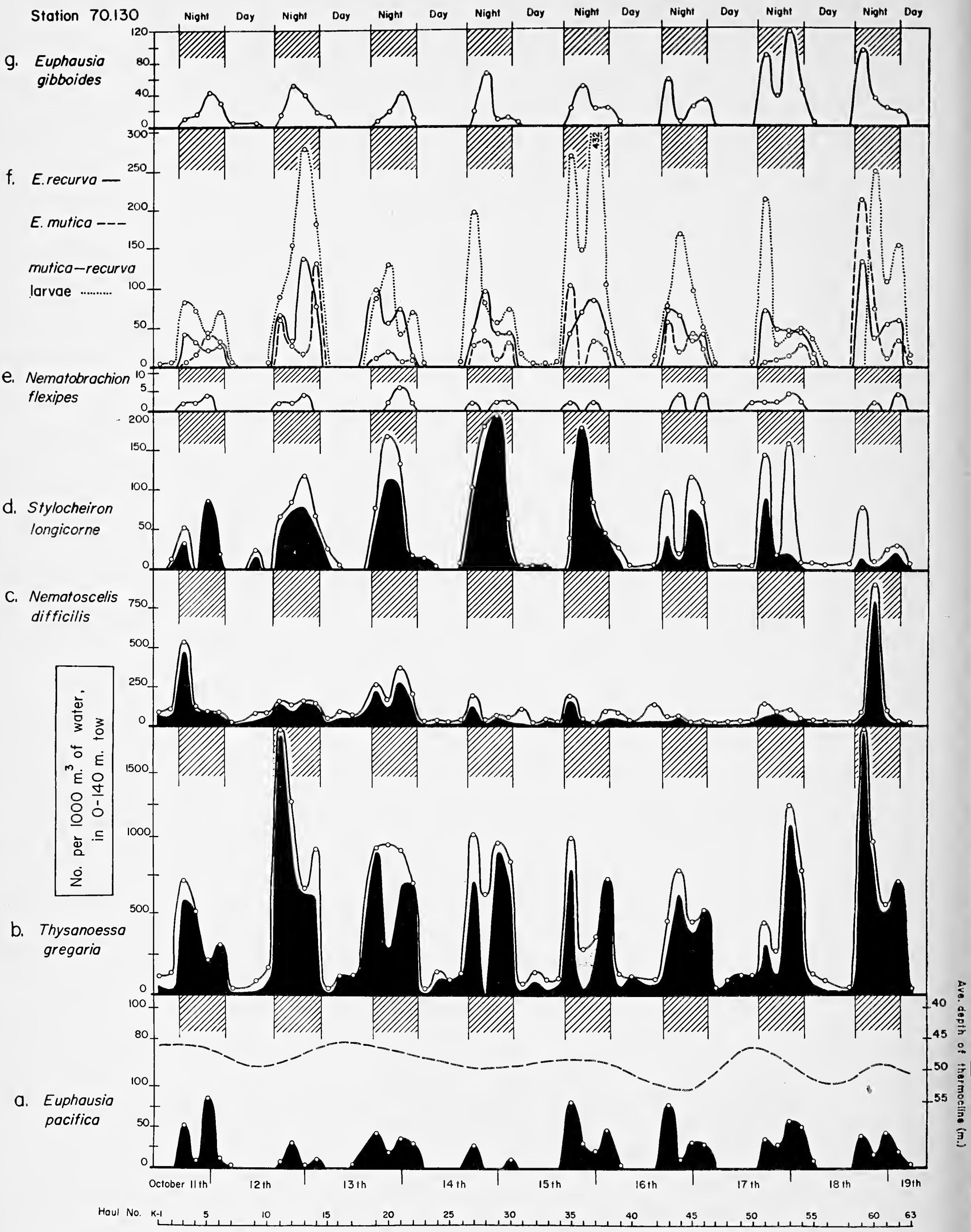


FIG. 11. Time variation in concentration of euphausiids at anchor station 70.130. Sampling was by standard oblique hauls to 140 m at 3-hr intervals over an 8-day period. Blackened areas under curves indicate concentrations of adults. Upper curves indicate total concentrations of each species, including furcilia and juvenile individuals.

concentrations in the 1–49 range, suggesting that a different population of *N. difficilis* had entered the area, or that the depth distribution of the species had changed.

Stylocheiron longicorne (Fig. 11*c*) was present in greater numbers than at the two previous stations. It showed greater diurnal periodicity in the 0–140-m layer than at the anchor stations nearer shore. This indicates a deeper average habitat for the species. Its daytime migration carried it entirely below the sampled layer, whereas at stations 70.90 and 72.60 some young individuals remained within the 0–140-m stratum throughout the 24-hr period.

Individuals of *Nematobrachion flexipes* (Fig. 11*e*) and *Euphausia gibboides* (Fig. 11*g*) appeared at station 70.130 with the same regularity shown at station 70.90. A few individuals were present in the samples each night.

The temperate character of the water at station 70.130 is reflected in the fact that the adults and larvae of *Euphausia recurva* and *E. mutica* begin to form a significant part of the night population sampled (Fig. 11*f*). These larvae were also present in small numbers in seven daytime hauls, but the station is still shoreward of the optimal environment of these *Euphausia* species. Westward of this station larvae were consistently taken in 0–140-m daytime hauls by "Transpacific" and "Norpac" expeditions.

The counts of five warm-water species are shown in Figure 12. At station 70.130, these species are near the eastern limits of their ranges. The numbers are largely made up of larval and immature individuals. Larvae of *Stylocheiron abbreviatum* (Fig. 12*a*) consistently appeared in greatest numbers at night. Immature and adult individuals of *Nematoscelis tenella*, *Nematoscelis atlantica*, and *Thysanopoda aequalis* (Fig. 12*c–e*) were not often caught except at night, but the total concentrations of these species did not always peak at night.

Counts of the euphausiids from the three anchor stations showed that the number of individuals of each species within the 0–140-m stratum varied from hour to hour at each locality. Variation in the numbers of the *Euphausia* species and *Thysanoessa gregaria* were most extensive and regular in respect to time. All size groups of the several *Euphausia* species showed

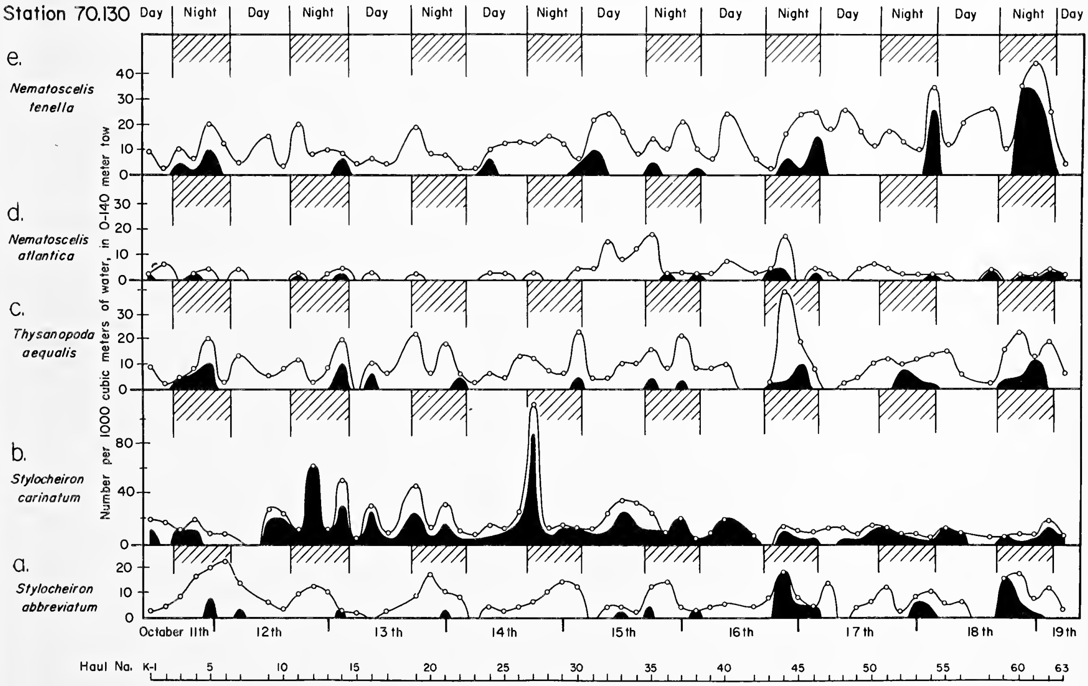


FIG. 12. Time variation in concentration of euphausiids at CCOFI anchor station 70.130; a continuation of Fig. 10, showing the central (warm-water) species.

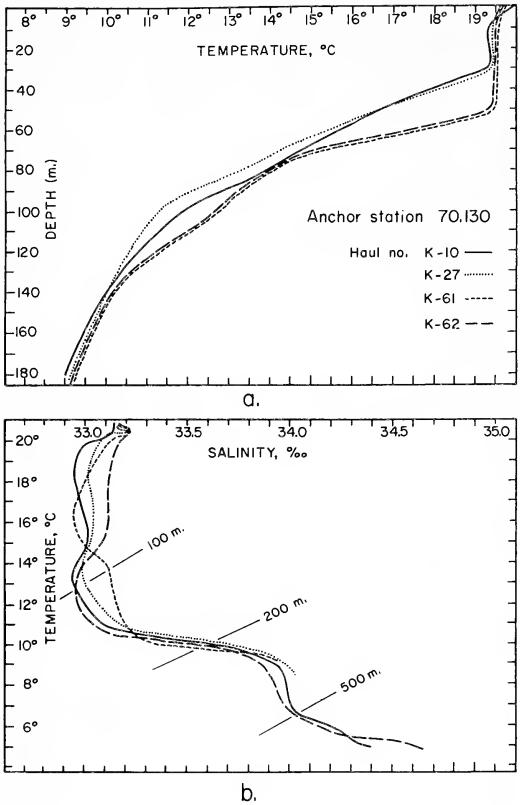


FIG. 13. *a,* Temperature and, *b,* temperature-salinity characteristics at selected times during occupancy of anchor station 70.130.

a consistent tendency to migrate into and out of the 0–140-m layer. The several species of *Nematoscelis* showed less diurnal variability in numbers, apparently owing to the near-surface habitat of the larvae and the fact that they are less inclined to migrate to depths below 140 m. The warm-water species at station 70.130 showed the least variability within the 24-hr period. Here, near the northeastern limits of their range, these species live in the thin peripheral part of the central Pacific warm-water lens.

LOCAL SEQUENCE COMPARED WITH INDIVIDUAL POPULATION SUCCESSION

The series of changes taking place with time in a plankton population occupying a moving or stationary mass of water has been called an "individual population succession" (Sverdrup, Johnson, and Fleming, 1942). The series of changes observed at a locality because different populations and masses of water are passing is called a "local sequence."

The examples in the preceding section show changes in estimated concentrations observed at three fixed localities off central California in the cool northern part of the California Current. If, during the 8-day sampling period, the plankton was carried southward at a mean current velocity of 0.3 knots, measured between the surface and 500 decibars (U. of Calif., Scripps Inst. Ref.

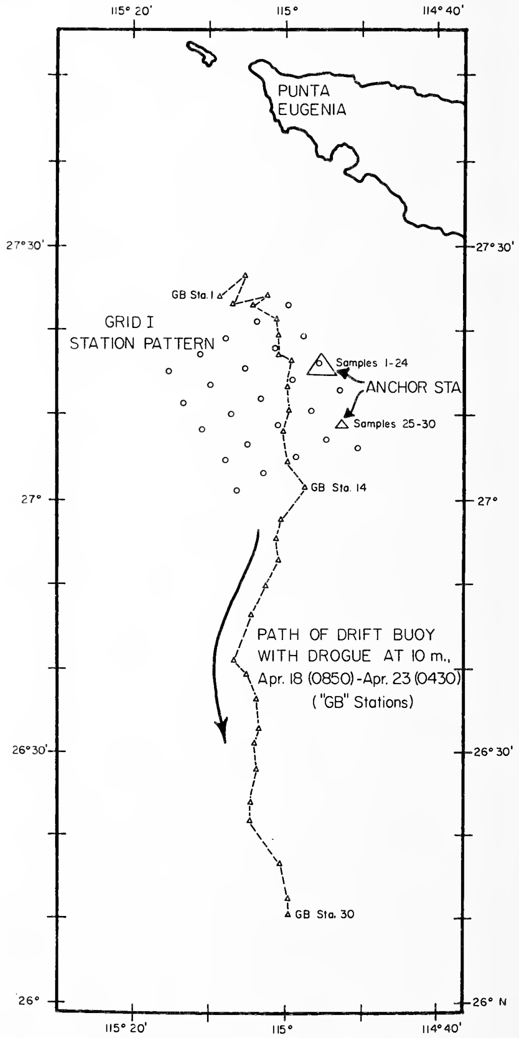


FIG. 14. Region off Punta Eugenia, Baja California, showing locations of anchor stations, drift-buoy stations, and close-grid survey carried out Apr 18–23, 1952.

52-37), these samples of euphausiids represented local sequences. It is known, however, that in the course of 24 hr vertically migrating plankton populations may occupy currents that move in different directions. In the region of the California Current these currents may be opposite in direction at the extremes of the vertical range of the adult euphausiids (0 and 300–500 m). In general, this will tend to keep the adult component of the population, which migrates through a 300–500-m span, at a given locality, while furcilia larvae living near the surface will be carried by the superficial currents through a horizontally distributed sequence of adult populations. Local sequence and individual population succession, therefore, could not be certainly differentiated at the central California anchor stations. However, most of the variability in estimated species concentrations can be interpreted as a measure of population replacement at the anchor station localities, because the trends in concentration-change extended for periods of several days.

A three-ship study, carried out in Baja California waters as part of the CCOFI survey cruise of Apr 1952 provided material for a comparison of local and time change in population composition and concentration. Simultaneous observations were made at (1) an anchor station located 30 miles offshore, south of Punta Eugenia, mid-Baja California; (2) a drifting buoy to which a metal drogue was attached at a depth of 10 m; (3) 25 stations forming a 20-mile square grid (Fig. 14). The entire grid was occupied on each of 5 consecutive days. Only the first 2 days of grid samples were analyzed for euphausiids. Sampling at the buoy and anchor stations was carried out at 4-hr intervals for a 5-day period. All plankton hauls were oblique to a depth of 140 m. Hydrographic measurements were made at the buoy and anchor stations, in conjunction with the plankton hauls.

Samples from the anchor station measured change at a fixed locality. The sampling program at the buoy station was designed to measure time change in the plankton populations inhabiting the superficial layers. Although it cannot be assumed that the flow of the current at a depth of 10 m approximates the average flow of the current in the 0–140-m layer sampled by the plankton net, euphausiid populations in the area were composed mainly of young individuals (larvae and juveniles) whose habitat is known to be the upper part of the vertical range of the species as a whole.

Six species were present throughout the sampling period at the anchor and buoy stations. These were *Euphausia gibboides, E. eximia, Thysanoessa gregaria, T. spinifera, Nematoscelis difficilis,* and *Nyctiphanes simplex* (Fig. 15). *Euphausia recurva* and *Stylocheiron affine* were sometimes present but were numerous only to the east of the buoy and anchor stations, as shown by the grid survey distributions (Figs. 16, 17). The distributions of *E. recurva* and *S. affine* were to some extent determined by the proportion of nighttime sampling stations, (cf grid distribution, and Apr 1952, CCOFI cruise). Records for *Euphausia pacifica* were also not consistent; the study was carried out near the southern limit of the Apr 1952 range of this species (Fig. 18).

The anchor station did not represent a fixed point. The area in which samples 1–24 were taken (the large triangle, Fig. 14) and in which samples 25–30 were taken (the small triangle, 10 miles farther south) were approximately 4 and 1 sq miles, respectively. The southward shift of the position of the anchor station did not appear to affect the composition of the euphausiid population which was sampled.

Counts of the most abundant species, *Nyctiphanes simplex,* varied a good deal (Fig. 15): the first six hauls (Apr 18) fell in the 50–499 range; hauls 7–29 (Apr 19–23), with three exceptions, fell in the 500–4,999 range; hauls 24 and 30 contained more than 5,000 *Nyctiphanes,* per 1000 m^3. It was thought that if these differences meant that different populations were being sampled, this might be indicated by differences in the mean size of the furcilia larvae which made up the bulk of the population. The average sizes of *N. simplex* for each 24-hr period (dawn to dawn), determined from all individuals caught in all anchor station samples, were as follows:

APR	ANCHOR STATION HAULS	MM
18–19	1–6	3.99
19–20	7–12	3.87
20–21	13–18	3.45
21–22	19–24	3.17
22–23	25–30	3.84

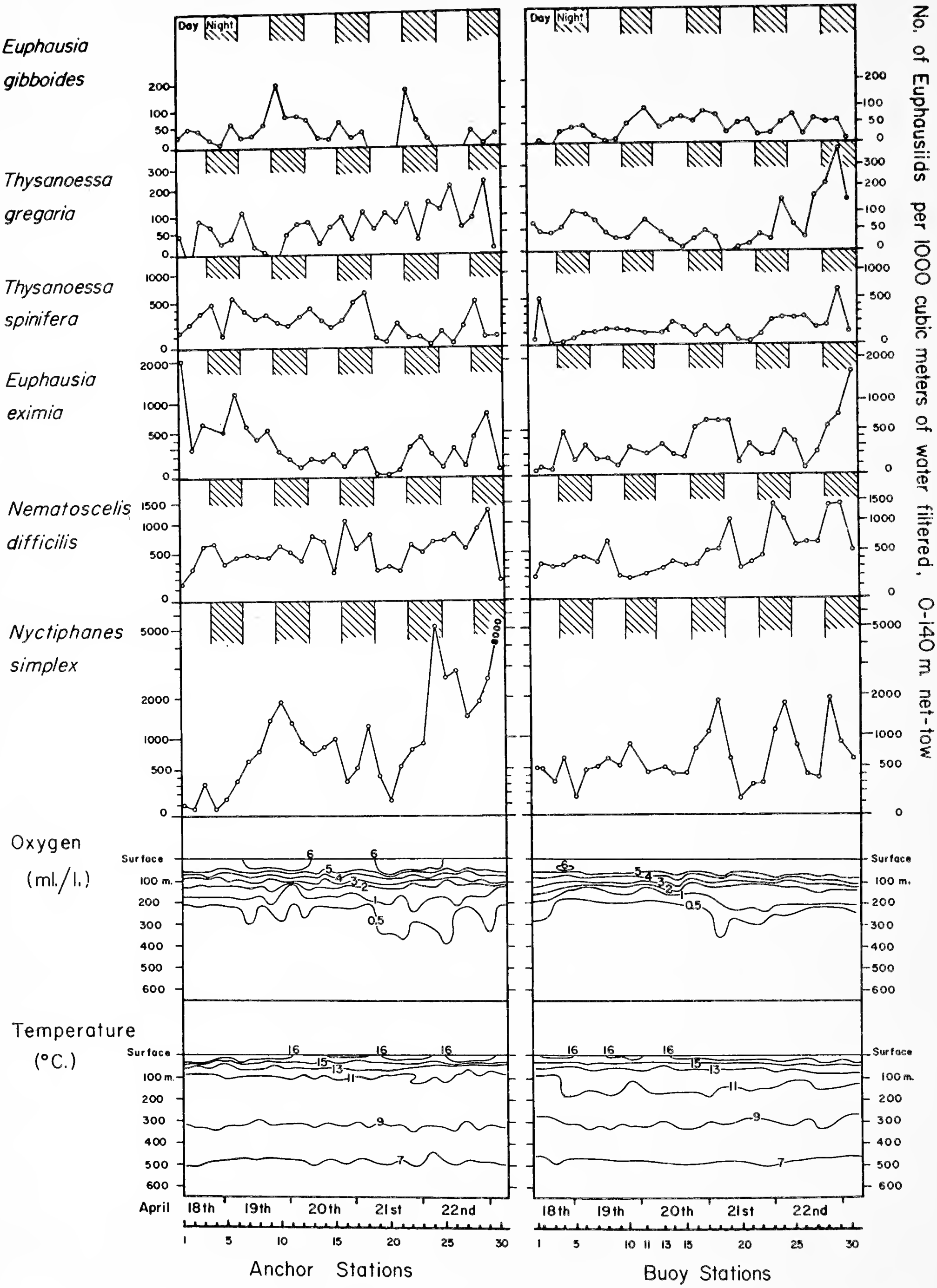
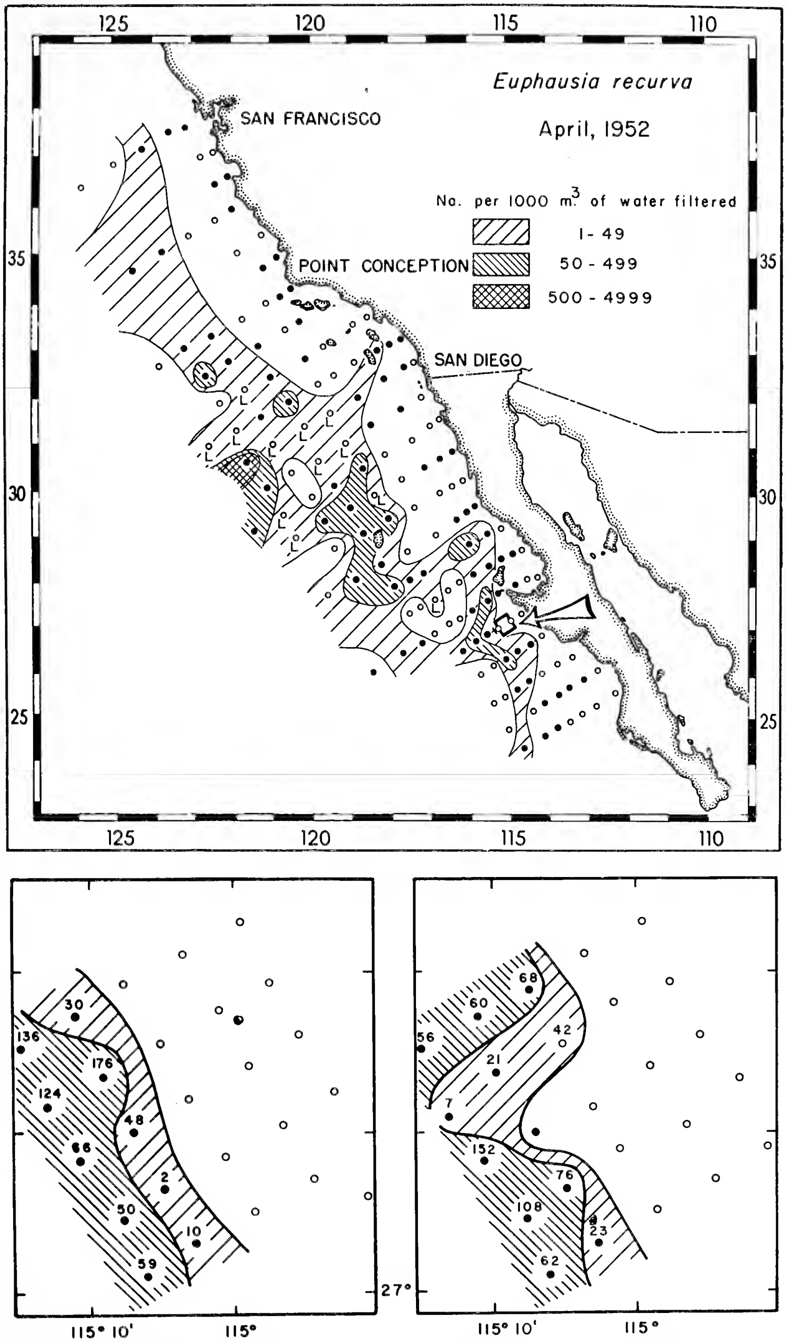


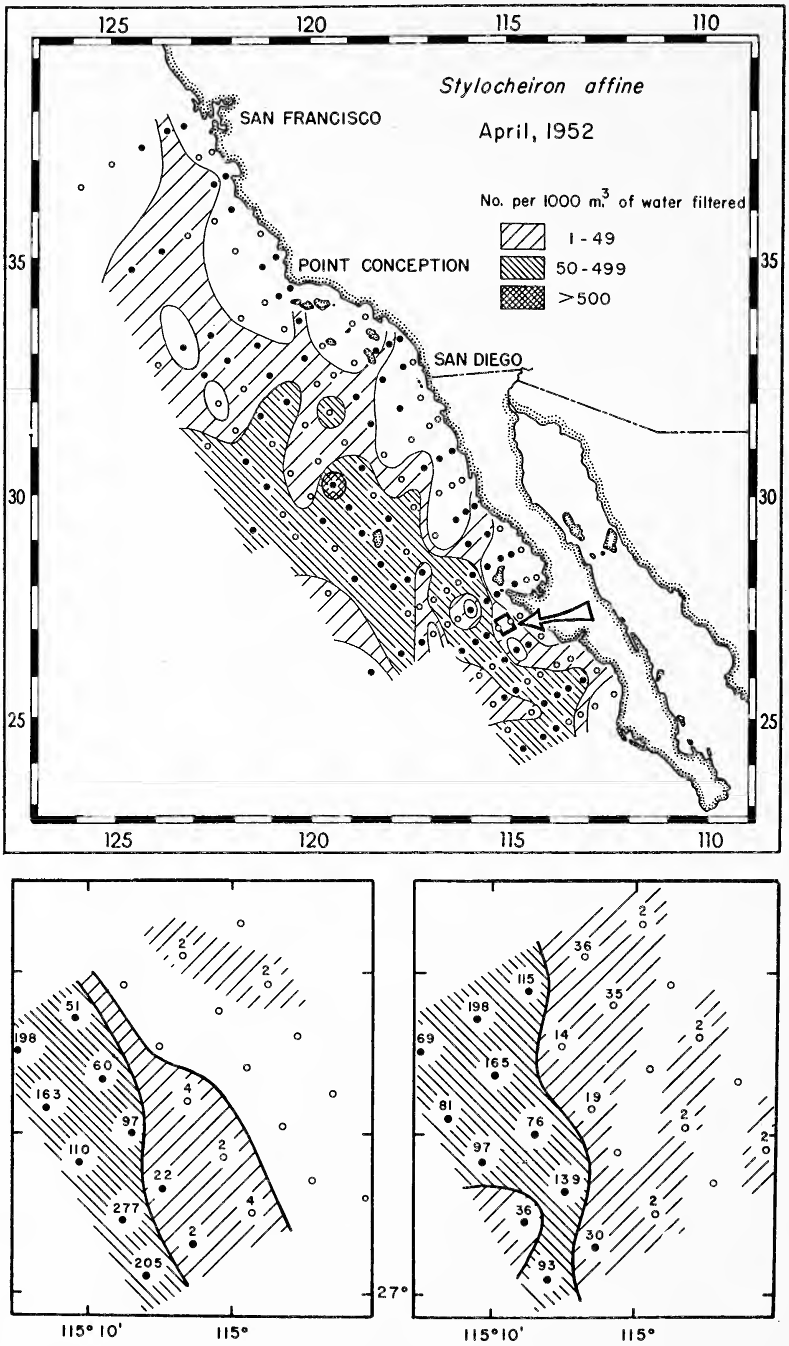
FIG. 15. Time changes in concentrations of euphausiids sampled at anchor and buoy stations off Baja California, Apr 18–23, 1952. Sampling was by standard oblique hauls, 0–140 m, at 4-hr intervals. Oxygen and temperature profiles for the two series of observations are plotted to a depth of 600 m.



E. recurva, Grid I, April 18

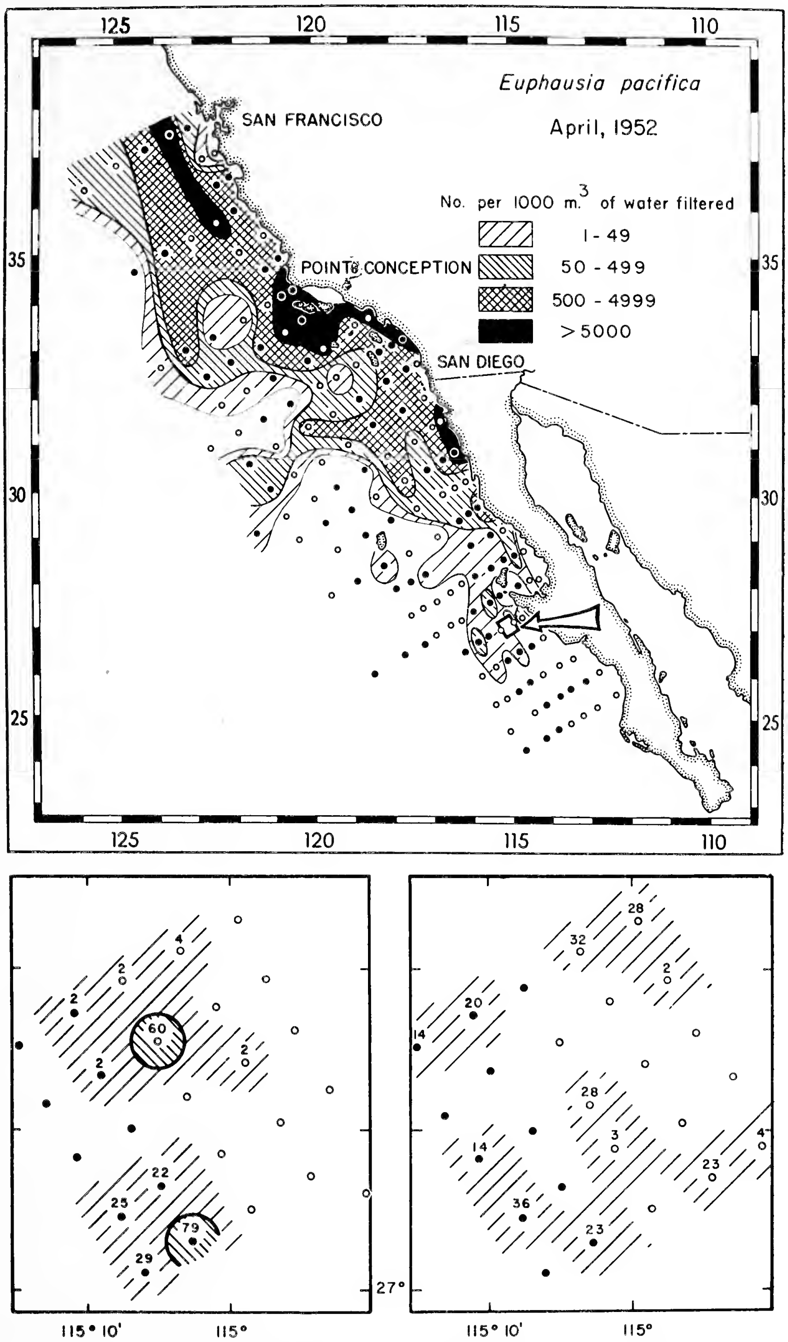
E. recurva. Grid II, April 19

FIG. 16. *Euphausia recurva,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close grid survey. The letter *L* indicates occurrence of larvae *probably* belonging to *E. recurva.*



S. affine. Grid I, April 18 S. affine. Grid II, April 19

FIG. 17. *Stylocheiron affine,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.



E. pacifica. Grid I, April 18

E. pacifica. Grid II, April 19

FIG. 18. *Euphausia pacifica,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.

As single *Nyctiphanes* furcilia stages of development may include individuals that differ from each other in length by 1.0–1.5 mm, the differences in average length are not sufficient to suggest that populations of different age or size were sampled at the anchor station. A comparison of the distribution of *N. simplex* in grids I and II (Fig. 19) suggests that from Apr 18 to 19 the water containing high concentrations of this species moved in a southeast or eastward direction. According to the grid samples, the numbers of this species near the anchor station were in the 50–499 per 1000 m^3 interval on Apr 18, and in the 500–4,999 interval on Apr 19; the concentrations actually sampled at the anchor station (Fig. 14) on these 2 days were within this range.

Of the other species occurring at the anchor station, *Euphausia eximia* had a high amplitude of variation, while *Thysanoessa gregaria* had the most up-down sequences in abundance, during the 5-day period. Concentrations of *Nematoscelis difficilis* were near 250–750 per 1000 m^3, except in the first sample (156 per 1000 m^3) and the last two samples (1,291 and 190, per 1000 m^3, respectively).

The concentration of *Euphausia eximia* fell in the 500–4,999 per 1000 m^3 interval in six of the first nine anchor station hauls (Fig. 15). This was in agreement with the grid sampling (Fig. 20). After anchor station haul no. 9, Apr 19, *E. eximia* numbers were in the 50–499 interval, except for three hauls, until the end of the sampling period.

Thysanoessa spinifera was in the 50–499 range, with the exception of four samples, during the anchor station sampling (Figs. 15, 21). *T. gregaria* was consistently in the 50–499 range after Apr 19, the second day at the anchor station. During the first 2 days it was often less numerous, agreeing with the grid concentrations shown in Figure 22.

The anchor station counts of *Euphausia gibboides* were erratic. As in the grid distributions (Fig. 23), the numbers of this species were most often in the 1–49 per 1000 m^3 interval during the first day and a half of sampling at the anchor station.

Samples were taken at the drift-buoy at the same times as those at the anchor station. The two series of observations can be compared in Figure 15. The path of the buoy (Fig. 14) indicates that, until haul no. 14, the current at a depth of 10 m traveled in a direction that was east of south. According to J. L. Reid (personal communication), who conducted operations on the R/V "Black Douglas" which followed the buoy, the apparently erratic path of the buoy during the first day may have been due to early difficulties in ascertaining the ship's position. After buoy haul no. 14, the buoy moved in a direction west of south. At haul no. 20 the buoy appeared to resume its original course.

At the buoy stations five species were evidently in a favorable environment, judging from their numbers. Thus, *Nyctiphanes simplex, Nematoscelis difficilis, Thysanoessa spinifera, T. gregaria,* and *Euphausia eximia* were most regular in hauls 1–14. After haul no. 14, the course of the buoy changed, and diurnal periodicity of these species was observed. *Nyctiphanes simplex, Nematoscelis difficilis,* and *Euphausia eximia* were most extreme in this respect. (However, the apparent density of *Nyctiphanes* did not change as extremely at the buoy stations as at the anchor stations).

Daytime concentrations of the above five species were compared (Table 5) with nighttime concentrations for the two parts of the buoy stations series, hauls 1–14 and hauls 15–30. Levels of significance of the differences between the two series of hauls were determined according to the distribution of the rank sum T'.

Daytime concentrations for hauls 1–14 did not differ significantly from concentrations in hauls 15–30, except in the case of *Euphausia eximia* which was more numerous after haul 14. Nighttime concentrations of *Nematoscelis difficilis* and *Nyctiphanes simplex,* two species showing conspicuous nocturnal peaks in abundance after haul 14, were significantly higher after the course of the buoy changed. *Euphausia eximia* also became more numerous (as stated above for the daytime hauls), though the nighttime values for hauls 15–30 were greater than those for hauls 1–14 only at the level $p-.06$. Nighttime means for *Thysanoessa spinifera* and *T. gregaria* were higher after haul 14, but the ranked values of the hauls did not differ significantly from the haul 1–14 series.

The euphausiid assemblage remained the same after haul 14. The character of the water

TABLE 5

DRIFT BUOY STATION HAULS 1–14 COMPARED WITH HAULS 15–30

SPECIES	HAULS	MEAN DAY DENSITY	LEVEL OF SIG. OF DIFFERENCE	MEAN NIGHT DENSITY	LEVEL OF SIG. OF DIFFFRENCE
Nyctiphanes simplex	1–14 15–30	494 446	.280	529 1146	.028
Nematoscelis difficilis	1–14 15–30	356 565	.152	326 841	.006
Euphausia eximia	1–14 15–30	102 251	.040	265 609	.060
Thysanoessa spinifera	1–14 15–30	152 139	.612	70 189	.112
T. gregaria	1–14 15–30	44 38	.190	72 114	1.000

mass also remained stable, according to the temperature and oxygen profiles plotted in Figure 15. However, temperature at a depth of 9 m was at all times colder than 16 C before haul 14 (15.71–15.98 C), and warmer than 16 C after haul 14 (16.02–16.26 C). This could not be interpreted as a gradual time increase in temperature accompanying southward movement of the water, but probably reflected replacement of surface water. The changed abundance and behavior of euphausiids therefore probably indicates a more dense population brought in with this surface water. *E. eximia, N. difficilis,* and *N. simplex* then exhibited diurnal vertical migration.

The behavior of *N. simplex* changed conspicuously at haul no. 14. However, the mean sizes of individuals, determined for each of the 5 days of sampling, did not differ significantly from one another or from the mean sizes of *N. simplex* measured at the anchor station, listed above:

APR	BUOY STATION HAULS	MM
18–19	1–6	3.91
19–20	7–12	4.32
20–21	13–18	3.99
21–22	19–24	3.86
22–23	25–30	3.48

SAMPLES FROM 45-CM NET AND 1-M NET COMPARED

During the Aug–Sep 1956 cruise of the R/V "Stranger," transects were made of the mid-equatorial Pacific using two types of net. A net, 45 cm in mouth diameter and 0.33 mm in mesh width,[2] was attached to the wire at a distance of 10 m above a 1-m net of the standard 0.65-mm mesh width. The nets were towed obliquely to a depth of 140 m.

The paired samples were counted for 10 of the "Equapac" stations. These were standardized for 1000 m^3 of water, assuming that the large net strained 4.94 times as much water as the small net (that is, in the ratio of the areas of the mouths of the two nets). The large nets strained 325–463 m^3 of water, the small nets 66–94 m^3.

The relative catching ability of the two nets is summarized in Table 6. Furcilia larvae (2.5–4.5 mm long) of the most abundant species, *Euphausia tenera,* were sampled in greater numbers by the 45-cm net than by the 1-m net at 9 of the 10 stations. Furcilia of *E. diomediae* and *Stylocheiron abbreviatum* were better sampled by the small net at all stations where they were present, furcilia of *Thysanopoda aequalis* at all but 1 station, and those of *Nematoscelis gracilis, Thysanopoda tricuspidata,* and *S. affine* at all but 2 stations. In the most extreme case, larvae in a 45-cm net sample outnumbered by a factor of

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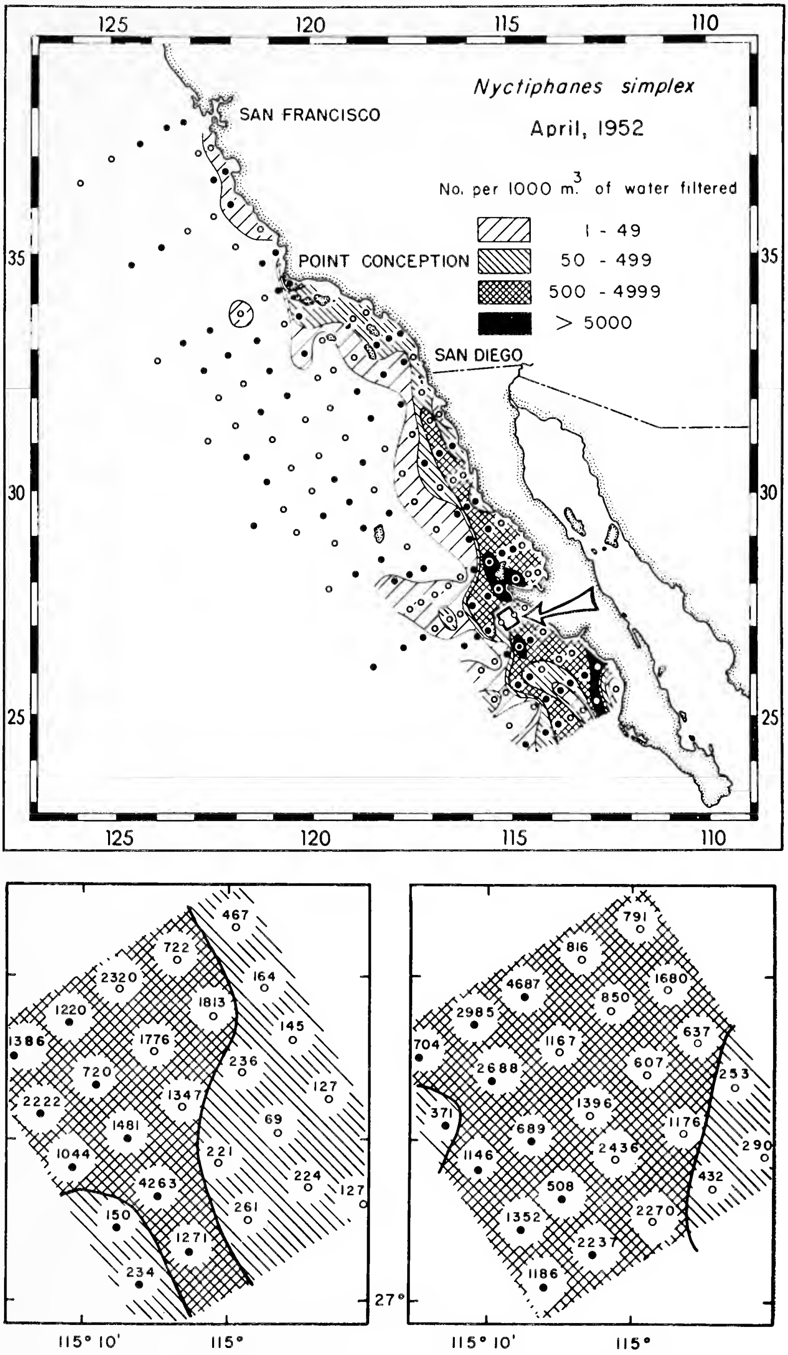
[2] At a meeting in Hawaii, Apr 1956, the 45-cm net was adopted as one of the standard plankton nets for sampling in the Pacific. The meeting was attended by oceanographers from Canada, Japan, and the United States for the purpose of coordinating publication of "Norpac" expedition data. It was agreed that the 45-cm net was to be used to supplement other standard nets.

TABLE 6

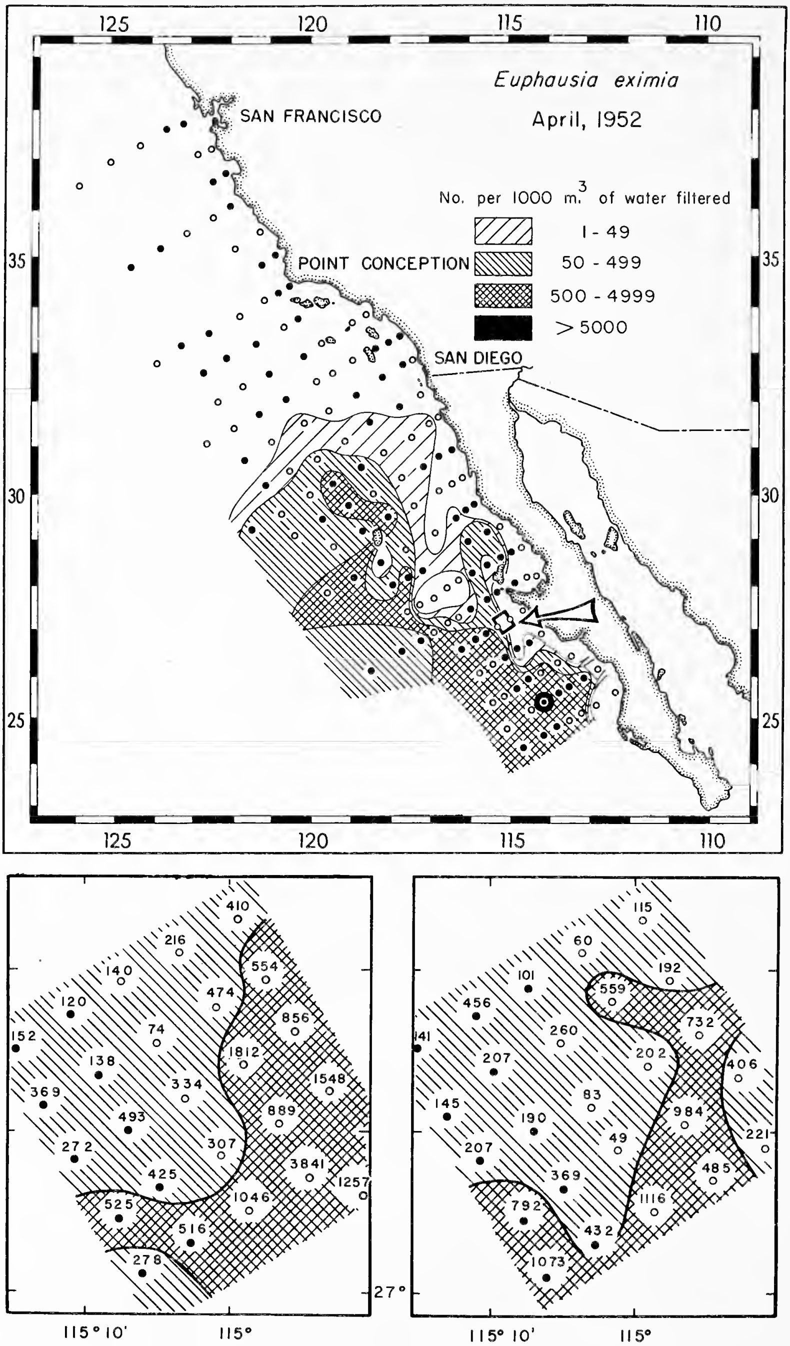
EUPHAUSIID CATCHING ABILITY OF 45-CM NET COMPARED WITH 1-M NET, AT 10 "EQUAPAC" EXPEDITION STATIONS, 12° N–3° S, 166.5°–175° W

SPECIES	STAGE	DENSITY MEASURED BY 45-CM NET EXCEEDED DENSITY MEASURED BY 1-M NET (no. of hauls)	DENSITY MEASURED BY 1-M NET EXCEEDED DENSITY MEASURED BY 45-CM NET (no. of hauls)	DENSITY MEASURED BY 45-CM NET EQUAL TO DENSITY MEASURED BY 1-M NET (no. of hauls)
Euphausia tenera	adults	2	3	6
	juvs.	2	6	2
	furcilia	9	1	0
E. diomediae	adults	0	5	5
	juvs.	2	4	4
	furcilia	6	0	4
E. paragibba	adults	1	3	6
	juvs.	1	4	5
	furcilia	1	1	8
Nematoscelis gracilis	adults	0	1	9
	juvs.	4	5	1
	furcilia	8	2	0
N. tenella	adults	0	0	10
	juvs.	1	3	6
	furcilia	6	2	2
N. microps	adults	0	0	10
	juvs.	1	1	8
	furcilia	6	3	1
Stylocheiron affine	adults	4	6	0
	juvs.	4	5	1
	furcilia	8	2	0
S. carinatum	adults	4	4	2
	juvs.	6	4	0
	furcilia	5	5	0
S. microphthalma	adults	4	4	2
	juvs.	4	5	1
	furcilia	3	4	3
S. abbreviatum	adults	0	0	10
	juvs.	2	2	6
	furcilia	8	0	2
S. suhmii	adults	1	0	9
	juvs.	1	1	8
	furcilia	0	1	9
S. longicorne	adults	0	1	9
	juvs.	0	1	9
	furcilia	1	0	9
Thysanopoda aequalis	adults	2	0	8
	juvs.	4	3	3
	furcilia	4	1	5
T. tricuspidata	adults	0	0	10
	juvs.	4	4	2
	furcilia	8	2	0
T. monacantha	adults	0	1	9
	juvs.	2	1	7
	furcilia	1	4	5
Totals (all species)	adults	18	28	($p = .18$)
	juvs.	38	49	($p = .28$)
	furcilia	74	28	($p < .01$)



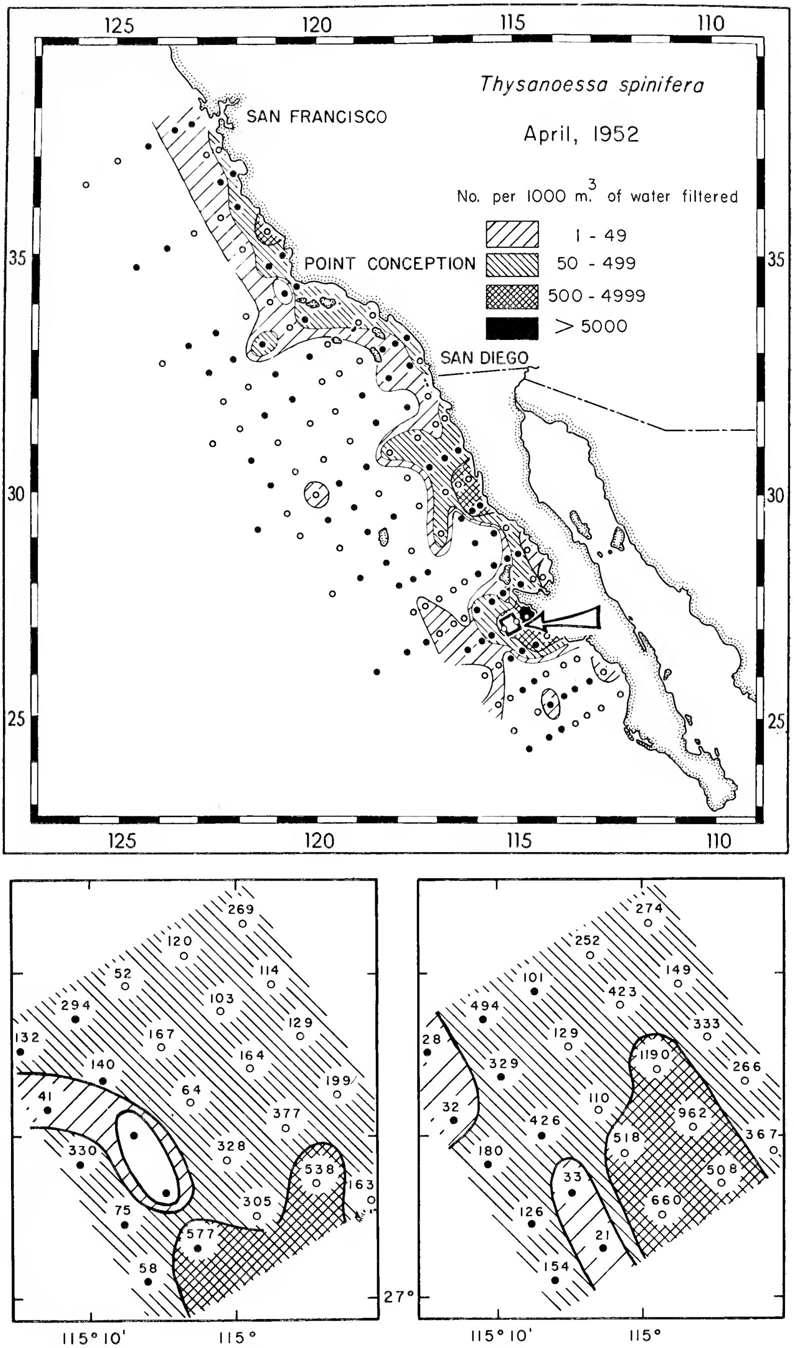
N. simplex. Grid I, April 18 *N. simplex.* Grid II, April 19

FIG. 19. *Nyctiphanes simplex,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.



E. eximia, Grid I, April 18 *E. eximia*, Grid II, April 19

FIG. 20. *Euphausia eximia*, Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.



T. spinifera. Grid I, April 18

T. spinifera. Grid II, April 19

FIG. 21. *Thysanoessa spinifera,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.

4.1 larvae in a 1-m net sample. More often the values differed by factors smaller than 3.0.

Adults of the large *Euphausia* species, *E. diomediae,* appeared to be more numerous when sampled by the 1-m net than by the 45-cm net. Adults of the other species, generally low in concentration, were not consistently better sampled by either type of net.

In 21 instances the estimated concentration interval for the total count of a species differed between the two samples (using intervals of 1–49, 50–499, 500–4,999, > 5,000 per 1000 m^3). In 86 instances the interval was the same.

On 41 occasions both samples were negative for a species listed in Table 6 (these accounted for all but 4 of the instances in which the density of a species measured by the 45-cm net was equal to the density measured by the 1-m net); on 98 occasions both samples were positive (Table 7).

Eight stations were positive for a species on the basis of the 1-m net sample and negative on the basis of the 45-cm net sample: *Euphausia diomediae* (1 sta.), *E. paragibba* (1 sta.), *Nematoscelis microps* (1 sta.), *N. tenella* (1 sta.), *Thysanopoda monacantha* (4 sta.). *T. monacantha* was present only in the 45-cm net sample at two stations and *Stylocheiron abbreviatum* at one station. It is evident, therefore, that in terms of presence and absence the two nets did not clearly differ in sampling.

The total euphausiid concentrations at each station (all species summed), determined by the two samples, differed by maximum factors of 1.89 and 1.94. At 8 of the 10 stations the total euphausiid concentration based upon the 45-cm net sample was larger. This was related to the greater number of furcilia larvae retained by the fine-mesh net.

The numbers of adults, juveniles, and furcilia larvae, totalled for all of the euphausiid species caught by each type of net, were as follows:

	45-CM NET	1-M NET	RATIO
Adults	6,716	6,682	1.01 : 1.00
Juveniles	11,780	16,086	0.73 : 1.00
Furcilia larvae	23,362	11,706	2.00 : 1.00
Total	41,858	34,474	1.21 : 1.00

Only the furcilia larvae were sampled in very different concentrations: the 45-cm net with a mesh size of 0.33 mm retained on the average twice as many as the 1-m net. The larger net evidently allowed some furcilia to pass through the meshes, 0.65 mm apart. Though the over-all length of the larva is greater than the mesh width of both nets, larvae with a height or width of 0.33–0.65 mm were more often retained by the small net.

CONCLUSIONS AND SUMMARY

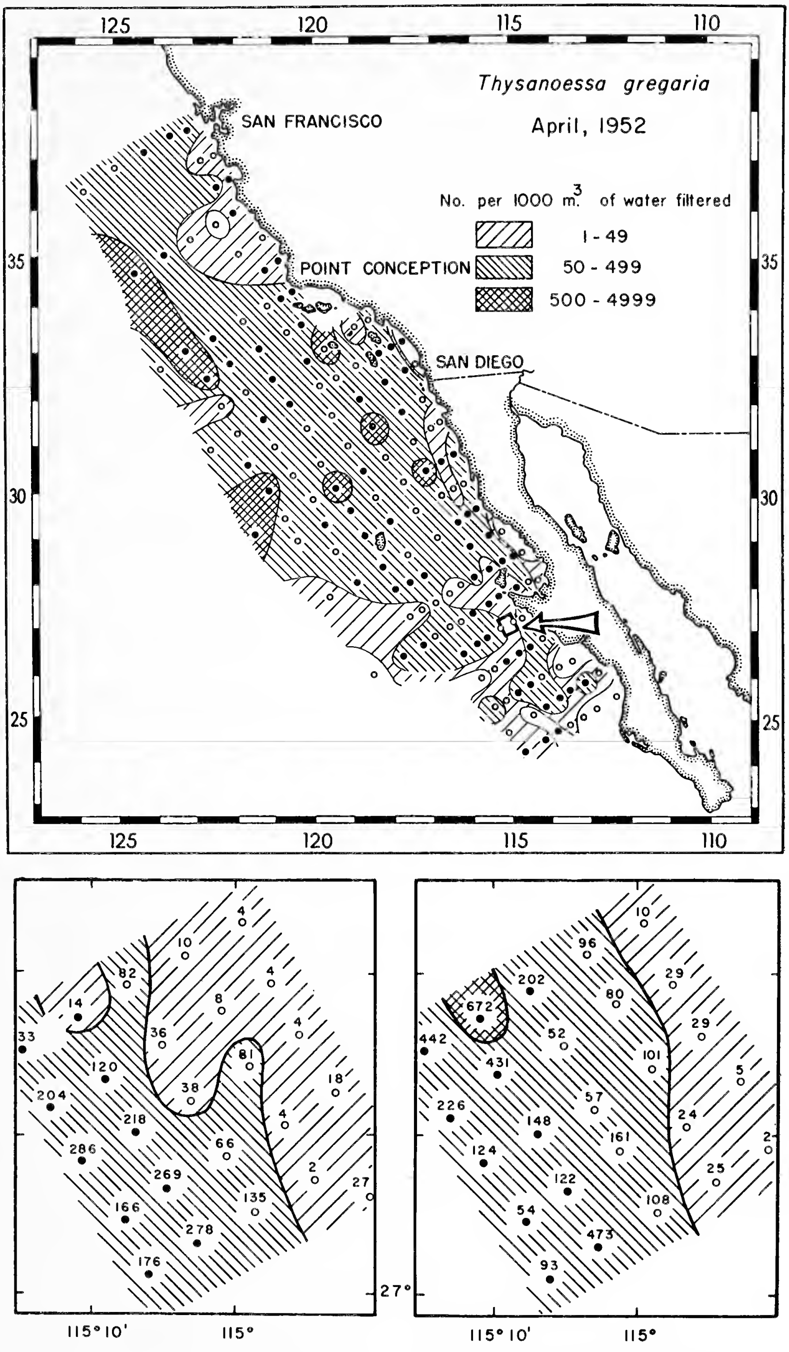
A precise picture of the concentrations of the euphausiid species, with attention to geographical distribution and time variation, can be established only if the effective artificial variables are recognized, and the estimated concentrations corrected. The data included here suggest that a standard basis for such corrections would be difficult to establish.

The qualitative aspect of the counting procedure is accurate. All euphausiid species present in a sample are recorded. An aliquot is counted so that the concentrations of the plentiful species (more than about 25 specimens per 1000 m^3) can be determined. The method of taking aliquots using a graduated cylinder to measure a fraction of the total volume of plankton and fluid was tested for reliability. Replicate counts of three samples indicated that the ali-

TABLE 7

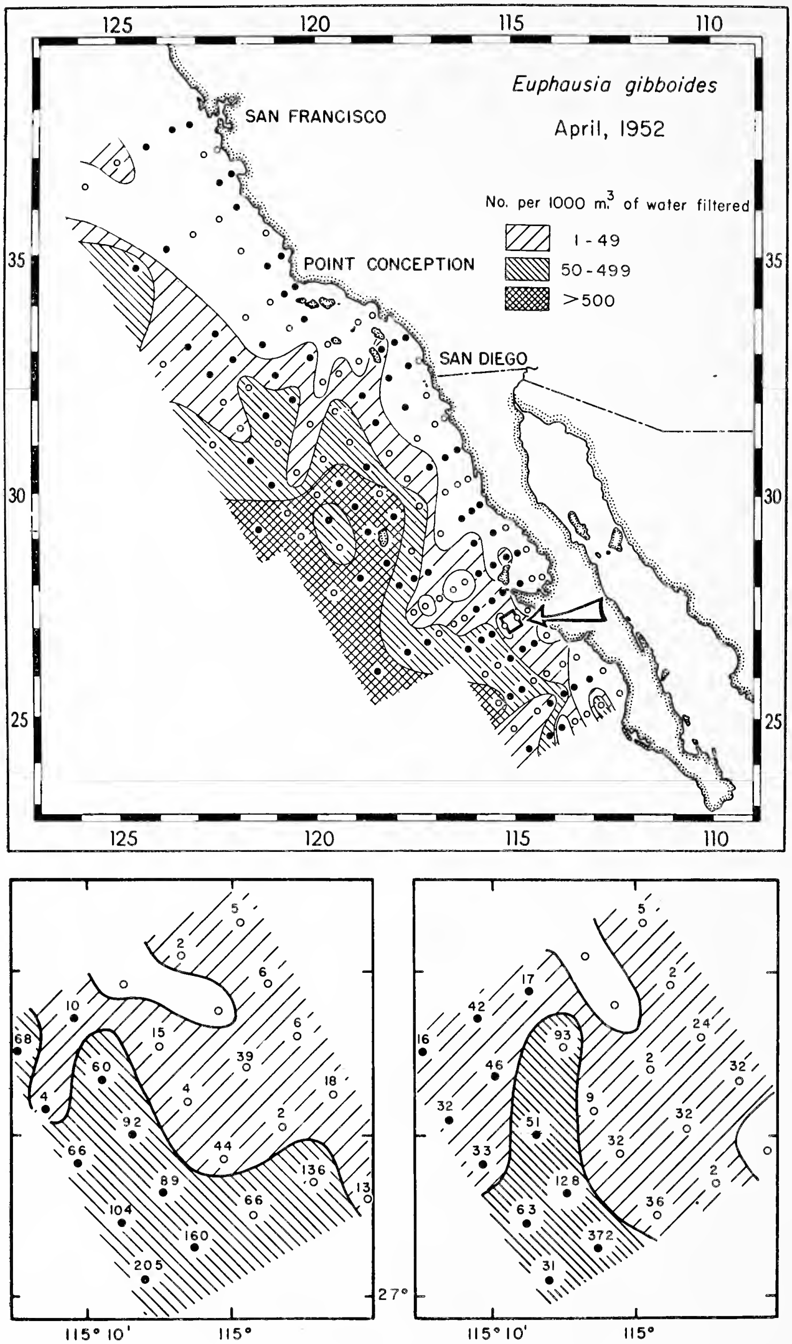
Presence and Absence of Species; 1-m Net Samples Compared With 45-cm Net Samples

		1-M NET		
		Present	Absent	
45-cm net	Present	98	3	101
	Absent	8	41	49
		106	44	150



T. gregaria. Grid I, April 18 *T. gregaria*. Grid II, April 19

FIG. 22. *Thysanoessa gregaria,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.



E. gibboides. Grid I, April 18

E. gibboides. Grid II, April 19

FIG. 23. *Euphausia gibboides,* Apr 1952 (CCOFI Cruise 5204), and two close-grid surveys carried out at the conclusion of the CCOFI cruise. Nighttime station dots are blackened. Daytime stations are open circles. The arrow on the upper chart indicates the area of the close-grid survey.

quots were obtained in a random manner and provided reliable estimates of species composition and concentration.

The catching ability of the standard 1-m net (mesh width of 0.65 mm) did not differ greatly from that of a smaller net, constructed of material with a mesh width of 0.33 mm. As great or greater numbers of adult and juvenile euphausiids were taken by the larger net of coarser mesh, but about twice as many furcilia larvae, which made up a large proportion of the total population, were obtained by the 45-cm net.

The "Equapac" collections established that the 45-cm net samples, filtering 66–99 m^3 of water, were almost as complete with respect to the number of species present as those taken by the 1-m net. The latter filtered a volume of water five times as great. Both nets sampled obliquely to a depth of 140 m, integrating the catch across a horizontal distance of about 1 mile.

Populations that are patchy between the horizontal extremes of the oblique towing distance will not be sampled as adequately by single vertical hauls as by single oblique tows. Numbers fluctuated in an erratic way in the samples taken at anchor station 72.60 by vertical hauls. Diurnal periodicity in numbers of the cool-water species was observed at the offshore anchor stations 70.90 and 70.130 (Figs. 9, 11). The warm-water species (Fig. 12) were consistent within the 1–49 concentration interval and, except for *Stylocheiron abbreviatum,* did not show diurnal peaks. The difference between stations may be due to (1) the relatively smaller amount of water filtered by the vertical hauls at station 72.60, and (2) irregular fluctuations in current speed and direction at the near-shore locality. The time-concentration series at anchor stations 70.90, 70.130, and at the Baja California anchor and buoy stations (Fig. 15) indicated that most concentrations were constant and were representatively sampled.

All species at station 70.130 were uniform in estimated numbers or in their diurnal period of availability during the 8-day sampling period. Similarly, at station 70.90, only *Nematoscelis difficilis* and *Euphausia pacifica* underwent real changes in concentration during the 8-day sampling period. The former species replaced the latter in dominance.

Euphausiid species showing no significant density change, or showing a regular change with a diurnal period, were either (1) homogeneously distributed in a segment of the current stream, at least 50–100 miles long, that passed the ship during the time the station was occupied, or (2) relatively stationary at the anchor station locality. Species that underwent gradual concentration changes of nondiurnal period were either carried from different parts of their distributional ranges, across which there were concentration gradients, or were changed locally in apparent numbers as the mean depth of the population changed. A mechanism for replacement can be seen in the differential lateral movement of species in relation to each other, owing to differences in their vertical ranges. Species having similar vertical ranges remain longer in association with each other than those having dissimilar vertical ranges. The latter may be transported in different directions horizontally. For example, *Thysanoessa gregaria* and *Nematobrachion flexipes* at station 70.90 remained in association with each other, but not with *Nematoscelis difficilis* and *Euphausia pacifica,* the numbers of which increased and decreased respectively.

Data from the grid–buoy–anchor station survey off Baja California agreed with the data from the central California anchor station 72.60, in that the 24-hr periodicity in concentration was *least* where larval euphausiids were dominant, and *most* where juveniles and adults were numerous. The central populations found at anchor station 70.130, composed mainly of larvae and postlarvae, showed little 24-hr fluctuation in the 0–140-m layer.

Populations of larvae and postlarvae sampled from a vessel following a drogue which drifted with the current at a depth of 10 m, were little, if at all, more constant in numbers during the 5-day period than those sampled at the anchor station, a fixed geographical locality. Only *Nyctiphanes simplex* changed extremely in concentration at the anchor station but not at the drift buoy. Diurnal periodicity, not evident at the anchor station, was found for the three most numerous species in the samples taken at the drift buoy after the second day, when the course of the buoy changed.

Concentrations of species sampled by the grid surveys showed agreement with concentrations at the concurrent anchor station. Species boundaries and concentration intervals were in close agreement with the generalized boundaries and concentration intervals determined from the Apr 1952, CCOFI Cruise, which was followed by the Punta Eugenia survey. The determination of the distributions of some species, notably *Euphausia recurva* and *Stylocheiron affine,* was to a considerable extent dependent at their southern limits upon the presence of night stations.

Distribution patterns plotted on the scale of the California Current or the entire North Pacific appeared discrete, notwithstanding the inconsistency in the time of day of sampling. Distributions based upon sampling to a depth of 280 m (Figs. 2, 3) were less patchy than those based on sampling to 140 m.

Nevertheless, the species distributions plotted for the CCOFI survey region on the basis of the 0–140-m samples show some regions of high density that are based on day stations, and some regions of low density based on night stations. Of the stations shown (Figs. 1, 16–23) at which the concentration of a species was greater than 50 per 1000 m^3, only 346 out of a total of 603 (57.4%) were occupied at night (twilight to dawn).

REFERENCES

AHLSTROM, E. H. 1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. U.S. Fish and Wildlife Serv. Spec. Sci. Rept. 54: 1–76.

BAKER, A. DE C. 1959. Distribution and life history of *Euphausia triacantha* Holt and Tattersall. "Discovery" Repts. 29: 309–340.

BARY, B. M. 1959. Species of zooplankton as a means of identifying different surface waters and demonstrating their movements and mixing. Pacif. Sci. 13(1): 14–54.

BIERI, R. 1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. Limnology and Oceanog. 4(1): 1–28.

CUSHING, D. H. 1953. Studies on plankton populations. J. du Conseil 19(1): 1–22.

DAVID, P. M. 1958. The distribution of the Chaetognatha of the Southern Ocean. "Discovery" Repts. 29: 199–228.

GLOVER, R. S. 1952. Continuous plankton records: The Euphausiacea of the north-eastern Atlantic and the North Sea, 1946–1948. Hull Bull. Mar. Ecol. 3(23): 185–214.

——— 1957. An ecological survey of the driftnet herring fishery off the north-east coast of Scotland, Part II. The planktonic environment of the herring. Bull. Mar. Ecol. 5(39): 1–43.

JOHNSON, M. W. 1953. Some outlines of plankton concentration in the eastern and tropical Pacific. 8th Pac. Sci. Congress of Pac. Sci. Ass. Oceanogr. Proc. 3: 379–390.

——— 1956. The plankton of the Beaufort and Chuckchi Sea areas of the Arctic and its relation to the hydrography. Arctic Inst. North Amer. Tech. Pap. 1: 1–132.

KING, J. E., and J. DEMOND. 1953. Zooplankton abundance in the central Pacific. U.S. Fish and Wildlife Serv. Fish. Bull. 54(82): 111–144.

LEAVITT, B. B. 1938. The quantitative vertical distribution of macrozooplankton in the Atlantic Ocean basin. Biol. Bull. 74(3): 376–394.

MCEWEN, G. F., M. W. JOHNSON, and T. R. FOLSOM. 1954. A statistical analysis of the performance of the Folsom plankton splitter, based upon test observations. Arch. Met. Geophysik Bioklimatol., series A, vol. 7.

SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING. 1942. The Oceans, Their Physics, Chemistry, and General Biology. Prentice-Hall, Inc., New York. 1,087 pp.

THRAILKILL, J. R. 1957. Zooplankton volumes off the Pacific Coast, 1956. U.S. Fish and Wildlife Serv. Spec. Sci. Rept. Fish. 232: 1–50.

UNIVERSITY OF CALIFORNIA, Scripps Institution of Oceanography, 1952. Ref. 52–37.

Revision of the Genus *Pandanus* Stickman, Part 13
Pandanus in the Northern Territory, Australia

HAROLD ST. JOHN[1]

IN PREVIOUS LITERATURE there have been but few species of *Pandanus* reported for the Northern Territory, Australia. These were *P. spiralis* R. Br., *P. de-Lestangii* Martelli, *P. Basedowii* C. H. Wright, *P. Whitei* Martelli, and *P. Solms-Laubachii* F. Muell.

The first, *P. spiralis* R. Br., was described from the type collection made on the Wellesley Group, Island Bay, Gulf of Carpentaria, in Queensland. Later collections to match it have not been seen, and all those so labeled from the Northern Territory seem to be misdetermined.

The second, *P. de-Lestangii* Martelli, is well known from its type locality on the Gregory River, which flows into the Gulf of Carpentaria in northwest Queensland. A recent collection of a similar plant from Arnhem Land is here described as new. Records of *P. de-Lestangii* (under the name *P. aquaticus* F. Muell.) pub-

KEY TO SPECIES

- Carpels 1–2, (section *Microstigma*),
  - Drupes 3.9–4.4 cm long, 8–12 mm wide, narrowly oblanceoloid; (stigmas when 2 approximate); leaves 3.9–4.5 cm wide……1. *P. Spechtii*
  - Drupes 4.3–6.4 cm long, 3.1–5.5 cm wide, suborbicular-pyriform; (stigmas when 2 remote); leaves 1–3.9 cm wide……5. *P. Basedowii*
- Carpels 7–20; phalange apex convex,
  - Intercarpellary apical sinuses 0–0.5 mm deep, mostly merely a tessellate marking, (section *Eydouxia*),
    - Phalange sides rounded and smooth; stigmas 3–4 mm long……4. *P. integer*
    - Phalange sides with numerous longitudinal valleys and rounded ridges; stigmas 1–2.5 mm long……2. *P. arnhemensis*
  - Intercarpellary apical sinuses 1.5–12 mm deep, conspicuous,
    - Phalanges 5–6.3 cm long, the apex mostly low convex; central apical sinuses 1.5–7 mm deep,
      - Phalanges 5.9–6.3 cm long, the apex rounded convex; stigmas 4–5 mm long, (section *Eydouxia*)……3. *P. convexus*
      - Phalanges 5–5.7 cm long; stigmas 1–2 mm long, (section *Pandanus*),
        - Phalange apex low convex; carpels 7–8; central apical sinuses 4–7 mm deep……10. *P. yirrkalaensis*
        - Phalange apex semiorbicular; carpels 12–20; central apical sinuses 3–4 mm deep……7. *P. latifructus*
    - Phalanges 6.5–7.7 cm long, (section *Pandanus*),
      - Phalanges 6.5–6.8 cm long, the apex truncate or subtruncate; carpel sides smooth and gently convex; central apical sinuses 1–3 mm deep; leaf apex unarmed……8. *P. semiarmatus*
      - Phalanges 7.1–7.7 cm long, the apex semiorbicular; carpel sides with longitudinal ridges and valleys; leaf apex serrulate,
        - Central apical sinuses 2–4.5 mm deep; phalanges 7.1–7.5 cm long; near the base the leaf margins with prickles 4–6 mm long……9. *P. thermalis*
        - Central apical sinuses 7–12 mm deep; phalanges 7.5–7.7 cm long; near the base the leaf margins with prickles 0.3–1.3 mm long……6. *P. darwinensis*

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[1] B. P. Bishop Museum, Honolulu 17, Hawaii, U. S. A. Manuscript received June 28, 1961.

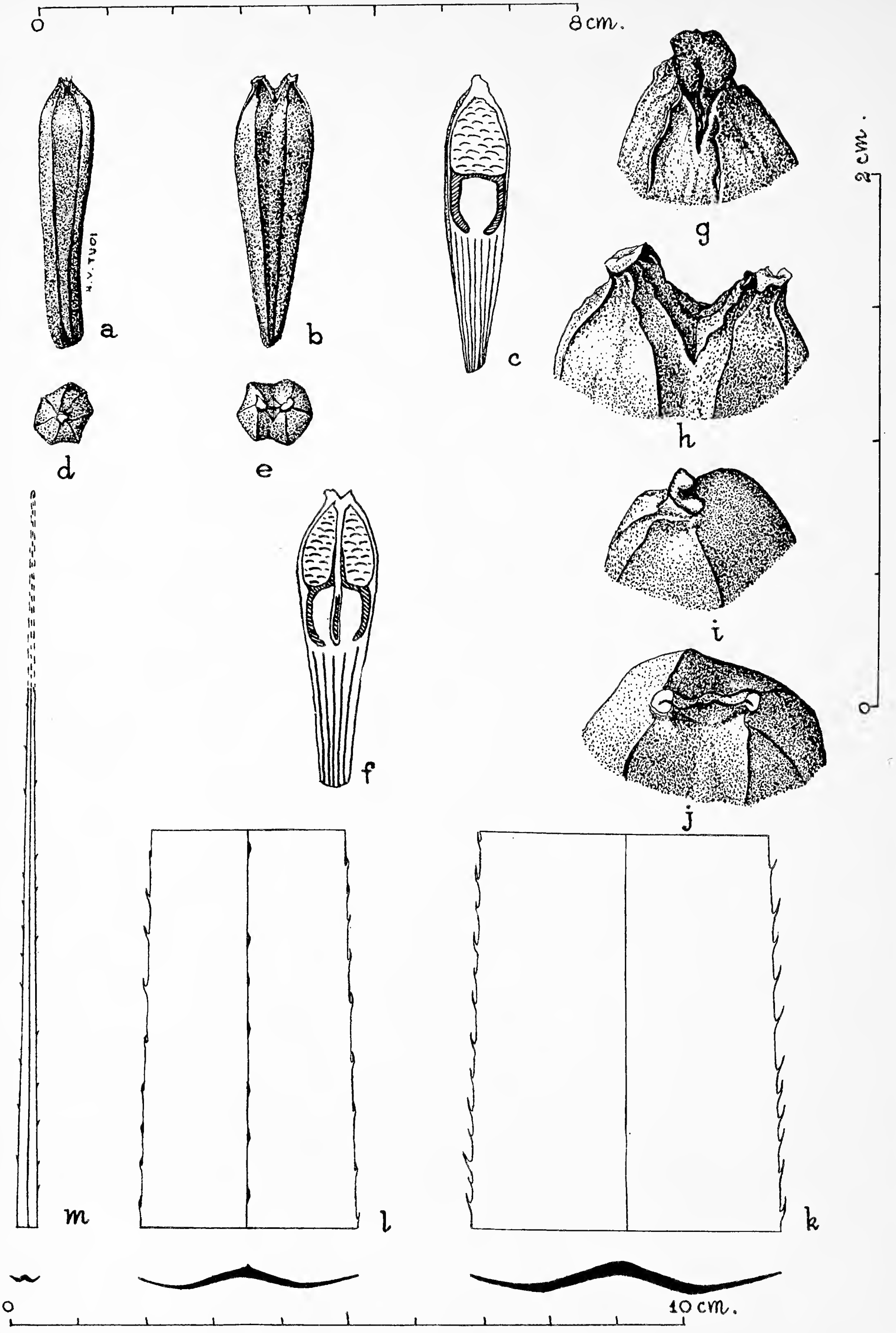

FIG. 139B. *Pandanus Spechtii* St. John, from holotype. *a, b,* Drupes, lateral view, × 1; *c,* drupe, longitudinal median section, × 1; *d, e,* drupes, apical view, × 1; *f,* 2-celled drupe, longitudinal median section, × 1; *g, h, i, j,* carpel apices and stigmas, oblique view, × 4; *k,* leaf base, lower side, × 1; *l,* leaf middle, lower side, × 1; *m,* leaf apex, lower side, × 1.

lished by Blake (1954: 130) indicate its occurrence from the Gregory River, Queensland, to the Daly River, Northern Territory. The specimens so determined from the Katherine River and from the Daly River are now placed in *P. Spechtii* St. John.

The report by Martelli (1933: 24) of the Queensland species *P. Whitei* Martelli from Darwin, is now to be discounted, as this collection by Allen is here described as the new *P. darwinensis* St. John.

P. Solms-Laubachii F. Muell. was based on type material from the Endeavour River, north Queensland, collected by Persich. With this, Warburg (1900: 46) identified the collection, Fr. Shultz 613, from Nord-Australien. This locality may have been in the Northern Territory or in Queensland. No material identical with this species has been seen by the writer from the Northern Territory. The Schultz specimen was doubtless in the Berlin herbarium, but its classification has not been verified. For the present, the record of *P. Solms-Laubachii* for the Northern Territory is to be considered doubtful.

With the benefit of more collections and study, there can now be recorded for the Northern Territory 10 species. They occur at localities all the way from the eastern to the western borders, but mostly near the northern edge of the continent, especially in Arnhem Land. Only in the southwestern part, in the Kimberley district, does the genus approach the southern boundary of the territory. Here occurs *P. convexus* St. John, and it crosses the boundary and is also found in Western Australia.

Of special interest is *P. Basedowii* C. H. Wright. This occurs along valley bluffs in the interior of Arnhem Land in very arid habitats. The phalanges are from 4.3 to 6.4 cm long, suborbicular pyriform. The great part of their contents is of dry, medullary pith, and in consequence, these large phalanges weigh ½ ounce or less apiece. It is thought that wind is the principal agent for their seed dispersal.

1. ***Pandanus Spechtii*** sp. nov. (sect. *Microstigma*)

Figs. 139B, 140

DIAGNOSIS HOLOTYPI: Arbor 4 m alta 15 cm diametro, cortice griseo-brunneo exlaevibus et in parte 60 cm infera cum spinulis [radicillis adventiviis], cum radicibus fulturosis, foliis 1.04–1.27 m longis 3.9–4.5 cm latis coriaceis supra midnervum late 1-sulcatis 2-plicatis in sectione mediali cum 43 nervis parallelis secundariis in quoque medio in tertia infera nervis tertialis conspicuis et oblongis longis formantibus, lamina gladiformati et ex basi sensim in apice trigono subulato diminuenti eo in puncto 10 cm ex apice 3.5 mm lato, basi amplexicauli et inermi sed ex 6–7 cm marginibus cum aculeis 1–2.5 mm longis 2–8 mm separatis subulatis subrectis adscendentibus apicibus rubris, midnervo infra ex 20 cm cum aculeis 2 mm longis 12–15 mm separatis acicularibus valde adpressi-adscendentibus rubris, in sectione mediali marginibus cum aculeis 1.5–3 mm longis 6–12 mm separatis subulatis valde adpresse adscendentibus, midnervo infra angusto salienti cum aculeis simulantibus 2.5–3 mm longis 8–16 mm separatis, proxima apicem marginibus et midnervo infra cum serrulis 0.2–0.3 mm longis 5–15 mm separatis brunneis, syncarpio in pedunculo folioso, syncarpio 18 cm diametro subgloboso, drupis multis 39–44 mm longis eis 1-carpellatis numerosis 8–11 mm latis 6–9 mm crassis lineari-oblanceoloideis parte ¼ supera libera 5–6-angulosa lateribus laevibus subcurvatis sublucidis apice pyramidali sed obliquo, drupis 2-carpellatis paucis simulantibus sed 10–12 mm latis apice bilobato sinu 2 mm profundo sed in parte grandi cum stigmate occupato, stigmate 1.5–2 mm longo late ellipsoideo vel obovato sulcato papilloso obscure brunneo terminali vel obliquo quando 2 centripetali, endocarpio minime supramediali 9 mm longo osseoso mahogani-colorato apice subtruncato lateribus lateralibus 1 mm crassis intra lucidis, semine 6 mm diametro doliformato, mesocarpio apicali ellipsoideo infra truncato cum membranis transversis fortibus pallidis multis, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 4–6 m tall, with or without stilt roots; trunk 15 cm in diameter; bark gray-brown and rough with leaf scars, and on the lower 60 cm with short needle growths [adventitious rootlets] from the scars; leaves 1.04–1.3 m long, 3.9–5 cm wide, coriaceous, broadly channeled above the midrib, with 2 lateral pleats, at midsection with 43 secondary veins on each side, in the

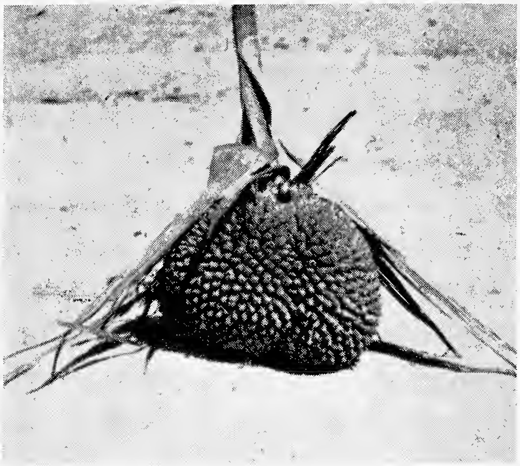

FIG. 140. *Pandanus Spechtii* St. John, from holotype. Syncarp, lateral view. Photo by R. L. Specht.

lower third on both sides the tertiary cross veins conspicuous, forming elongate, oblong meshes, blade swordlike and from the base gradually tapering to the subulate, trigonous apex, this at the point 10 cm down 3.5 mm wide, the base amplexicaul and unarmed, but beginning 6–7 cm up the margins with prickles 1-2.5 mm long, 2–8 mm apart, subulate, nearly straight, ascending, red-tipped; the midrib below unarmed for 20 cm, then with prickles 2 mm long, 12–15 mm apart, acicular, closely appressed ascending, red; at midsection the margins with prickles 1.5–3 mm long, 6–12 mm apart, subulate, closely appressed ascending; the midrib below narrow, salient, with similar prickles 2.5–3 mm long, 8–16 mm apart; near the apex the margins and midrib below with serrulations 0.2–0.3 mm long, 5–15 mm apart, brownish; syncarp borne on a leafy peduncle; syncarp about 15–18 cm in diameter, subglobose; drupes numerous, 39–44 mm long, the abundant 1-celled ones 8–14 mm wide, 6–12 mm thick, linear-oblanceoloid, upper ¼ free, 5–6-angled, the sides smooth, gently curving, somewhat shiny, the apex pyramidal but the actual summit oblique; the infrequent 2-celled drupes similar, but 10–18 mm wide, the apex bilobed, the cleft 2 mm deep, but most of it occupied by the stigmas; stigma 1.5–2 mm long, broadly ellipsoid to obovate, creased, papillose, dark brown, terminal or oblique from the summit, when 2 centripetal; endocarp slightly supramedian, 9 mm long, bony, mahogany-colored, the apex subtruncate, the lateral walls 1 mm thick, the inner surface shining; seed 6 mm in diameter, barrel-shaped; apical mesocarp ellipsoid, truncate below, with numerous strong, transverse, pale membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Northern Territory, Arnhem Land, Oenpelli (12° 18′ S. lat., 133° 4′ E. long.), along stream at foot of sandstone scarp, 2 Oct. 1948, *R. L. Specht 1,120* (BRI). Isotypes: (AD, Lae, SYD).

SPECIMENS EXAMINED: Northern Territory: Katherine, sandy bank of Katherine River, 100 m alt., 23 June 1946, *S. T. Blake 16,085* (BRI); Daly River, 14° 5′ S., 131° 15′ E., close to edge of water (dry season), 1 July 1946, *S. T. Blake 16,256* (BRI).

DISCUSSION: *P. Spechtii* is a member of the section *Microstigma,* as is its closest relative, the Australian species *P. de-Lestangii* Martelli, which species has the drupes 31–35 mm long; endocarp supramedian, leaves 1.8–2.7 m long, near the base 7.5–8 cm wide, at midsection with 62 secondary parallel veins in each half, near the base the margins with prickles 2.5–3.5 mm long, 5–12 mm apart, arcuate subulate. *P. Spechtii* has the drupes 39–44 mm long; endocarp median; leaves 1.04–1.27 m long, near the base 3.9–4.5 cm wide, at midsection with 43 secondary parallel veins in each half, near the base the margins with prickles 1–2.5 mm long, 2–8 mm apart, subulate, nearly straight.

This new species is named in honor of Prof. Raymond Louis Specht of the University of Melbourne, who made noteworthy collections of *Pandanus* while on the Arnhem Land Expedition in 1948.

2. ***Pandanus arnhemensis*** sp. nov. (sect. *Pandanus*)

Fig. 141

DIAGNOSIS HOLOTYPI: Trunco foliisque incognitis; phalangibus 5–5.4 cm longis 5.3–5.4 cm latis 4.8–4.9 cm crassis quadrato-cuneatis plerumque 5-angulosis suturis lateralibus angustis sed distinctis in parte supera ½ libera, superficie brunneo-stramineo lucido, apice subconvexo, sinibus apicalibus centralibus 0–0.5 mm profundis paene evidentibus, carpello quoque cum

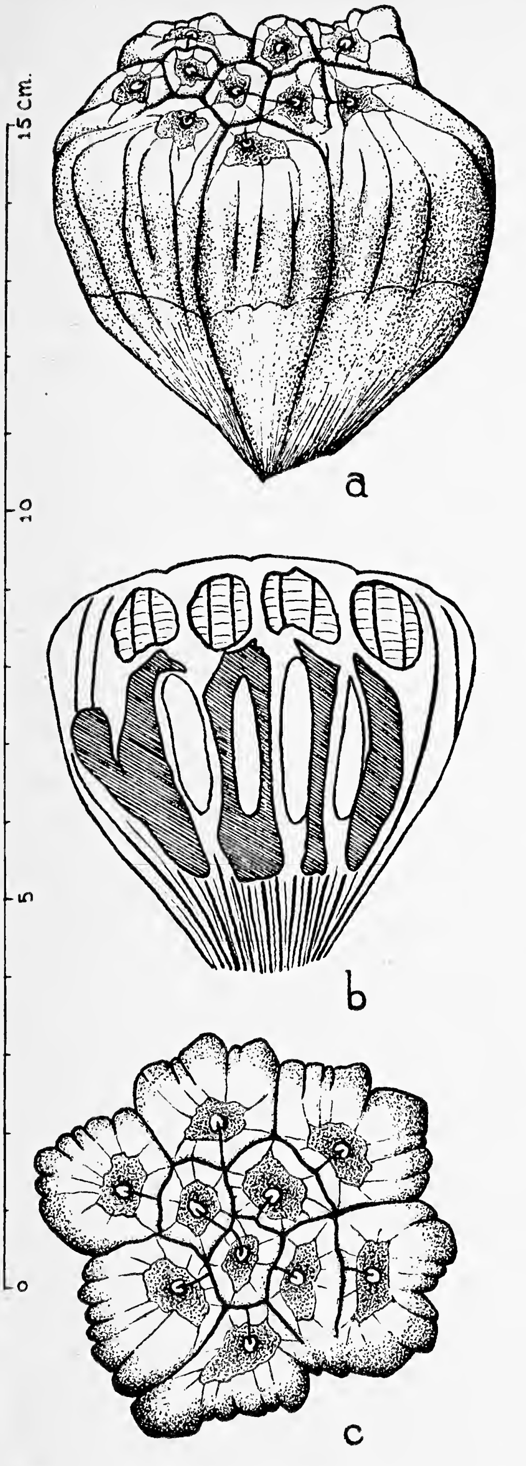

FIG. 141. *Pandanus arnhemensis* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1.

2–6 sulcis angustis deinde phalangibus interobseratis, carpellis 9–10, apicibus carpellarum centralium subconcavis et in eo brunneo-maculatis et frequenter cum fissuris vel dorsis, stigmatibus 1–1.5 mm longis suborbicularibus sulcatis centripetalibus, endocarpio centrali 3.1 cm longo solido osseoso marginibus lateralibus 5–7 mm crassis, seminibus 21 mm longis 4 mm diametro ellipsoideo, mesocarpio apicali in carpello quoque caverna rotundata 8–12 mm longa fibrosa et cum membranis medullosis formanti, mesocarpio basali fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Trunk and leaves unknown; syncarps "about 20 × 12.5 cm., probably ovoid," phalanges 5.1–5.4 cm long, 5.1–5.4 cm wide, 4.6–5 cm thick, quadrate cuneate, mostly 5-angled, the lateral sutures narrow but distinct on upper free half, the surface brownish stramineous, shining, apex low convex, central apical sinuses 0–0.5 mm deep, scarcely evident, each carpel with 2–6 additional narrow furrows so that the adjacent phalanges are mortised; carpels 9–10; apices of central carpels with a central shallow concavity containing a dark brown maculation, often with cracks and swellings; stigmas 1–2.5 mm long, suborbicular, creased, centripetal; endocarp central, 3.1 cm long, massive, bony, brown, the lateral walls 5–7 mm thick; seeds 21 mm long, 4 mm in diameter, ellipsoid; apical mesocarp forming in each carpel a rounded cavern 8–12 mm long, traversed by a few fibers and with medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Northern Territory, Arnhem Land, Yirrkala, 12° 12′ S. lat., 136° 47′ E. long., common along fresh-water stream, Aug. 19, 1948, *R. L. Specht 929C* (AD). This was mixed with *929A and B* which are here described as *P. yirrkalaensis* St. John. There is an isotype in Melbourne.

SPECIMENS EXAMINED: Australia, Northern Territory, Darwin, cult., April 3, 1957, *M. S. Doty* no. *A* (BISH), mixed with no. *B* which is *P. darwinensis* St. John.

DISCUSSION: *P. arnhemensis* is a member of the section *Pandanus.* It finds there its closest relative, *P. truncatus* St. John, also of Australia, but from northern Queensland. It has the phalanges 4.5–5 cm long, 3.1–4.4 cm wide, 2.9–3.3 cm thick; central apical sinuses 3–4 mm deep;

and the carpel apices pyramidal-suborbicular. On the other hand, *P. arnhemensis* has the phalanges 5–5.4 cm long, 5.1–5.4 cm wide, 4.6–5 cm thick; central apical sinuses 0–0.5 mm deep; and the carpel apices low convex or the interior ones with a shallow central concavity.

Eydouxia sect. nov.[2]

Arbores, syncarpiis terminalibus solitariis, phalangibus grandibus apicibus integris convexis latissimis cum stigmatibus sessilibus cordatis vel suborbicularibus centripetalibus aequaliter dispersis, staminibus in columna forti racemosis.

Trees; syncarps terminal, solitary; phalanges large, 7–50-celled, the apex unlobed, very broad convex, with the sessile, flush, cordate or suborbicular stigmas evenly distributed on it, centripetal; stamens racemose on a stout column.

HOLOTYPUS: *Pandanus Eydouxia* Balf. f. in Baker, Fl. Mauritius & Seychelles 401, 1877; Engler's Pflanzenreich IV, 9: 55–56, fig. 15B, 1900; Linn. Soc. Bot. Jour. 55: 21–22, fig. 3F, pl. 2F, 3C, 1953; *Eydouxia macrocarpa* Gaud., Bot. Voy. La Bonite, Atlas pl. 18, figs. 1–6, (1843) = [1841], an invalid name. Gaudichaud's genus contained two species, but no generic description. Other species in this new section are the following, all from Australia: *P. arnhemensis* St. John, *P. convexus* St. John, *P. integer* St. John, and *P. spiralis* R. Br.

3. *Pandanus convexus* St. John, Pacif. Sci. 15(2): 182–184, fig. 10 (repr. pp. 21–23), 1961. (sect. *Eydouxia*)

HOLOTYPE: Western Australia, Dillens Springs, Oct. 1906, *W. F. Fitzgerald 2,394* (SYD).

NORTHERN TERRITORY: Escape Cliffs, *Hulls* [an error for *W. Hulse*], (MEL).

The collector of the specimen from Escape Cliffs was published by Bentham (1878: 149) as Hulls. This was an error. The collector's name was really W. Hulse, as indicated by F. von Mueller (1869: 20).

4. ***Pandanus integer*** sp. nov. (sect. *Eydouxia*) Fig. 142

DIAGNOSIS HOLOTYPI: Arbor, foliis 1.47 m longis 6 cm latis coriaceis infra subglaucis gladiformatis sensim ex basi in apice longe subulato diminuentibus apice 10 cm ex puncto 4 mm lato, in sectione mediali cum 55–58 nervis secundariis in uno latere sed 62–64 in altero, basi amplexicaule integra et inermi sed ex 10 cm marginibus cum aculeis 2.5–3 mm longis 5–9 mm distantibus subulatis adscendentibus brunneis excepta in basi, midnervo infra toto inermi, in sectione mediali et ad apicem marginibus inermibus, phalangibus 5–5.5 cm longis 5–6.2 cm latis 4.8–6 cm crassis late cuneiformis, apice valde convexo parte ½ supera libera, lateribus 4–5-angulosis laevibus lucidis in sicco pallide luteo-brunneis subcurvatis et in aetate cum fissuris longitudinalibus brunneis, suturis lateralibus plerumque nullis, sinibus centralibus apicalibus 0–1 mm profundis plerumque subnullis et suturis solum tessellatis, carpellis 7–10 apicibus subaequalibus sed lateribus inclinatis hinc marginalibus majoribus apparitis, circum stigmatem regione nigro-brunneo lucido folioso, stigmatibus 3–4 mm longis cordatis brunneis intra vel extra subinclinatis sulcatis centripetalibus, suturis proximalibus dimidio distantia ad fondam extentis, endocarpio inframediali solido 34 mm longo osseoso obscure brunneo lateribus 8–9 mm crassis, seminibus 20–23 mm longis 4 mm diametro fusiformibus, mesocarpio apicali in carpello quoque cavernam parvam cum fibris paucis et membranis transversis medullosis formanti, mesocarpio basali minuto sed fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 5–7 m tall, 15 cm in diameter; trunk pale gray; leaves 1.45–1.47 m long, 6 cm wide, cori-

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[2] This new section *Eydouxia* may be inserted in the author's key to the sections (Revision of *Pandanus* Stickman, Part 1, Pacif. Sci. 14(3)) as follows, on page 226 (reprint, p. 3); replacing the first heading T. by:

T. Stigmas 1–50, centripetal, not on a ring,
  d. Stigmas approximate in central area of broad, low convex apex; staminate column fasciate, bearing short, terminal, free filaments, or filaments united ⅙–½ way into groups............*Vinsonia*
  d. Stigmas evenly dispersed over the broad convex apex of the phalange; stamens racemose..*Eydouxia*

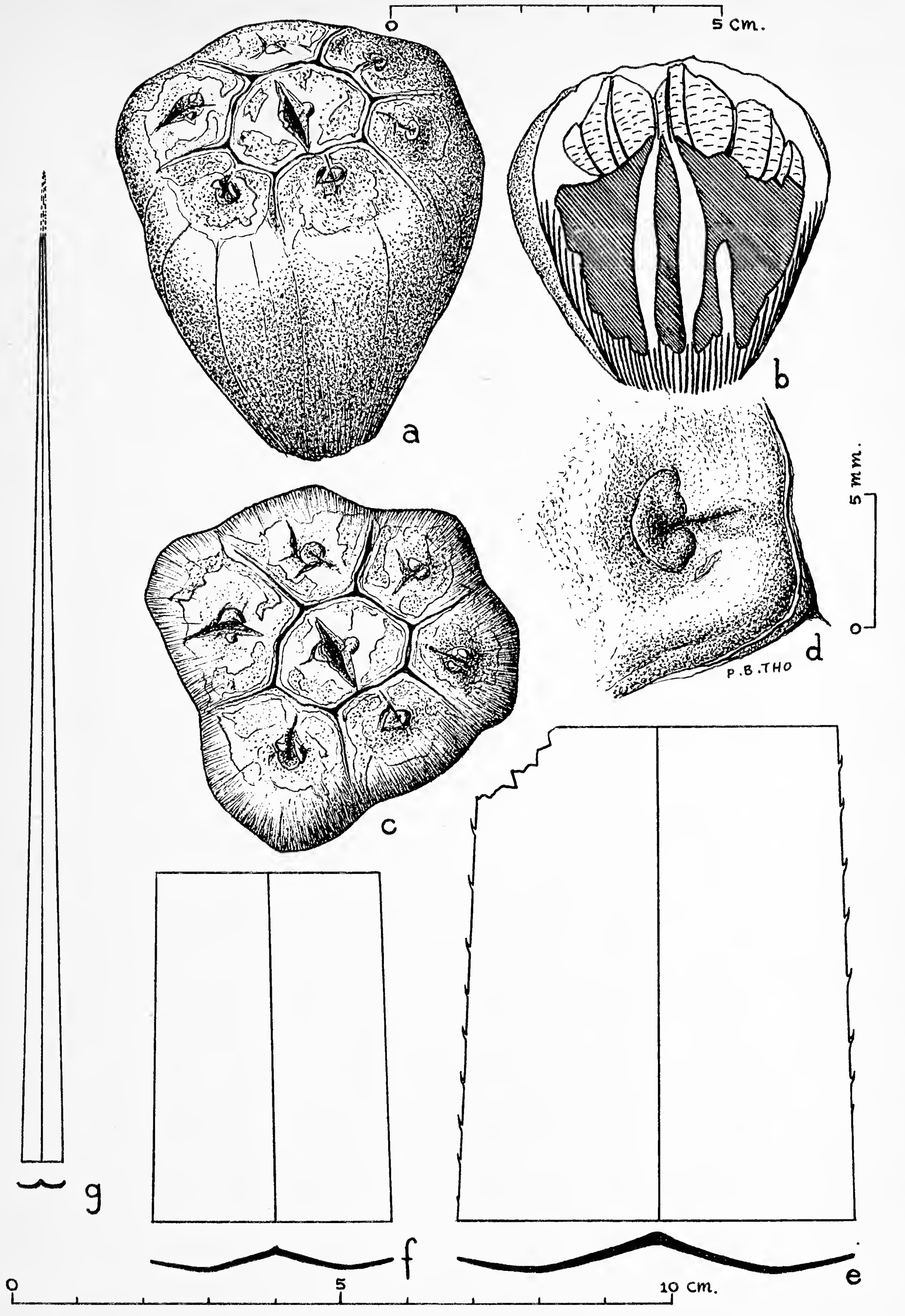


FIG. 142. *Pandanus integer* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, apical view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

aceous, somewhat glaucous below, swordlike, gradually tapering from the base to the long subulate tip which 10 cm down is 4 mm wide, at midsection with 55–58 secondary parallel veins in one half and 62–64 in the other, the base amplexicaul and unarmed, but beginning 10 cm up the margins with prickles 2.5–3 mm long, 5–9 mm apart, subulate, ascending, brown except at base; the midrib below unarmed throughout; at the midsection and from there to the apex the margins unarmed; peduncles 30–45 cm long; syncarp 22 cm long, 15 cm in diameter; phalanges 5–6.5 cm long, 5–7 cm wide, 4.3–6 cm thick, broad cuneiform, the apex strongly convex, upper ½ free, the sides 4–5-angled, smooth, shining, when dry pale yellowish brown, gently curved, developing brown longitudinal cracks; lateral sutures mostly none; central apical sinuses 0–1.5 mm deep, usually so shallow as to be scarcely perceptible and the sutures making a dark tessellate pattern; carpels 6–10, the apices subequal, though the sloping sides make the marginal ones somewhat the larger and with a distal concavity forming about half of the apex and being darker brown and more shiny in a leaflike area surrounding the stigma; stigma 3–4 mm long, cordate, brown, slightly inclined inward or outward, sulcate, centripetal; proximal sinus running from halfway to all the way to the valley bottom; endocarp inframedian, massive, 34 mm long, bony, dark brown, the lateral walls 8–9 mm thick; seeds 20–23 mm long, 4 mm in diameter, fusiform; apical mesocarp forming in each carpel apex a small cavern with a few fibers and white, delicate transverse medullary membranes; basal mesocarp minute, but fibrous and fleshy.

HOLOTYPUS: Australia, Northern Territory, 20 miles s.w. of Leguna Station, alluvial deep sandy yellow podsol with *Eucalyptus polycarpa* and *Banksia* sp., July 28, 1949, *R. A. Perry 2,630* (BRI).

SPECIMENS EXAMINED: Australia, Northern Territory, 20 miles s. of Victoria River Downs Station, near creek, June 12, 1949, *R. A. Perry 2,141* (BRI); 12 miles n.e. of Leopold Downs Station, common on levee of creek near semipermanent spring with *Eucalyptus papuana* and *Dicanthium fecundum,* 10 Sept. 1959, *M. Lazarides 6,521* (BRI).

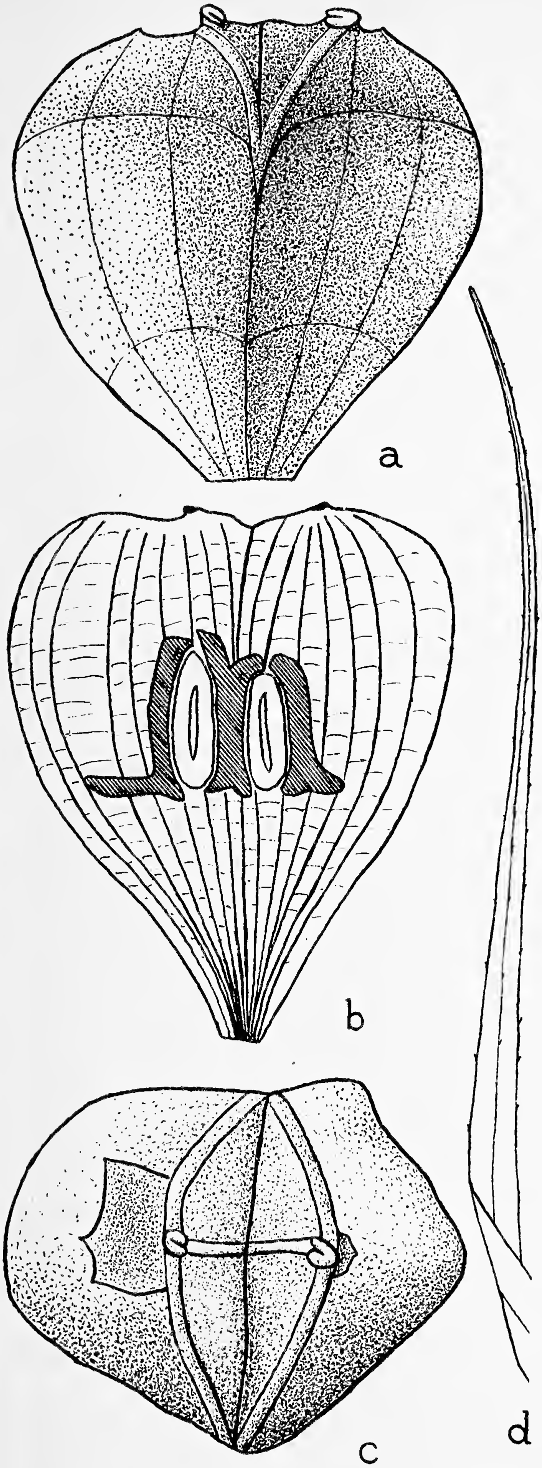
DISCUSSION: *P. integer* is a member of the section *Eydouxia,* and in that section is its closest relative, *P. convexus* St. John, of Western Australia. The latter species has the phalanges 5.9–6.3 cm long, broad cuneate, the upper ⅓ free; central apical sinuses 1.5–3 mm deep; and the stigmas 4–5 mm long. *P. integer* has the phalanges 5–5.5 cm long, turbinate, the upper half free; central apical sinuses 0–1.5 mm deep, wholly or partly lacking; and the stigmas 3–4 mm long.

The new epithet is the Latin adjective *integer,* entire, given because so much of the leaf margin is smooth, lacking prickles.

5. *Pandanus Basedowii* C. H. Wright, Kew Bul. 158–159, pl. 6 (habitat), 1930; S. T. Blake, Austral. Jour. Bot. 2(1): 130, pl. 7, fig. 4, 1954, (sect. *Microstigma*)
Fig. 143

HOLOTYPE: Australia, Arnhem Land, high tablelands, ca. 310 m. alt., *Basedow* (not seen). The type locality was probably to the eastward of the East Alligator River and the head of the Liverpool River (*fide* S. T. Blake).

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 3–5 m tall; prop roots present; crown broad; branchlets 0.5–3 m long, 2.5 cm in diameter; leaves 30–67.5 cm long, 1–4.6 cm wide, ligulate, at midsection with 42–54 secondary parallel veins in each half, long tapering to a subulate apex, firm, the tip at 10 cm down only 5 mm wide, at 20 cm only 14 mm wide, the base amplexicaul, the midrib below armed sometimes 7 cm from the base with a few slender prickles 2 mm long, 6–8 mm apart, subulate, reflexed, near the middle with slender subulate prickles 2.5 mm long, 8–20 mm apart, reflexed or ascending, and then near the apex with spines 0.2 mm long, 10–15 mm apart, appressed ascending, brown; the margins beginning at 3 cm up with prickles 1–2 mm long, 3–20 mm apart, ascending, dark brown; at the midsection the margins with prickles 1–2 mm long, 8–20 mm apart, closely appressed ascending, brown; near the apex the margins with serrulations 0.1–0.2 mm long, 6–10 mm apart, ascending, brown, or wanting; pistillate heads terminal, solitary; peduncle 10 cm long, 10 mm in diameter, trigonous, few bracted except for the numerous



terminal bracts, these green, 15–30 cm long, 15–28 mm wide, long acuminate, the margins acicular serrulate, the teeth 0.3–1 mm long; syncarps globular, about 20 cm in diameter, bearing 8–13 phalanges; the phalanges 4.3–6.4 cm long, 3.1–5.5 cm wide, 2.6–5.6 cm thick, suborbicular pyriform, a little compressed, obtusely 4–5-angled, pale brown or stramineous when dried, lateral sutures none, sides smooth, convex, apex convex, but when 2-carpellate with a shallow concavity distal of the stigmas, and arcuate ridges running to each lateral suture, proximal sinus running to the valley bottom, a whole phalange weighing ½ ounce or less, well rounded "and could easily be dispersed by the wind" (*fide* Wright, 1930: 159), about one-third of the phalanges 1-celled; central apical sinus superficial, level with the stigmatic base; carpel apices low convex, mostly with a quadrangular concavity distal of the stigma; stigmas 3–3.5 mm long, suborbicular to cordate, creased, oblique; endocarp bony, 2 cm long, with basal horizontal flanges, the lateral walls 2–3 mm thick; seeds 15–18 mm long, 5 mm in diameter, ellipsoid; apical and basal mesocarps extensive, continuous, with longitudinal fibers and light medullary pith, the basal fleshy part only 1 cm long.

SPECIMENS EXAMINED: Australia: Northern Territory, Oenpelli, near dry watercourse on sandstone scarp, Oct. 1, 1948, *R. L. Specht 1,106* (AD, SYD); Northern Territory, Cannon Hill, about 12° 24′ S., 132° 55′ E., exposed rocky slopes, on cliffs, 2 Oct. 1946, *S. T. Blake 17,134* (BRI).

6. ***Pandanus darwinensis*** sp. nov. (sect. *Pandanus*)

Figs. 144–145

DIAGNOSIS HOLOTYPI: Foliis 92–135 cm longis 5.5–6 cm latis subcoriaceis in sectio M-formatis ligulatis fere ex basi in apice subulato sensim diminuentibus apice 10 cm ex puncto 10 mm lato, in sectione mediali cum 68 nervis secundariis parallelis in quoque latere, basi amplexicaule et integra sed ex 14–15 cm mar-

FIG. 143. *Pandanus Basedowii* C. H. Wright, from Oenpelli, *R. L. Specht 1,106*. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* leaf apex, lower side, × 1.

ginibus cum aculeis 0.3–1.3 mm longis 3–8 mm distantibus adscendentibus arcuato-subulatis punctis brunneis, midnervo omnino inerme, in sectione mediali marginibus cum serris 0.5–1 mm longis 3–7 mm distantibus, circa apicem marginibus cum serris umbonatis 0.1–0.2 mm longis 1.5–3 mm distantibus, phalangibus 7.5–7.7 cm longis 6.2–7.5 cm latis 6–6.7 cm crassis obovoideo-suborbicularibus in sicco pallide brunneis, summo dense minute punctato, lateribus cum 5–6 angulis majoribus et carpello quoque cum 5–8 dorsis acutis et valleculis angustis et igitur phalangibus proximis interobseratis, parte ½ supera libera, apice semiorbiculari, suturis lateralibus angustis sed profundis et ad basem extentis, sinibus centralibus apicalibus 7–12 mm profundis latis cum in fundo V-formato contractis, carpellis 11–13 subaequalibus apicibus centralibus semiorbicularibus vel ellipsoideo-semiorbicularibus pluri-angulosis, sinibus sinuatis, apicibus carpellorum marginalium obliquiter semiorbicularibus 6–8 mm altis valde angulosis sed latere exteriore oblique truncato, stigmatibus 3–3.5 mm longis suborbicularibus vel obdeltoideis sulcatis vel lobatis obliquis centripetalibus, sinu proximo profundo ¼–⅕ ad fondam extento, endocarpio maximo 4.5 cm longo osseoso albo sed cavernis seminiferis brunneis lucidis, lateribus exterioribus 8–10 mm crassis, seminibus 3.5–4 cm longis 5 mm diametro ellipsoideis, mesocarpio apicali in carpello quoque cavernam formanti cum fibris multis validis longitudinalibus et membranis albis medullosis, mesocarpio basali minimo carnoso et cum fibris multis.

DIAGNOSIS OF HOLOTYPE: Leaves 92–135 cm long, 5.5–6 cm wide, subcoriaceous, M-shaped in cross section, ligulate, tapering gradually from near the base to the subulate tip which 10 cm down is 10 mm wide, at midsection with 68 secondary parallel veins in each half, at base amplexicaul and entire but 14–15 cm up the margins with ascending prickles 0.3–1.3 mm long, 3–8 mm apart, arcuate subulate, brown-tipped; the midrib unarmed throughout; at midsection the margins with serrations 0.5–1 mm long, 3–7 mm apart; near the tip the margins with umbonate serrations 0.1–0.2 mm long, 1.5–3 mm apart; phalanges 7.5–7.7 cm long, 6.2–7.5 cm wide, 6–6.7 cm thick, obovoid-suborbicular, when dried pale brown, the surface closely minutely punctate, the sides with 5–6 major angles and each carpel with 5–8 sharp secondary ridges and valleys so that the adjacent phalanges are many times mortised in the syncarp, upper ½ free, the apex semiorbicular; lateral sutures narrow but deep and distinct to the base; central apical sinuses 7–12 mm deep, wide, then narrowing to the V-shaped base; carpels 11–13, subequal, the central apices semiorbicular to ellipsoid-semiorbicular, with several sharp angles which account for the mortising of each with its neighbors and the sinuous or zigzag sutures; apices of the marginal carpels obliquely semiorbicular, 6–8 mm high, also sharply angled but the outer side with one or more truncate or curved surfaces extending almost to the apical stigma; stigmas 3–3.5 mm long, suborbicular to obdeltoid, deeply lobed or creased below, oblique, centripetal; proximal sinus deep but running only ¼–⅕ way to valley bottom (except when coinciding with a distal valley); endocarp massive, 4.5 cm long, bony, white except for the brown, shiny lining of the seed cavities, the lateral walls 8–10 mm thick; seeds 3.5–4 cm long, 5 mm in diameter, ellipsoid; apical mesocarp forming a cavity in each carpel apex, crossed by many, strong, longitudinal fibers and with white medullary membranes; basal mesocarp sparse, fleshy and with many fibers.

HOLOTYPUS: Australia, Northern Territory, near Darwin, Jan. 1927, *C. E. F. Allen* (BRI). Isotype in A, BISH, BO.

DISCUSSION: *P. darwinensis* is a member of the section *Pandanus*. There, its closest relative is *P. Whitei* Martelli, of Queensland, a species with: leaves 7–8 cm wide, unarmed for the lower third; phalanges 6–6.5 cm wide, the lateral sutures wide; carpels 9–10; central apical sinuses 3–5 mm deep; endocarp 3 cm long; and basal mesocarp 20 cm long. In contrast, *P. darwinensis* has the leaves 5.5–6 cm wide, the margins of the lower third with prickles 0.3–1.3 mm long, 3–8 mm apart; phalanges 7.1–7.5 cm wide, the lateral sutures narrow; carpels 11–13; central apical sinuses 7–12 mm deep; endocarp 4.5 cm long; and the basal mesocarp 12–13 mm long.

These specimens bear a manuscript name that indicates that Martelli at one time considered it a new species. The present writer concurs, but refrains from adopting an unpublished name from an herbarium.

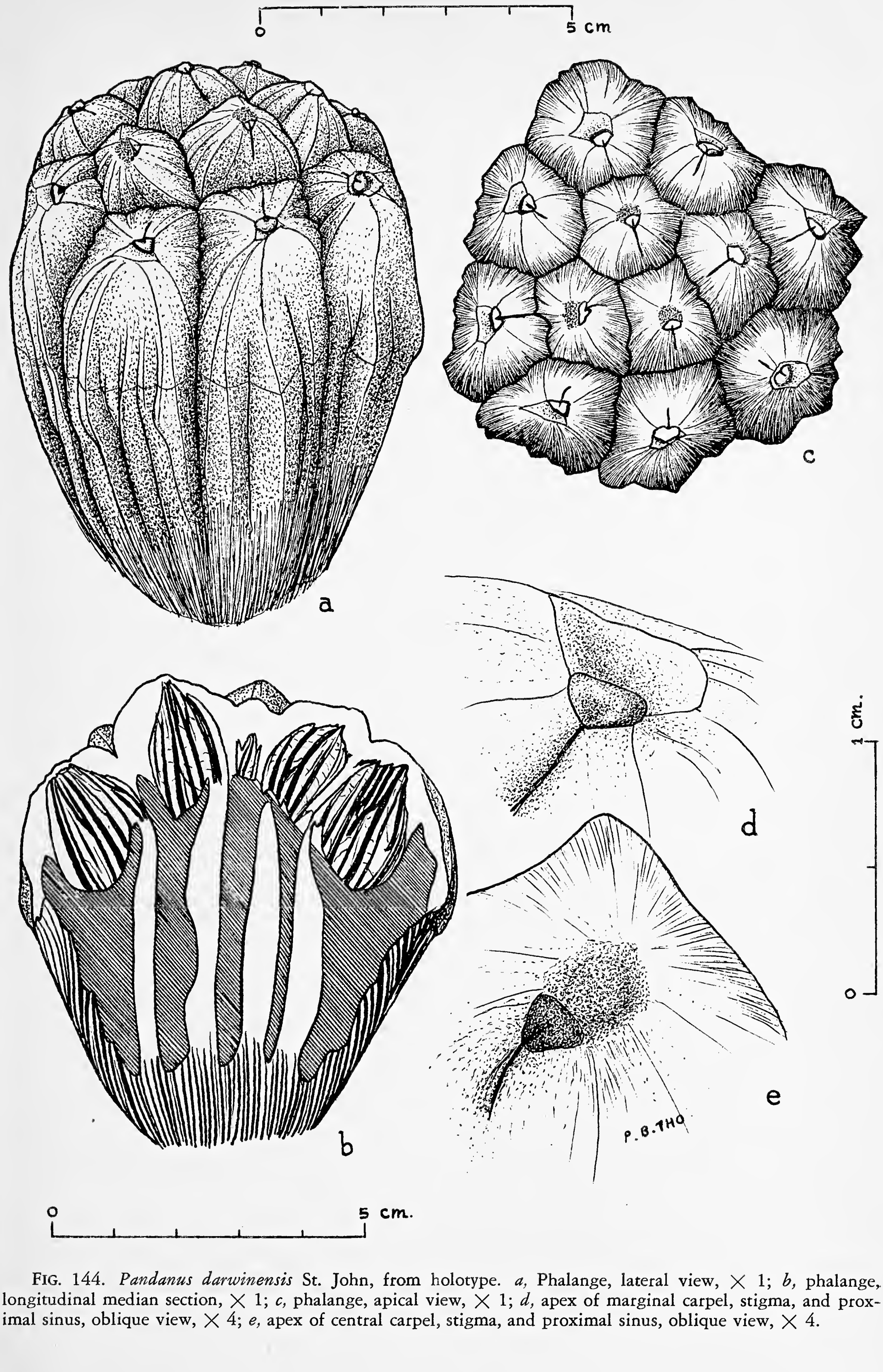


FIG. 144. *Pandanus darwinensis* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* apex of marginal carpel, stigma, and proximal sinus, oblique view, × 4; *e,* apex of central carpel, stigma, and proximal sinus, oblique view, × 4.

Mixed with three uniform phalanges, like the one illustrated, is a much smaller one, perhaps from some other source. It is here excluded.

The new specific epithet is formed from the name of the type locality, plus *-ensis,* the Latin adjectival place suffix.

7. *Pandanus latifructus* sp. nov. (sect. *Pandanus*)

Fig. 146

DIAGNOSIS HOLOTYPI: Arbor 6 m alta 1 dm diametro, foliis 120 cm longis 5.5 cm latis subcoriaceis in sectione mediali cum 59 nervis secundariis in quaque latere ligulatis sensim in apice acuto longiter diminuentibus cum sulcum medialem basi inermi, marginibus ex 12–15 cm cum aculeis 1.5–2.5 mm longis 7–10 mm distantibus subulatis rectis adscendentibus, midnervo infra inermi, in regione mediali marginibus cum aculeis simulantibus gracilibus 4–11 mm distantibus sed plerumque eis majoribus cum minoribus 1–1.5 mm longis alternantibus, midnervo infra cum aculeis 2–2.5 mm longis 8–22 mm distantibus simulantibus adscendentibus, apice non preservato, phalangibus 5–5.3 cm longis 6.2–7.5 cm latis 4.6–5.4 cm crassis in imagine obliqua subrotundatis sed in basi truncata compressis superficie laeve sublucida in sicca brunnea parte ⅓ supera libera sinibus lateralibus V-formatis profundis etiam ad basem apice alte rotundato lateribus cum dorsis et valleculis angustis et interobseratis, sinibus apicalibus centralibus 3–4 mm profundis, carpellis 12–30 apicibus carpellorum rotundatis vel obliquiter rotundatis eis centralibus symmetricalibus rotundatis illis marginalibus obliquioribus et cum cavo centrali et omnibus cum dorsis parvis acutis, stigmatibus 1–2 mm longis obovatis vel obdeltoideis centralibus subobliquis, endocarpio centrali solido obscure brunneo osseoso lateribus 8–13 mm crassis, seminibus 15–17 mm longis 4–7 mm diametro ellipsoideo, mesocarpio in carpello quoque cavernam grandem cum fibris fortibus, mesocarpio basali cum fibris fortibus multis et cartilaginem parvam.

DIAGNOSIS OF HOLOTYPE: Tree 6 m tall, 1 dm in diameter, and to the best of my recollection without prop roots; leaves 120 cm long, 5.5 cm wide, subcoriaceous, ligulate and gradually long tapering to an acute tip, furrowed only

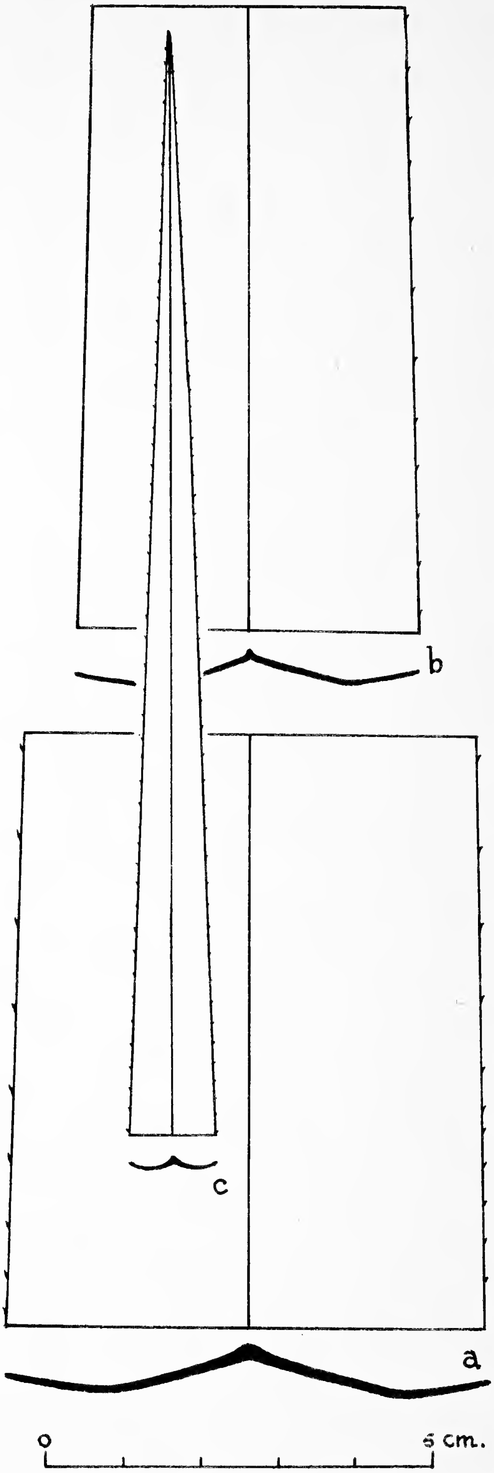


FIG. 145. *Pandanus darwinensis* St. John, from holotype. *a,* Leaf base, lower side, × 1; *b,* leaf middle, lower side, × 1; *c,* leaf apex, lower side, × 1.

along the midrib, at midsection with 59 secondary parallel veins in each half, the base unarmed, beginning 12–15 cm up the margins near the base with prickles 1.5–2.5 mm long, 7–10 mm apart, subulate, nearly straight, ascending; the nearby midrib below unarmed; at midsection the margins with similar slender subulate prickles 4–11 mm apart, but mostly these larger ones alternating with smaller ones 1–1.5 mm long; the midrib below with similar, ascending prickles 2–2.5 mm long, 8–22 mm apart; the tip not preserved; phalanges 5–5.3 cm long, 6.2–7.5 cm wide, 4.6–5.4 cm thick, in profile almost circular except for the truncate or concave base, distinctly compressed, the surface smooth, somewhat shiny, when dry brown, upper ⅓ free, lateral sinuses V-shaped, deep, distinct to the base, apex high rounded, the carpel sides with numerous narrow V-shaped furrows that are mortised with the ridges of the adjoining phalanges; central apical sinuses 3–4 mm deep; carpels 12–20; carpel apices rounded or obliquely rounded, the central ones rounded, symmetric, the marginal ones very oblique and with a broad central concavity, all with low sharp ridges; stigmas 1–2 mm long, obovate or obdeltoid, central, centripetal, slightly oblique; endocarp central, massive, dark brown, bony, occupying ¾ of the body, the outer walls 8–13 mm thick; seed cavities 15–17 mm long, 4–7 mm in diameter, ellipsoid; apical mesocarp in each carpel a large cavern, open but crossed by heavy longitudinal fibers; basal mesocarp small, with a slight amount of pulp but many strong fibers.

HOLOTYPUS: Australia, Northern Territory, 22 miles south of Darwin and 4 miles east of North-South Road, trees of open savannah, 24 Nov. 1950, *H. St. John 24,225* (BISH).

DISCUSSION: *P. latifructus* is a member of the section *Pandanus*. Its closest relative is the Queensland species *P. medialinermis* St. John, ined., which is now in press. The latter has the phalange with the upper ⅔ part free; carpels with the apical concavity 3–4 mm in diameter, suborbicular and well bounded; the apical central sinuses 1–2 mm deep, gently curved or straight. *P. latifructus* has the phalanges with the upper ½ free; carpels with the apical concavity 5–10 mm in diameter, irregular, and with radial ridges; apical central sinuses 3–4 mm deep, zigzag.

The new epithet is from the Latin *latus*, broad; *fructus*, fruit, in description of the unusually broad phalanges.

8. ***Pandanus semiarmatus*** sp. nov. (sect. *Pandanus*)

Fig. 147

DIAGNOSIS HOLOTYPI: Arbor gracilis 6 m alta pauce ramosa, foliis circa 1.5 m longis et proxima basem 5.5 cm latis in media 4 cm latis coriaceis supra viridibus infra pallidioribus et glaucis supra sulcatis et biplicatis in sectione mediali cum 46 nervis secundariis parallelis prominentibus in quoque latere, nervis tertialis infra ad basem evidentis in reticulo lineari-oblongo, laminis gladiformatis ex basi in apice subulato diminuentibus, basi amplexicauli et inermi pallida, marginibus ex 10–11 cm cum aculeis 2–3 mm longis 5–11 mm separatis arcuato-subulatis adscendentibus apicibus rubro-brunneis, midnervo toto inermi, in sectione mediali uno latere inermi sed altero cum aculeis 1–2 mm longis 7–21 mm separatis subulatis adscendenti-adpressis, apice subulato licet inermi, pedunculo curvato et pendenti 55 cm longo 18 mm diametro trigono bracteato, syncarpio solitario 20 cm longo 18 cm diametro late ellipsoideo subtrilaterato, phalangibus 6.5–6.8 cm longis 5.6–6.4 cm latis 4.1–4.9 cm crassis rubris late obovoideis lateribus laevibus lucidis partibus clausis subplanis partibus superis rotundatis parte ⅓ supera libera apice truncato vel subtruncato, suturis lateralibus nullis, sinibus apicalibus centralibus 1–3 mm profundis latissimis vadosis rectis, carpellis 8–9 apicibus vadose convexis eis centralibus et illis marginalibus subaequalibus, sinibus proximalibus latis ⅓–½ ad fondam extentis, stigmatibus 2–3 mm latis reniformibus vel suborbicularibus sulcatis pallide brunneis papillosis centripetalibus, endocarpio paene inframediali 4 cm longo osseoso solido partibus centralibus obscure mahogani-brunneis lateribus pallidis intra laevibus lucidis lateribus 15–17 mm crassis, seminibus 18–20 mm longis 5 mm diametro ellipsoideis, mesocarpio apicali cavernam unicam cum fibris fortibus et medulla membranacea alba formanti, mesocarpio basali parvo fibroso et carnoso.

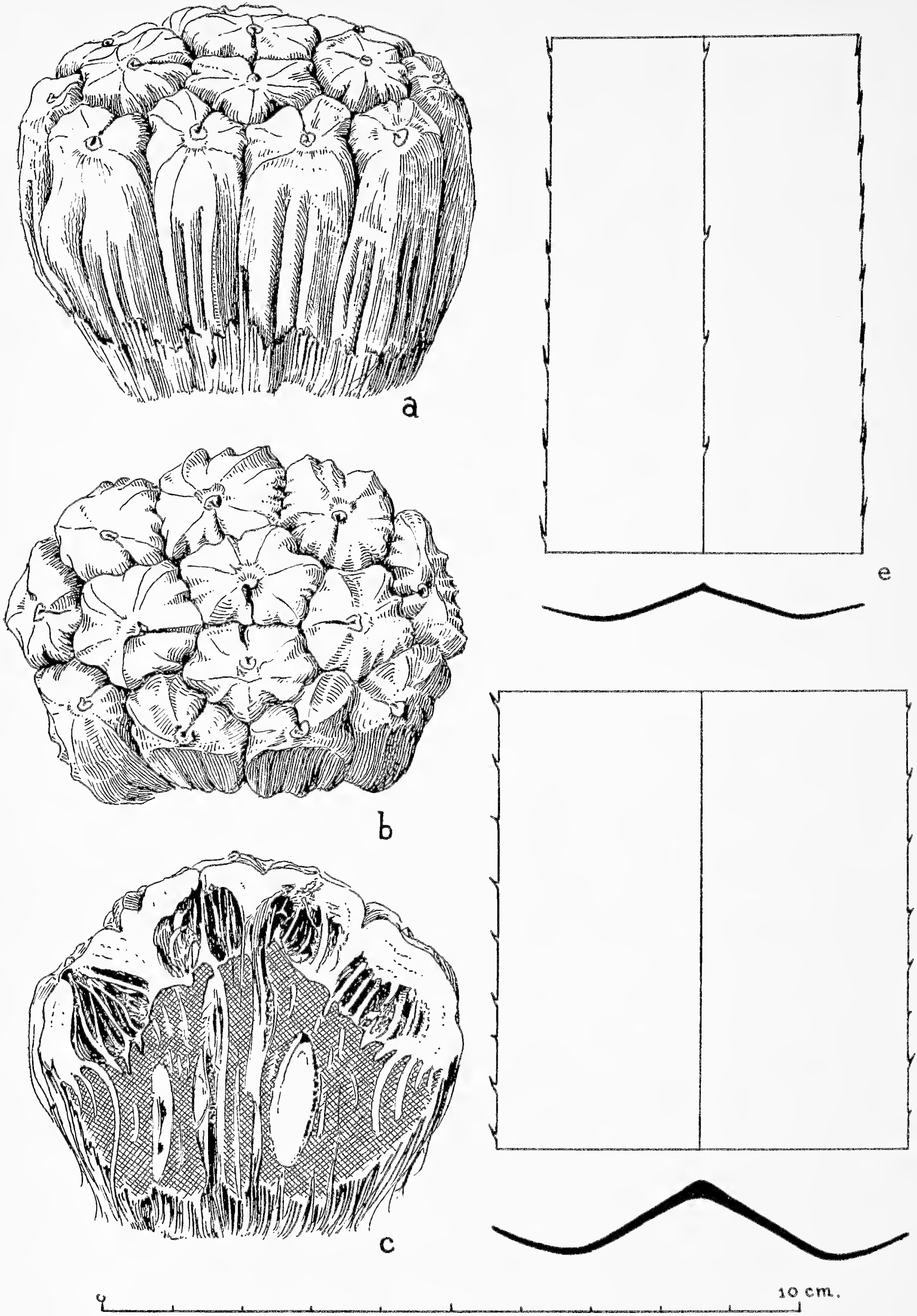


FIG. 146. *Pandanus latifructus* St. John, from holotype. *a*, Phalange, lateral view, × 1; *b*, phalange, apical view, × 1; *c*, phalange, longitudinal median section, × 1; *d*, leaf base, lower side, × 1; *e*, leaf middle, lower side, × 1.

DIAGNOSIS OF HOLOTYPE: Slender tree 6 m tall, few-branched; leaves about 1.5 m long, 5.5 cm wide near the base, 4 cm wide at the middle, coriaceous, green above, below paler green and glaucous, broad furrowed above the midrib and with 2 rounded pleats, at midsection with 46 prominent secondary parallel veins in each half, the tertiary cross veins visible below near the base, making linear oblong meshes, blade sword-shaped, tapering from base to the slender subulate apex which is only partly preserved, this about 10 cm down 2 mm wide, the base amplexicaul and unarmed, pale; the margins beginning at 10–11 cm up with prickles 2–3 mm long, 5–11 mm apart, arcuate subulate, ascending, the outer half reddish brown; the midrib unarmed throughout; at midsection one margin unarmed, the other with prickles 1–2 mm long, 7–21 mm apart, subulate, ascending appressed; the subulate apex apparently unarmed; peduncle curved and pendent, 55 cm long, 18 mm in diameter, 3-sided, leafy bracted; syncarp solitary, 20 cm long, about 18 cm in diameter, broad ellipsoid, somewhat 3-sided; phalanges 6.5–6.8 cm long, 5.6–6.4 cm wide, 4.1–4.9 cm thick, red, broadly obovoid, the sides smooth, shining, the covered parts almost flat, the upper part rounded, upper ⅓ free, the apex truncate or subtruncate, lateral sutures none, central apical sinuses 1–3 mm deep, very wide and shallow, straight; carpels 8–9, the apices very low convex, the central apices quite or nearly as large as the marginal ones; proximal sinus wide, running ⅓–½ way to valley bottom; stigmas 2–3 mm wide, reniform to suborbicular, creased, pale brown, papillose, centripetal; endocarp slightly inframedian, 4 cm long, bony, massive, all the central part dark mahogany brown, the sides and upper marginal flanges pale, inner surfaces smooth, shining, the lateral walls 15–17 mm thick; seeds 18–20 mm long, 5 mm in diameter, ellipsoid; apical mesocarp one large cavern, traversed by heavy fibers and with a white, membranous pith; basal mesocarp scant, fibrous and fleshy.

HOLOTYPUS: Australia, Northern Territory, Koolpinyah, 12° 25′ S., 131° 13′ E., small or large communities near edge of swampy grassland, 9 m. alt., 10 Sept. 1946, *S. T. Blake 16,964* (BRI).

DISCUSSION: *P. semiarmatus* is a member of the section *Pandanus*, as is its closest relative, *P. somersetensis* St. John, of the Cape York Peninsula of Queensland, a species with the syncarp 13 cm in diameter; phalanges 5–5.5 cm long, 4–5.1 cm wide, the apex low convex, central apical sinuses 0.5–1 mm deep; leaves 93 cm long, 6.8–7.2 cm wide, and at midsection the margins unarmed. *P. semiarmatus* has the syncarp 18 cm in diameter; phalanges 6.5–6.8 cm long, 5.6–6.4 cm wide, the apex truncate or subtruncate, the central apical sinuses 1–3 mm deep; leaves 150 cm long, 5.5 cm wide, at midsection one margin with prickles 1–2 mm long, 7–21 mm apart, the other unarmed.

The new epithet is formed from the Latin *semi,* half, *armatus,* armed, and is given in allusion to the leaf margins which are only partly armed with prickles.

9. ***Pandanus thermalis*** sp. nov. (sect. *Pandanus*) Fig. 148

DIAGNOSIS HOLOTYPI: Arbor 9 m alta plerumque congregata "erecta vel breviter decumbens et ita radicifera, radicibus fulturosis nullis, trunco spiraliter sulcato et cum projectionibus paucis brevibus erectis" [radicibus adventivis], foliis 2 m longis in basi 6 cm latis ex 30 cm 6.5 cm latis coriaceis pallide viridibus subglaucis parte tertia ultima pendenti supra costam late sulcatis 2-plicatis in sectione mediali cum 72 nervis secundariis parallelis in quoque dimidio, nervis tertialis non evidentis, laminis gladiformatis longiter in apice gracili subulato trigono diminuentibus eo circa 30 cm longo et circa 10 cm ex apice 2.5 mm lato, basibus non visis, proxima basem marginibus cum aculeis 4–6 mm longis 9–18 mm separatis subulatis paene rectis adscendentibus brunneo-rubris excepta basi, midnervo infra per 55 cm inermi tum cum aculeis simulantibus adscendentibus 3–4.5 mm longis 21–33 mm separatis, in sectione mediali marginibus cum aculeis 1.5–2 mm longis 5–10 mm separatis subulatis adscendentibus, midnervo infra cum aculeis 2 mm longis paucissimis remotis arcuato-adscendentibus, in apice subulato marginibus cum serrulis 0.2–0.4 mm longis 2–6 mm separatis, midnervo infra inermi, syncarpio 30 cm diametro subgloboso aurantiaco pendenti, phalangibus 7.1–7.5 cm longis 6.8–8.5 cm latis 7–7.5 cm crassis subglobosis sed ad basem cuneatis lateribus lucidis sublaevibus sed

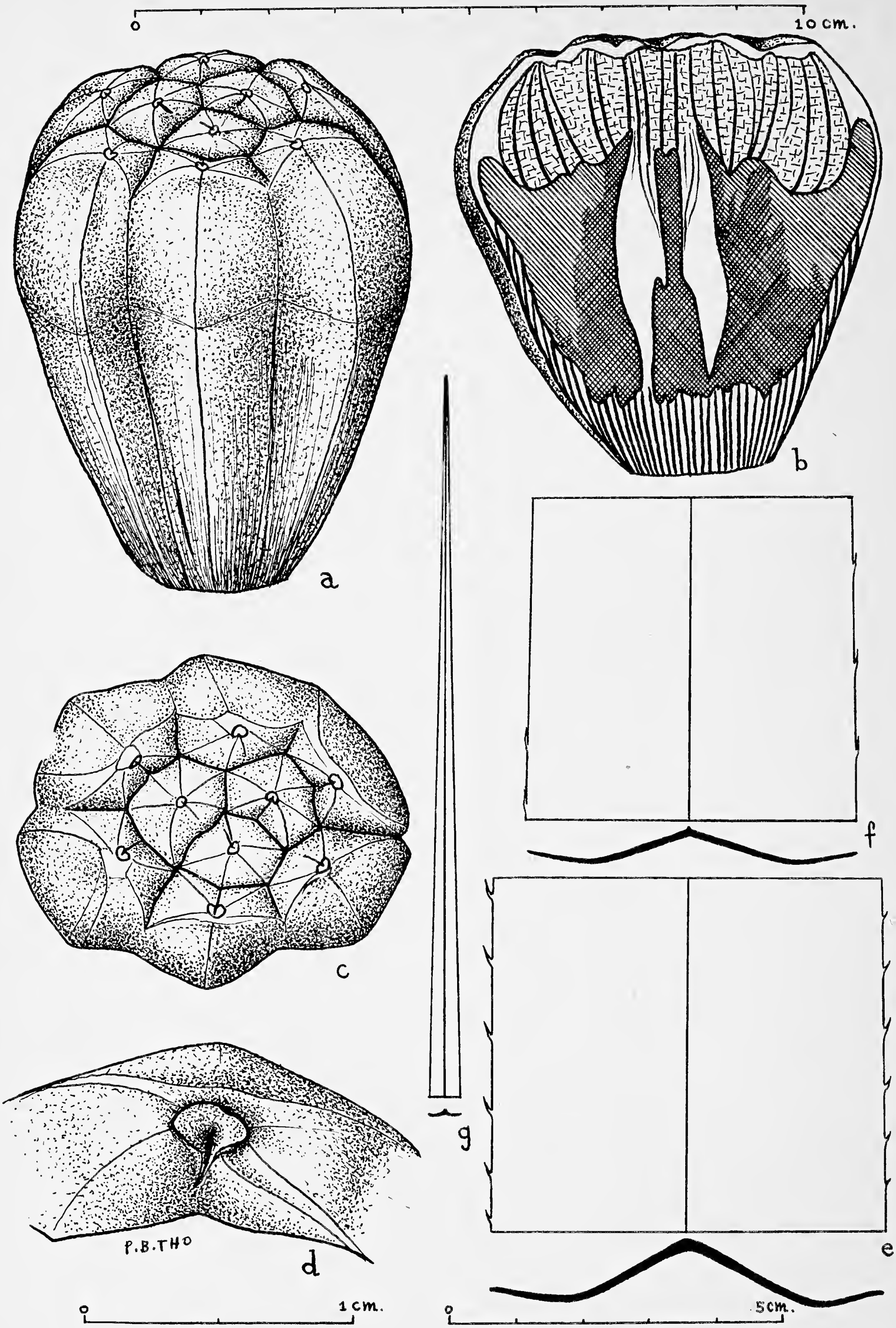


FIG. 147. *Pandanus semiarmatus* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex and stigma, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

cum dorsis et valleculis longitudinalibus parte ⅖ supera libera apice semiorbiculari suturis lateralibus profundis et conspicuis, sinibus centralibus apicalibus 2–4.5 mm profundis anguste V-formatis sinuosis et interobseratis, carpellis 9–11 apicibus centralibus truncatis vel subconcavis eis marginalibus ⅕–⅓ majoribus et valde obliquis et cum cavite apicali grande, sinibus proximalibus profundis et ⅓–½ ad basem extensis, stigmatibus 3.5–5 mm latis reniformibus vel late reniformibus sulcatis prostratis brunneis papillosis centripetalibus, endocarpio mediali 5 cm longo solido osseoso obscure brunneo lateribus 15 mm crassis intra lucidis, seminibus 25–27 mm longis 5 mm diametro ellipsoideo, mesocarpio supero in apice carpelli quique cavernam cum fibris paucis et membranis albis delicatis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree, often gregarious and 9 m tall, "erect or shortly decumbent at base and there rooting, no prop roots; trunk with loosely spiral shallow furrow and a few short erect processes" [adventitious rootlets]; leaves 2 m long, 6.5 cm wide, 30 cm up, 6 cm wide near the base, coriaceous, pale green, slightly glaucous, ⅓ way out breaking and the rest pendent, broad furrowed above the midrib, with two rounded pleats up the middle, beyond that plicate, at midsection with 72 prominent secondary parallel veins in each half, but no clearly visible tertiary veins, blade sword-shaped, long tapering to the trigonous slender subulate apex, this about 30 cm long, and at about 10 cm down 2.5 mm wide, the base not preserved, near the base the margins with prickles 4–6 mm long, 9–18 mm apart, subulate, nearly straight, ascending, brownish red except at base; the midrib below unarmed for about 55 cm, then with ascending similar prickles 3–4.5 mm long, 21–33 mm apart; at midsection the margins with prickles 1.5–2 mm long, 5–10 mm apart, subulate, ascending; the midrib below with a few very remote prickles 2 mm long, arcuate ascending; on the subulate apex the margins with serrulations 0.2–0.4 mm long, 2–6 mm apart; the midrib below unarmed; syncarp 30 cm in diameter, subglobose, orange, pendulous; phalanges 7.1–7.5 cm long, 6.8–8.5 cm wide, 7–7.5 cm thick, subglobose but cuneate towards base, the sides shining, almost smooth, but with longitudinal ridges and valleys, upper ⅖ free, the apex semiorbicular, lateral sutures well marked and deep, central apical sinuses 2–4.5 mm deep, narrow V-shaped, sinuous because of the ridged and mortised sides; carpels 9–11, the apices of the central ones truncate or slightly concave, of the marginal ones ⅕–⅓ the larger and very oblique and with a large apical concavity, proximal sinus deep, running ⅓–½ way to valley bottom; stigmas 3.5–5 mm wide, reniform or broadly so, flush, creased, brown, papillose, centripetal; endocarp median, 5 cm long, massive, bony, dark brown, the lateral walls 15 mm thick, the inner surfaces shining; seeds 25–27 mm long, 5 mm wide, ellipsoid; upper mesocarp forming in the apex of each carpel a cavern with a few fibers and delicate, white membranous pith; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Northern Territory, near Hot Springs, Douglas River, 13° 46′ S., 131° 27′ E., common in flat drainage channels, 11 July 1946, *S. T. Blake 16,433* (BRI).

DISCUSSION: *P. thermalis* is a member of the section *Pandanus,* as is its closest relative, the Australian species *P. latifructus* St. John, which latter has the phalanges 5–5.3 cm long, 6.2–7.5 cm wide; seed cavities 15–17 mm long; leaves 1.2 m long, 5.5 cm wide, at midsection with 59 secondary parallel veins in each half, the margins near the base with prickles 1.5–2 mm long, 7–10 mm apart. *P. thermalis* has the phalanges 7.1–7.5 cm long, 6.8–8.5 cm wide; seed cavities 30–35 mm long; leaves 2 m long, 6.5 cm wide, at midsection with 72 secondary parallel veins in each half; the margins near the base with prickles 4–6 mm long, 9–18 mm apart.

The new epithet is the Latin adjective *thermalis,* hot, and is given in reference to its habitat by the Hot Springs.

10. ***Pandanus yirrkalaensis*** sp. nov. (sect. *Pandanus*)

Fig. 149

DIAGNOSIS HOLOTYPI: Arbor 4.5 m alta, corona 2 m diametro, trunco 3 m alto 10 cm diametro, foliis 111.5 cm longis 4 cm latis coriaceis ligulatis gradatim in apice subulato acuto

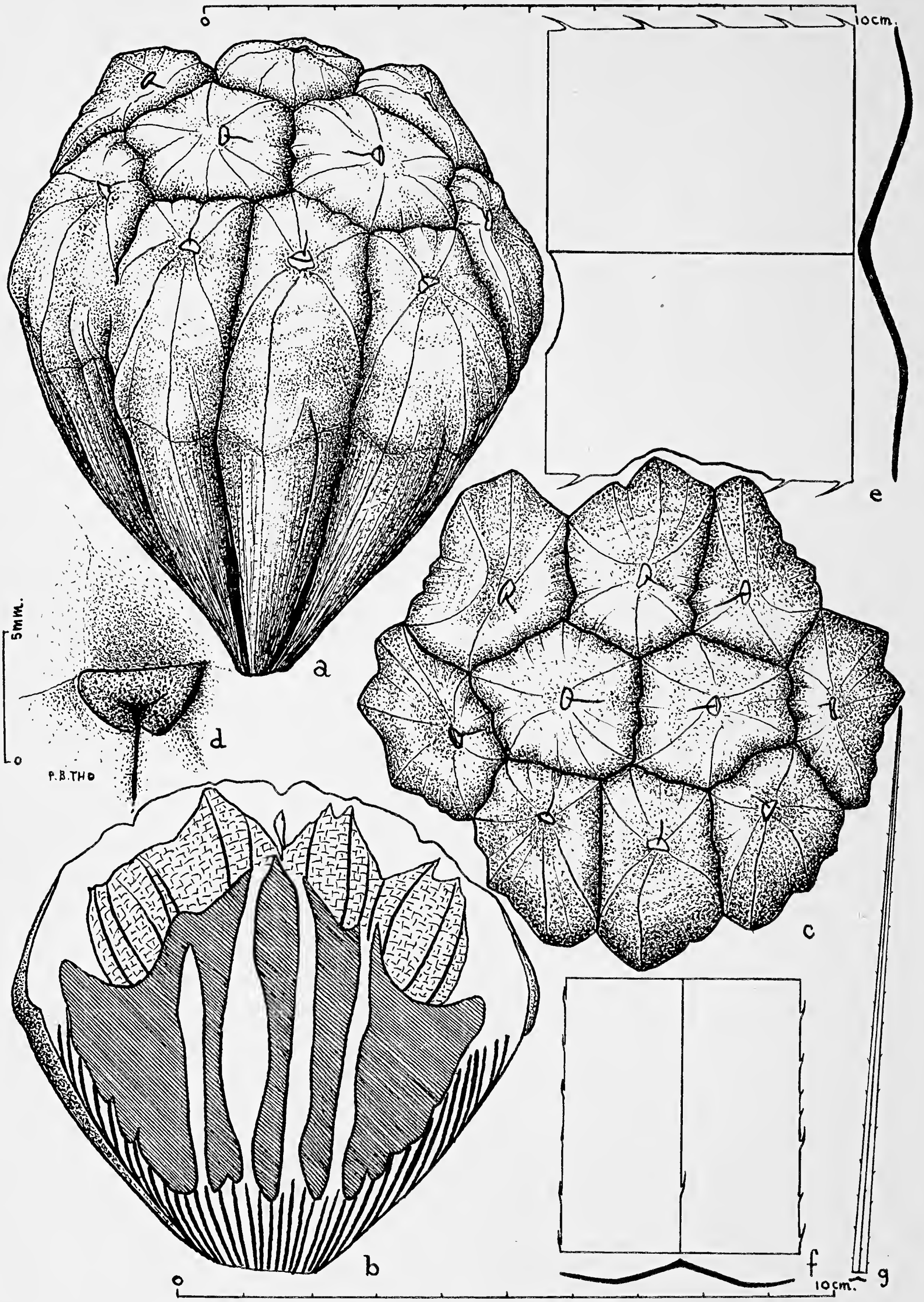


FIG. 148. *Pandanus thermalis* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, longitudinal median section, × 1; *c,* phalange, apical view, × 1; *d,* carpel apex, stigma, and proximal sinus, oblique view, × 4; *e,* leaf base, lower side, × 1; *f,* leaf middle, lower side, × 1; *g,* leaf apex, lower side, × 1.

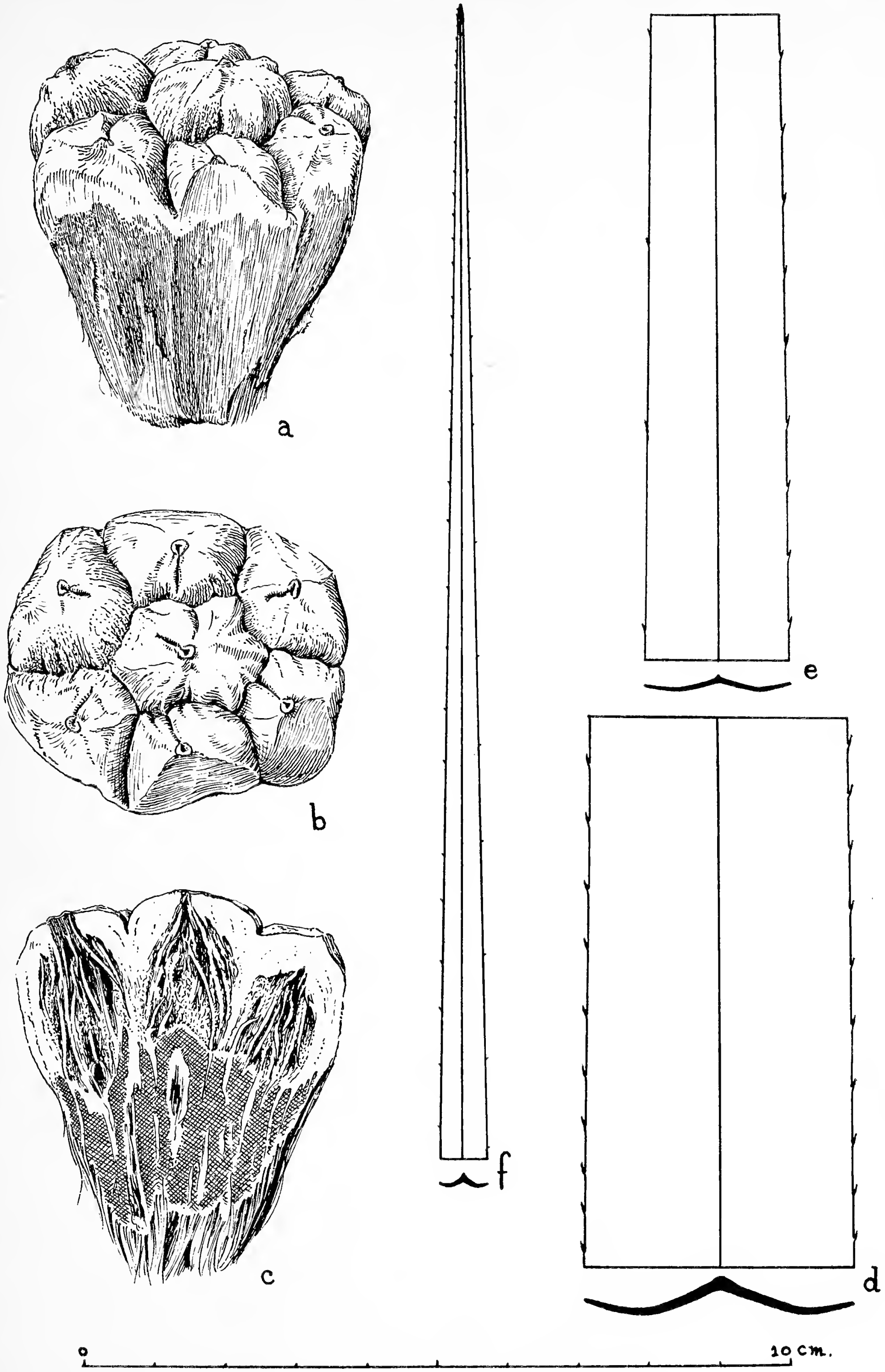


Fig. 149. *Pandanus yirrkalaensis* St. John, from holotype. *a,* Phalange, lateral view, × 1; *b,* phalange, apical view, × 1; *c,* phalange, longitudinal median section, × 1; *d,* leaf base, lower side, × 1; *e,* leaf middle, lower side, × 1; *f,* leaf apex, lower side, × 1.

diminuentibus eo ex 10 cm 4 mm lato, laminis plicatis solum in midnervo inermi sed ex 10 cm marginibus cum aculeis 1.5–2.3 mm longis 5–10 mm distantibus subulatis adscendentibus brunneis excepta basi, in medio marginibus cum aculeis simulantibus 0.5–1 mm longis 5–12 mm distantibus, proxima apice marginibus cum aculeis simulantibus 0.2–0.3 mm longis 1.5 mm distantibus, syncarpio unico terminali, phalangibus 5.5–5.7 cm longis 4.5–5.3 cm latis 3.2–4 cm crassis late cuneatis in apice latissimo paene compressis aurantiacis sed in sicco pallide brunneis pauciter brunneo rimosis, apice convexo, suturis lateralibus plerumque non evidentis, parte ¼ supera libera, apicibus carpellorum oblato-hemisphaericis prominentibus cum dorsis radiatis parvis pluribus, sinibus proximalibus angustis plerumque ad fondam extentis, sinibus centralibus apicalibus 4–7 mm profundis, stigmatibus apicalibus 1.3–2 cm longis deltoideo-ovalibus sulcatis vel cordatis centripetalibus obliquis, endocarpio in parte ⅖ infera osseoso brunneo solido marginibus lateralibus 2–3 mm latis, seminibus 17 mm longis 3 mm diametro ellipsoideo, mesocarpio apicali in carpello quoque caverna unica cum fibris fortibus paucis longitudinalibus et membranis medullosis paucis, mesocarpio basali fibroso et carnoso parvo.

DIAGNOSIS OF HOLOTYPE: Tree 4.5 m tall; crown 2 m in diameter; trunk 3 m tall, 10 cm in diameter; leaves 111.5 cm long, 4 cm wide, coriaceous, ligulate, long tapering to subulate acute tip which 10 cm down is 4 mm wide, the blade plicate only along the unarmed midrib, beginning 10 cm up from the base the margins with prickles 1.5–2.3 mm long, 5–10 mm apart, subulate, ascending, brown except at base; at the midsection the margins with similar teeth 0.5–1 mm long, 5–12 mm apart; near the tip the margins with similar teeth 0.2–0.3 mm long, 1–5 mm apart; syncarp single and terminal; phalanges 5.5–5.7 cm long, 4.5–5.3 cm wide, 3.2–4 cm thick, broad cuneate, widest at the apex, a little compressed, orange but drying light brown, with a few dark brown cracks, the surface smooth, somewhat shining, the apex convex, lateral sutures mostly not evident, upper ¼ free; carpel apices oblate hemispheric, prominent, with several low, radiating ridges, proximal sinus narrow, usually running to the valley bottom; central apical sinuses 4–7 mm deep; stigmas apical 1.3–2 mm long, deltoid-oval, creased or cordate, centripetal, oblique; endocarp in lower ⅖, bony, brown, massive, the lateral margins 2–3 mm wide; seeds 17 mm long, 3 mm in diameter, ellipsoid; apical mesocarp forming in each carpel a cavern crossed by a few heavy longitudinal fibers and a few medullary membranes; basal mesocarp fibrous and fleshy, sparse.

HOLOTYPUS: Australia, Northern Territory, Arnhem Land, Yirrkala, 12° 12′ S. lat., 136° 47′ E. long., common along fresh water stream, Aug. 19, 1948, *R. L. Specht 929A* (AD). Originally mixed with 929C here described as *P. arnhemensis* St. John, and 929B, a smaller narrower leaf, gathered from a sucker at the base of the same tree.

DISCUSSION: *P. yirrkalaensis* is in the section *Pandanus*. It is related to *P. Whitei* Martelli of Australia, which species has its phalanges 7–7.3 cm long, with lateral sutures deep and distinct at least ⅔ way down; and the carpel sides mortised by the many longitudinal furrows. *P. yirrkalaensis* differs by having the phalanges 5–5.7 cm long, the sides smooth and the lateral sinuses mostly not evident; and the carpel sides smooth, not mortised.

REFERENCES

BENTHAM, GEORGE, and FERDINAND VON MUELLER. 1878. Flora of Australia 7: xii + 806.

BLAKE, S. T. 1954. Botanical contributions of the northern Australia regional survey. II. Studies on miscellaneous northern Australian plants. Austral. Jour. Bot. 2(1): 99–140, pl. 1–7.

MARTELLI, U. 1933. Two Australian Pandani. R. Soc. Queensland Proc. 45: 23–26, pl. 1–2.

MUELLER, F. VON. 1869. Report of the Government Botanist and Director of the Botanic Garden, for 1868. Pp. 1–21.

WARBURG, OTTO. 1900. Pandanaceae. Engler's Pflanzenreich IV, 9: 1–97, figs. 1–22.

Additional Records of Folliculinids (Protozoa) in Hawaii[1]

DONALD C. MATTHEWS[2]

THUS FAR, only three species of folliculinids have been recorded for Hawaii: Andrews (1944) assigned folliculinids from Kaena Point to *Parafolliculina annulata* [reassigned by Hadzi (1951) to *Halofolliculina annulata* (Andrews)]; and Matthews (1953) assigned folliculinids from Waimanalo Creek to *Metafolliculina andrewsi* Hadzi and those from the Hawaii Marine Laboratory to *Lagotia simplex* Dons.

This paper records two additional species taken on glass-plate panels (vid. Moebius, 1887). Each panel (Fig. 1) resembled a large open slide box and contained six 8 cm × 10 cm unetched glass plates. These panels, with floats and anchors adjusted, were placed in the dock lagoon, Hawaii Marine Laboratory, where they floated freely approximately a meter above the sand and coral bottom.

The first plate was removed and examined May 16, having been submerged 1 week; the second plate was examined May 23, having been submerged 2 weeks, and so on, until all plates had been removed. The cycle was then repeated.

Although pelogloea formation (Fox et al., 1952: 30) and sequential fouling were beyond the scope of this study, both were noted. Whereas some sedentary polychaetes and folliculinids attached to the plates' upper surface, most fouling organisms adhered to the under surface. Noteworthy, too, is the fact that, although *Metafolliculina andrewsi* was present on all plates, *Lagotia simplex* and *Halofolliculina annulata* were present on none.

During May, June, and July, attached, fully extended folliculinids were abundant, and from this material all measurements were made. Of these, lorica (test) measurements were usually easy; body measurements rarely so. This was primarily because of body contractility which, while it seldom affected the size and shape of the nonmoniliform nucleus, often affected the size, shape, and apparent number of moniliform nuclear conglomerates. However, the clarity and uniformity of other characters made identification of the following two species fairly certain:

Parafolliculina violaceae (Giard) 1888, Fragments biologique XIII. Sur les genres Folliculina et Pebrilla. Bulletin Scientifique de la France et de la Belgique, 3. ser., 1: 310–317.

These beautiful folliculinids (Fig. 2) were observed on all plates from May to July. Rarely were they distributed over the entire plate surface but, rather, were limited to small, closely compact areas, sometimes near the plate's edge but just as often near its center. In contrast to only nine specimens taken at Woods Hole by Andrews (1942: 94), each compact area often contained from 25 to 50 fully extended folliculinids. Thus, during the course of this brief study, several hundred specimens were observed.

Although the genus (Dons, 1912) is characterized by the presence of unique valves (Fig. 2*c*) which separate sac (*d*) from neck (*b*), these are not the structures which first call one's attention to this unusual folliculinid. Whereas a typical folliculinid (Fig. 3) with horizontal sac (*c*), blue-green body (*b*), and upright neck (*a*), resembles a delicate Grecian lamp with spiral chimney, *P. violaceae* (Fig. 2) with perpendicular sac (*d*), reddish-blue body (*e*) and valves (*c*) resembles a minute, upright wine bottle with portions of broken cork pushed down into the neck.

No reclining lorica with collectoderm (*h*) along the side of the sac was ever observed (Hadzi, 1951: 189); and although Andrews (1942: 94) states that the shape of the lower end of the sac varies considerably, the lower end of the sac of *P. violaceae* from Hawaii was consistently rounded (Fig. 2*g*).

Pertinent loricae measurement averages in microns are listed in Table 1 for *P. violaceae*

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[1] Contribution No. 173, Hawaii Marine Laboratory, University of Hawaii, Honolulu, Hawaii. Manuscript received December 11, 1961.

[2] Department of Zoology, University of Hawaii.

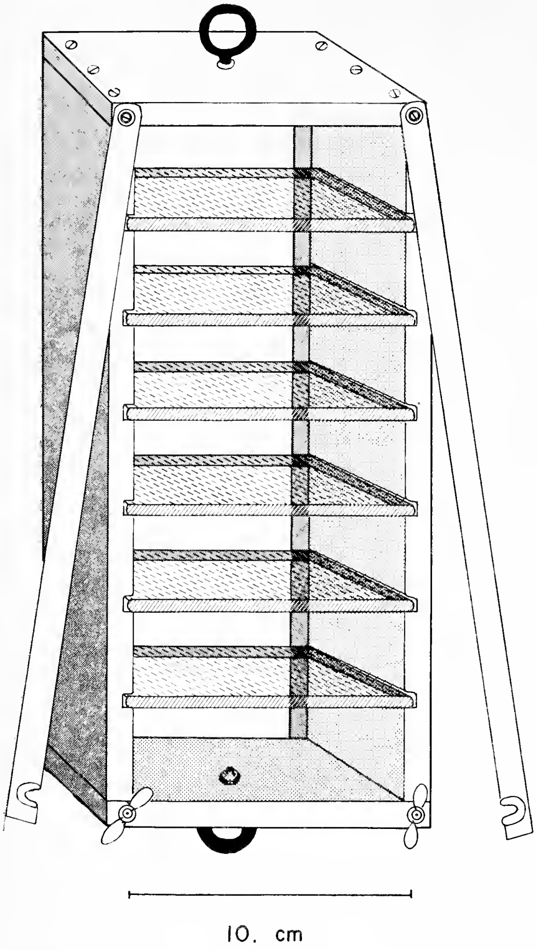


FIG. 1. Diagram of glass-plate panel showing float and anchor rings, inserted glass plates, and locking bars.

from British Columbia (Andrews, 1948: 63), Woods Hole (Andrews, 1942: 95), and from Hawaii.

Since loricae measurement averages for *P. violaceae* from British Columbia are based on extremes, with no knowledge of the actual number of individuals measured, these data cannot be adequately compared. However, measurements of the Hawaiian specimens usually fall well within those recorded elsewhere for this species.

Metafolliculina nordgardi Dons, 1924, Det. kgl. Norske Vidsk. Selskabs Shrifter. (1): 1–18.

These bizarre folliculinids (Figs. 4, 5, 6) were observed on plates May 16. Their numbers increased during June, decreased during July, and disappeared completely during August. Again, rarely were they evenly distributed over the plates' surface, but, rather, were limited to compact areas near the edges or, as frequently, near the center. The following lengths in microns are of 10 loricae taken at random: 1328, 1245, 1145, 1826, 1377, 1726, 1494, 1384, 1610, and 1261. Both Dons' (1924) specimens, collected on the Norwegian coast, and Hult's specimens (after Silén, 1947: 60), collected on the Swedish coast, were considerably smaller, ranging from 320–1130 μ.

Unlike other species of *Metafolliculina* which often attain lorica lengths of 500 μ or more and which have reduced but horizontal sacs (e.g., *M. perducta* Dons, 1934; *M. longicollis* Hadzi, 1938; *M. elongata* Das, 1949) (vid. Andrews, 1952: fig. B, and Fig. 3*a, c* of the present paper), *M. nordgardi* lacks a sac which can be

TABLE 1

MEASUREMENTS	BRITISH COLUMBIA (NO. NOT KNOWN)	WOODS HOLE (9 SPECIMENS)	HAWAII (25 SPECIMENS)
Total length	280	246	215
Sac length	196	159	149
Tube length	84	87	66
Mouth and collar width	*	40	66
Neck width	44	33	42
Vestibule width	50	49	58
Sac width	105†	62	58
Greatest sac depth	55	57	50
Least sac depth	30	28	36
Diameter of nucleus	*	22	25

* No measurements given.
† Obviously a mistake. Compare Andrews, 1948: figs. 1, 2.

differentiated either by shape, size, or position from the rest of the lorica. Hadzi (1951: 28) states, "One might say the abdominal part goes up into the throat."

Metafolliculina nordgardi in Hawaii agrees with its European counterpart in that both primary loricae (Fig. 4*b*) and primary and secondary loricae (Fig. 5 *de, bc,* and *cd*) are cylindrical (actually attenuated cones) but differ in that spiral thickenings are absent. According to Dons (1924), primary loricae (Figs. 4, 6) are the result of newly settled populations, whereas secondary loricae (Fig. 5) are the result of old populations. However, in Hawaii, primary lorica lengths of "newly settled" populations often exceeded the combined lengths of primary and secondary loricae of "old populations." For example, specimens 1 (1328 μ), 2 (1245 μ), 3 (1145 μ), 5 (1377 μ), 8 (1384 μ), and 10 (1261 μ) each possessed only a primary lorica. None had the slightest indication of a spiral thickening or region where primary lorica ended and secondary began. Yet in example 9 (1610 μ), which was composed of a primary lorica (697 μ) and two secondary loricae (415 μ and 498 μ respectively), the combined length of primary and first secondary (1112 μ) was less than any of the primaries given above.

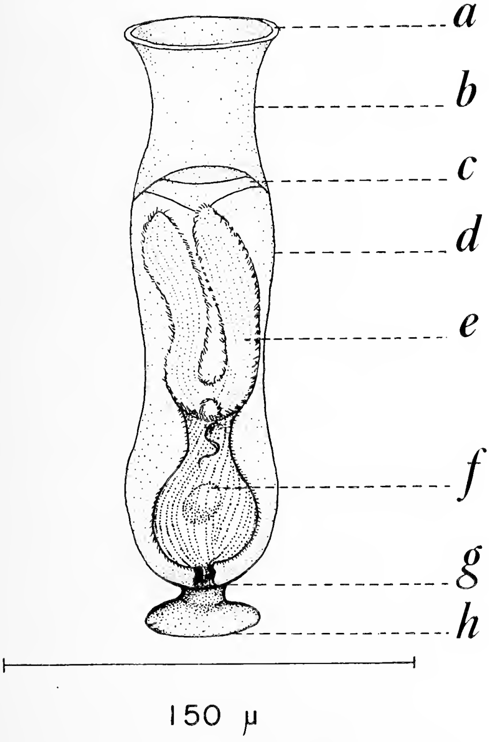


FIG. 2. Full-face view of partially contracted *P. violaceae* showing: *a,* lip; *b,* neck; *c,* dorsal valve; *d,* perpendicular sac; *e,* peristomal lobe of reddish-blue body; *f,* nonmoniliform nucleus; *g,* rounded, proximal portion of sac; *h,* collectoderm.

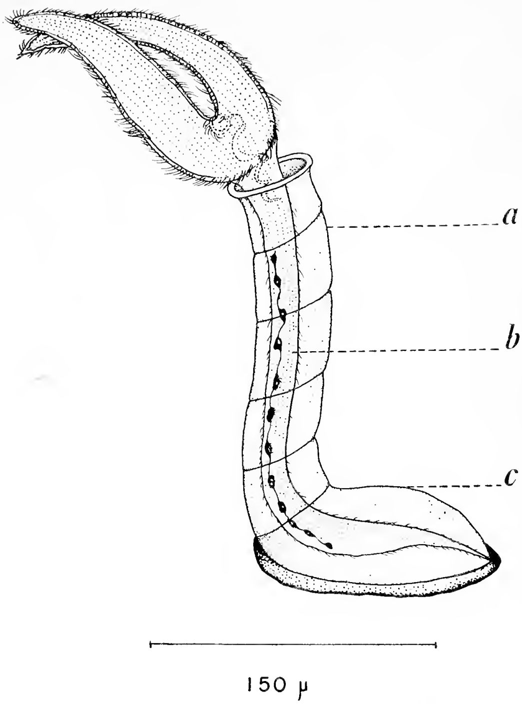


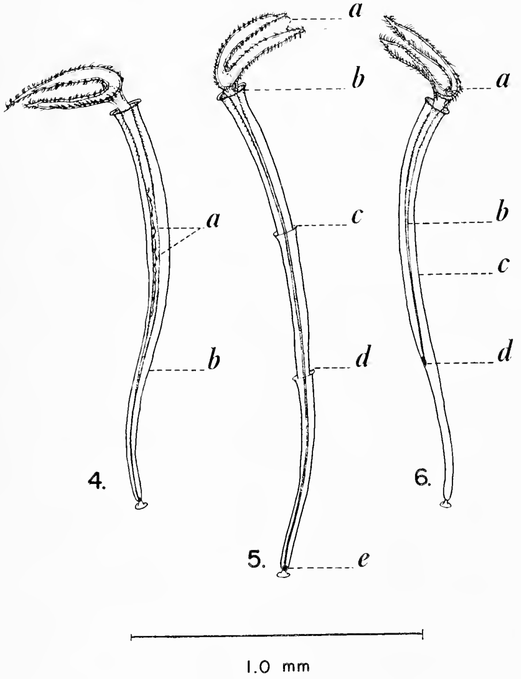
FIG. 3. Typical folliculinid as viewed from the left side showing: *a,* upright neck with spiral thickenings; *b,* extended, blue-green body with left and right peristomal lobes; *c,* horizontal sac.

Since on any one plate, lengths of certain primary loricae may be greater than the combined lengths of others with both primary and secondary loricae, and if the deposition rate for both is assumed to be the same, then some *M. nordgardi* with only primary loricae are older than others with both primary and secondary loricae; hence the notion that secondary loricae are adaptations of older colonies to compensate for the choking effect of a heightened fouling layer is placed in serious doubt.

The delicate, blue-green body usually lay contracted in the small proximal portion of the lorica and, in this condition, neither peristomal nor nuclear lobes could be discerned clearly. Although attempts to fix and stain these folliculinids in a relaxed condition failed, phase contrast microscopy and living material revealed moniliform nuclei (Fig. 4*a*) with up to 12 components.

In one specimen whose primary and two secondary loricae were 1826 μ long, the peristomal lobes of the relaxed body extended 253 μ above the test opening; yet the body still remained attached to the proximal end of the primary lorica by an extremely delicate, green filament. However, another specimen (Fig. 6), with a relaxed body 1128μ long, was able to extend its peristomal lobes (Fig. 6*a*) 249 μ above the opening of its 1244 μ-long primary lorica (*c*), apparently because its body (*b*) was attached (*d*) 365 μ above the proximal end of the lorica.

Much has been made of the relationship of these giant folliculinids to their substrate. Andrews (1952: 133) considered the extreme length of lorica an adaptation which raised the delicate body above the thick substrate and, at the same time, afforded protection from predators. Granted that the openings of certain loricae were located well above the fouling layer surface, the openings of very young loricae as well as those of smaller species were rarely so; yet, though these lacked protective height, they appeared not seriously affected.



FIGS. 4–6. Fig. 4: Fully extended *M. nordgardi* with primary lorica; *a,* moniliform nucleus with 12 components. Fig. 5: Fully extended *M. nordgardi; a,* peristomal lobes; *bc* and *cd,* secondary loricae; *de,* primary lorica. Fig. 6: Fully extended *M. nordgardi* with primary lorica; *a,* peristomal lobes; *b,* body; *c,* primary lorica; *d,* attachment of body to side of lorica.

Despite excellent, detailed studies of lorica formation by Andrews (1923) in *Folliculina producta,* Das (1947) in *Folliculinopsis producta,* Dewy (1939) in *Folliculina aculeata,* Fauré-Fremiet (1932) in *Folliculina simplex,* and Penard (1919) in *Folliculina boltoni,* the problem of whether secondary loricae (necks) are formed by (1) the original occupant of the primary lorica, (2) one of the daughter cells of the original occupant, (3) the dedifferentiated primary occupant, or (4) a new, free-swimming larva from some other lorica, still remains unsettled, yet might easily be solved by one well versed in the biological application of radioisotopes.

REFERENCES

ANDREWS, E. A. 1923. Folliculina: Case making, anatomy and transformation. Jour. Morph. 38: 207–278.

——— 1942. *Parafolliculina violacea* (Giard) at Woods Hole. Biol. Bull. 83: 91–96.

——— 1944. A folliculinid from the Hawaiian Islands. Trans. Amer. Micros. Soc. 63: 321–325.

——— 1948. Folliculinids and stentors in British Columbia. Trans. Amer. Micros. Soc. 67: 61–65.

——— 1952. *Metafolliculina producta* (Wright) on both sides of the Atlantic. Trans. Amer. Micros. Soc. 71: 129–134.

DAS, S. M. 1947. The biology of two species of Folliculinidae found at Cullercoats, with a note on the British species of the family. Proc. Zool. Soc. 117: 441–456.

DEWY, VIRGINIA C. 1939. Test secretion in two species of Folliculina. Biol. Bull. 77: 448–455.

DONS, G. 1912. Folliculina–Studien. Arch. Protistenk. 27: 73–93.

——— 1924. *Metafolliculina nordgardi* n.g. n.sp. Det. kgl. Norske Vidsk. Selskabs Shrifter. (1): 1–18.

FAURÉ-FREMIET, E. 1932. Division et morphogenèse chez *Folliculina ampulla* O. F. Müller. Bull. Biol. France et Belg. 66: 77–110.

FOX, D. L., J. D. ISAACS, and E. F. CORCORAN. 1952. Marine leptopel, its recovery, measurement and distribution. Sears. Found. Jour. Marine Res. 11: 29–46.

GIARD, A. 1888. Fragments biologiques XIII. Sur les genres *Folliculina* et *Pebrilla*. Bulletin Scientifique de la France et de la Belgique, 3. ser., 1: 310–317.

HADZI, J. 1951. Studien über Follikulinider. Academia Scientiarum et Artium. Slovenica Biology. 2: 1–390.

MATTHEWS, D. C. 1953. New Hawaiian records of folliculinids (Protozoa). Trans. Amer. Micros. Soc. 72: 344.

MOEBIUS, K. A. 1887. Das Flaschenthierchen: *Folliculina ampulla* beschrieben und abgebildet. Ahb. Naturwiss. Ver. Hamburg. 10: 1–14.

PENARD, E. 1919. On *Folliculina boltoni* (S. Kent). Jour. Roy. Micros. Soc., ser. 2, 39: 305–319.

SILÉN, L. 1947. On Folliculinidae (Ciliophora Heterotricha) from the west coast of Sweden. Ark. Zool., Stockholm 39: 1–68.

Julia exquisita Gould, A Bivalved Gastropod[1]

ALISON KAY[2]

THREE LIVING SPECIMENS of a bivalved gastropod identified as *Julia exquisita* Gould were collected near Koloa, Kauai, Hawaii, on February 2 and 3, 1962. Originally described by Gould from shells obtained from the Hawaiian Islands during the U. S. Exploring Expedition (Gould, 1862: 283–284), *J. exquisita* is one of nine named species of *Julia* which have heretofore been known only from shell valves and classified as Pelecypoda. Keen (1960: 29–30), comparing the shells of *Julia* with those of the recently described bivalved gastropod *Berthelinia limax* (Kawaguti and Baba, 1959) suggested that when living animals of *Julia* were found they would be gastropods rather than pelecypods. The purpose of this note is to report on the first living collection of a species of *Julia* and to present a preliminary account of the anatomy of *J. exquisita* which confirms Keen's hypothesis.

The animal of *J. exquisita* is similar to the bivalved gastropods which have been described, *B. limax* (Kawaguti and Baba), *B. typica* (Gatliff and Gabriel) (Burn, 1960: 45), and *Midorigai australis* Burn (1960: 46). Ranging in size from 4 mm to 6 mm in length, the animals are sluglike, bearing two convex shells dorsally. The body is long and slender, the foot nearly as wide as the neck. The head and neck extend some 2 mm from the anterior edges of the shells when the animal is moving. The rhinophores are slender, squared off at the tips, and at their bases is the slightly elevated eye prominence. The oral tentacles do not extend beyond the edge of the foot, and are prominent, rounded structures. The anterior edge of the foot is bilabiate, wide, extending laterally to the oral tentacles, and the sole is grooved its whole length by faint grooves. The foot is flattened posteriorly and medially.

The body is dark green, sparsely ornamented on the neck and foot with small white patches ringed with brown and with similar but much more prominent single patches on the rhinophores. The mantle is also green, but has horizontal brown and white bands at the hinge line and at the distal edge of the shells. The sole of the foot is lighter green than the rest of the animal. The eye prominence is white, the eyes black.

J. exquisita resembles the previously described bivalved gastropods in general organization of internal anatomy. As in *Berthelinia* and *Midorigai* the visceral mass is enclosed by the two shell valves and covered by the mantle, the ctendidia are attached to the inner surface of the right mantle as a series of thin lamellae, the external oviducal groove runs along the right side of the body, and the adductor muscle is oval and subcentral in the anterior third of the body. The radula is also similar: uniserial with six teeth in the ascending series, each tooth simple at the tip and bearing fine denticulations on both sides. *J. exquisita* differs from the described species of *Berthelinia* and *Midorigai* in some anatomical details which will be described more fully in a later paper: there is an area of black pigmentation in the region of the hypobranchial gland, the penis appears to be more complex than the simple penis without armature described in *B. limax* (Kawaguti and Baba, 1959: 179) and *M. australis* (Burn, 1960: 46), and the adductor muscle appears to be larger in proportion to body length than it is in other species.

The shells conform closely to Gould's (1862: 283–284) description. They are broadly oval in outline, the anterior margin rounded, the posterior deeply excavated. The sculpture consists of concentric incremental lines only. It is noteworthy that Gould did not mention any other sculpture, although Dall, Bartsch, and Rehder (1938: 126), recording *J. exquisita* from the Hawaiian Islands, described ". . . 10 low, broad,

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[1] Contribution No. 172, Hawaii Marine Laboratory. Manuscript received April 15, 1962.

[2] General Science Department, University of Hawaii.

feebly rounded, radiating cords" on the posterior portion of the shell. The shells from living animals are bright green, with narrow, radiating, interrupted bands of red-brown and white extending from the hinge to the ventral margin. Beachworn specimens may be white. The hinge consists of a shelf which forms posteriorly a toothlike knob on the left valve and a depression in the right valve into which the left valve fits.

The animals were found in sand patches on small rocks some 3 ft under water. Three genera of algae also occurred on the rocks: *Laurencia, Gracillaria,* and *Gracillariopsis.* The animals readily crawled and hung by mucous threads on all three genera of algae when confined to aquaria in the laboratory. Although the described species of *Berthelinia* and *Midorigai* are associated only with the alga *Caulerpa,* it has not been possible to associate *J. exquisita* with a single algal genus.

Keen and Smith (1961: 49–50) separated *Julia,* subfamily Juliinae, from *Berthelinia* and *Midorigai,* subfamily *Bertheliniinae,* in the Juliidae on the basis of differences in shell characters. Although, in general, anatomically similar, it appears that *Julia* is also to be distinguished from the Bertheliniinae on the basis of habitat.

REFERENCES

BURN, R. 1960. Australian bivalve gastropods. Nature 187: 44–46.

DALL, W. H., P. BARTSCH, and H. A. REHDER. 1938. A manual of the recent and fossil marine pelecypod mollusks of the Hawaiian Islands. B. P. Bishop Mus. Bull. 153. 233 pp., 58 pls.

GOULD, A. 1862. Descriptions of new genera and species of shells. Boston Soc. Nat. Hist., Proc. 8: 280–285.

KAWAGUTI, S., and K. BABA. 1959. A preliminary note on a two-valved sacoglossan gastropod, *Tamanovalva limax,* n. gen., n. sp., from Tamano, Japan. Biol. J. Okayama Univ. 5(3–4): 177–184.

KEEN, M. 1960. The riddle of the bivalved gastropods. Veliger 9(1): 28–30.

——— and A. SMITH. 1961. West American species of the bivalved gastropod genus *Berthelinia.* Calif. Acad. of Sci., Proc. 30(2): 47–66.

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BURN, R. 1960. Australian bivalve gastropods. Nature 187: 44–46.

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