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A QUARTERLY DEVOTED TO THE BIOLOGICAL
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Pattern and Ontogeny of the Foliar Venation of *Bobea elatior* (Rubiaceae)

THOMAS R. PRAY¹

BEFORE A FULL UNDERSTANDING and appreciation of the various patterns of foliar venation can be attained there must be a greater knowledge of the ontogenetic processes which result in the diverse patterns of veins. The ontogenetic investigations to date suggest that there is a correlation between the shape and arrangement of the plate-meristem cells of the young leaf which produces the minor vein system and the pattern of the mature venation. In the case of the prevalent pattern in dicotyledons of polygonal areoles as exemplified by *Liriodendron* (Pray, 1954, 1955a), the plate meristem concerned is composed of small isodiametric cells whose planes of anticlinal division (with respect to the surface) are random; i.e., they are not oriented in any particular direction. The veins which comprise the mature minor venation are similarly disposed. In *Hosta* (Pray, 1955b, c), a monocotyledon, on the other hand, the intercostal venation (i.e., that between the primary veins), whose course is roughly at right angles to the course of the primaries, is derived from a plate of cells elongated at right angles to the primaries. Likewise, the study of Foster (1950, 1952) on the distinctive foliar venation of *Quina* shows that the lineolate minor venation is derived from similarly oriented elongate cells in the plate meristem of the developing leaf.

The present study was initiated therefore to examine the ontogeny of another distinctive pattern of foliar venation as displayed by the leaf of *Bobea elatior*. The genus *Bobea* with five species is endemic to the Hawaiian Islands. An extensive survey (Pray, 1953: 172-264) of the tribe of the Rubiaceae in which it is placed, the Guettardeae (composed entirely

of woody trees and shrubs), has revealed an astonishing variety of foliar venation patterns which exhibit varying degrees of expression of a lineolate disposition of the minor veins. The simpler patterns present in the Guettardeae appear to represent initial phases in the evolution of a markedly lineolate pattern of minor venation. *Bobea*, as a representative of those genera which display a lineolate pattern to a slight degree only, is of particular interest in broadening our understanding of variation in foliar venation and the ontogenetic processes which lead to such variation.

MATERIALS AND METHODS

The writer is indebted to Dr. Sherwin Carlquist for providing the material which formed the basis for the present study. The material was collected on the Palolo-Mt. Olympus trail on the island of Oahu, Territory of Hawaii. Vegetative buds and leaves in various stages of development were preserved in FPA. A voucher specimen of the same material has been deposited in the Herbarium of the University of California, Berkeley (Carlquist H6, August 1953). Mature leaves and those in several stages of development were cleared with 2½ per cent NaOH to facilitate the study of the overall venation pattern. Sections were made at 7 and 8 μ , with a great predominance of paradermal sections which have been found to be especially important in ontogenetic studies of venation patterns. All sections were stained with tannic acid—ferric chloride—safranin with a weak solution of fast green used to further differentiate the safranin.

VENATION PATTERN

The leaf blade of *Bobea elatior* is broadly lanceolate and varies from 4.5 to 11 cm. in length and 2 to 4.5 cm. in width. As is true

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of all members of the Guettardeae (indeed, of almost all Rubiaceae), the major venation of the leaf consists of a midrib with a pinnate series of secondary veins arranged in a campodromous manner (Ettinghausen, 1861: xvi); that is, the extremities of the secondaries curve acropetally near the leaf margin. In addition to the secondaries there are other prominent but smaller veins which diverge from the midrib and extend toward the margins. These intermediate veins (Foster, 1950: 163) are, however, entirely enclosed within the panels or areas delimited by the secondary veins. Such areas will henceforth be referred to as intersecondary or intercostal panels. In actuality the distinction between some intermediate veins and strong tertiaries is arbitrary because the two do intergrade.

In the mature leaf, tertiary veins and veins of lesser categories are not readily distinguishable. Hence it is convenient to refer to the entire intercostal venation exclusive of the obvious intermediates as the minor venation. It is the pattern, histology, and ontogeny of the minor venation with which the present study is particularly concerned. In a cleared leaf (Fig. 1) the minor veins, except for occasional obvious tertiaries, are fairly uniform in size and relative prominence. The ultimate areoles (smallest units of mesophyll completely enclosed by veins) are delimited for the most part by veins of the fifth and sixth orders. However, for the above mentioned reason, vein categories within the system of the minor venation will not be considered in descriptions to follow.

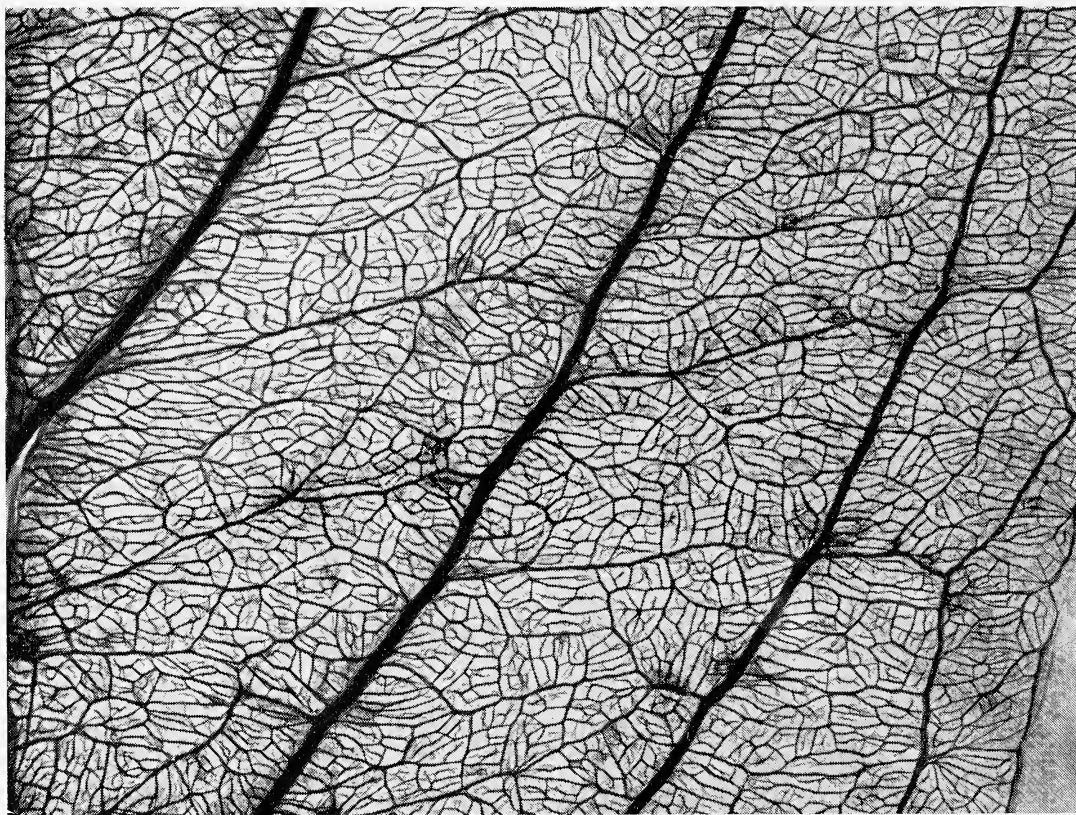
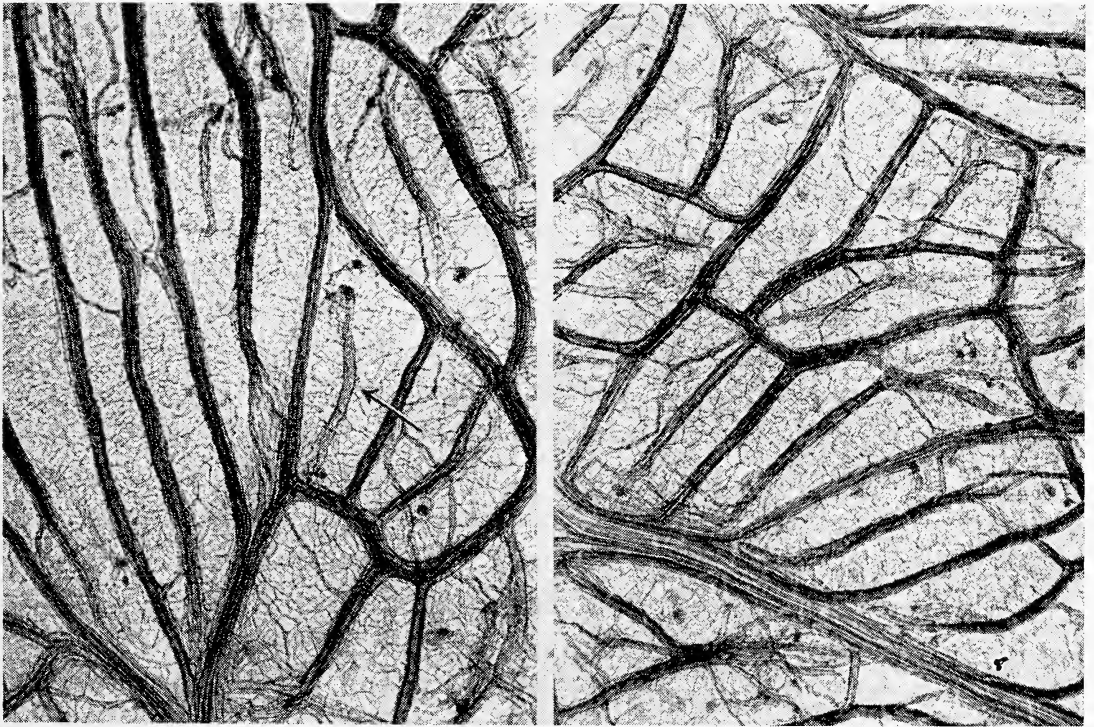


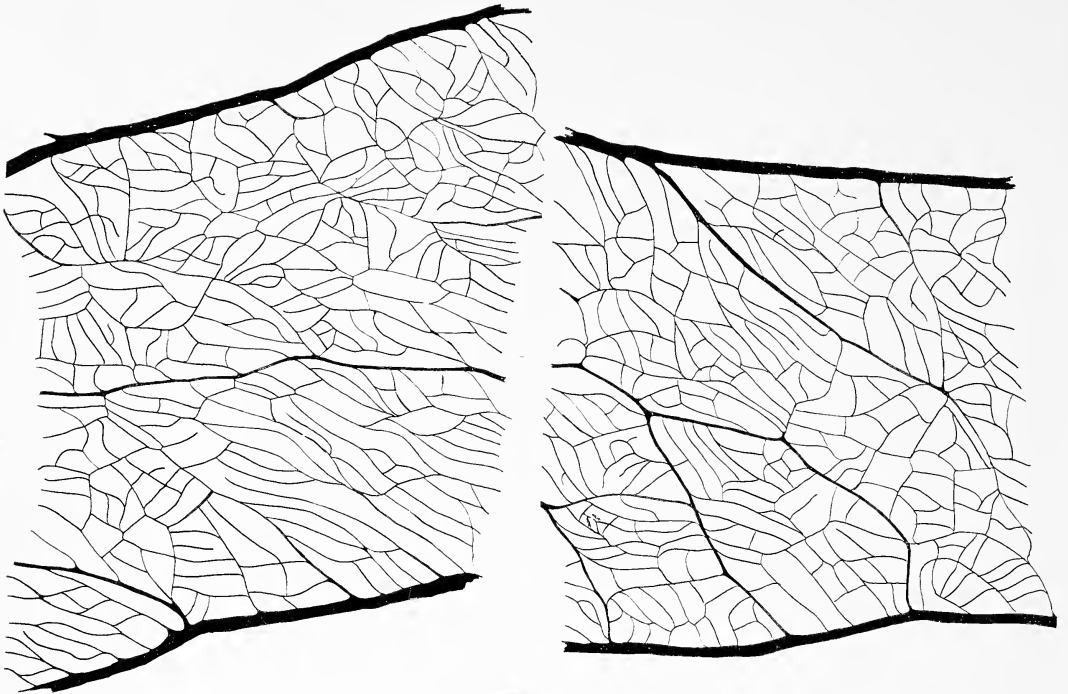
FIG. 1. Portion of a cleared lamina showing the general nature of the mature venation, $\times 7$. Midrib at left; several secondary veins in part extend diagonally toward upper right.

The ultimate areoles of *Bobea* display a marked tendency to be rectangular and often distinctly elongated. While actual areole shape is extremely variable the tendency toward rectangularity is well enough expressed to give the minor venation a distinctive character which is readily distinguishable from the minor venation of such a leaf as that of *Liriodendron* and many other dicotyledons with their polygonal areoles. The tendency of the minor venation to be made up of elongated areoles is interpreted as a weak expression of the lineolate type of venation which becomes highly developed in some members of the tribe Guettardeae (Pray, 1953: 174–233). While the cleared leaf at low magnifications (as in Fig. 1) displays quite obviously the general character of the minor venation, the abundant sclerenchyma in the blade does obscure the details, particularly as regards the occurrence and nature of vein endings. There

are fibers associated with every vein. In transverse section (Fig. 6) the fibers, which are located adaxial to the tracheary elements, are shown to comprise in fact the greater part of the vascular bundles. Strands of fibers and individual fiber cells extend from the vascular bundles into the mesophyll, in the region within the palisade layer, and between the palisade and hypodermal layers (Figs. 2, 3, 6). Careful study of cleared leaves at higher magnifications (Figs. 2, 3) shows that structures appearing to be vein endings are actually devoid of conductive tissues as such and consist of sclerenchyma only. Thus drawings of the true conductive system (Figs. 4, 5) show that most of the areoles lack vein endings. The latter are rather rare, in fact, in the present material. Apparently areoles without freely terminating vein endings are infrequent in the foliar venation patterns of dicotyledons in general (Esau, 1953: 424).



FIGS. 2 (left), 3. Small areas of the cleared lamina showing the nature of the ultimate areoles, $\times 65$. Note fibers extending from the veins into the mesophyll. Arrow in Figure 2 indicates an idioblastic sclerenchymatous element.



FIGS. 4, 5. Drawings of portions of two intersecondary panels (secondary vein at top and bottom of each figure), $\times 10$. Note scarcity of free-terminating vein endings.

LEAF HISTOLOGY

The general arrangement of tissues of the lamina of *Bobea* is distinctive enough to merit comment in this account. The epidermis is uniseriate on both leaf surfaces with the stomata limited to the lower. Beneath the upper epidermis there is a two-layered hypodermis (Fig. 6) of rather large, closely-packed cells apparently lacking chloroplasts. Ontogenetically, the hypodermis is derived from a single ground meristem layer. The latter is the adaxial subprotodermal layer which in many leaves produces the palisade layer of the mesophyll or its equivalent. The systematic significance, if any, of the hypodermis in the Rubiaceae is not known. It does occur in the only other species of *Bobea* (*B. timonioides*) available for study and in at least one species of *Timonius*, a closely related genus, but has not thus far been found in other genera of the tribe (Pray, unpublished). Solereder (1908: 445) and Metcalfe and Chalk (1950: 761)

record the sporadic occurrence of this feature in several other genera of the family. The palisade layer, which is nearly medially situated in the leaf, is biseriate for the most part. The spongy layer is quite loosely arranged, with the individual cells of rather irregular form.

The smaller vascular bundles which constitute the minor venation extend from the lower limits of the hypodermis into the spongy mesophyll, with the conductive tissues located within the latter. As noted above, the greater part of the vascular bundle is sclerenchymatous, with individual fibers and fiber strands extending beyond the limits of the conductive tissues. There are rarely idioblastic sclerenchymatous elements in the areoles (Fig. 2, center). These often appear to be intermediate between typical fibers and elongate foliar sclereids, such as certain of the unbranched types described in *Trochodendron* (Foster, 1945: pl. IV).

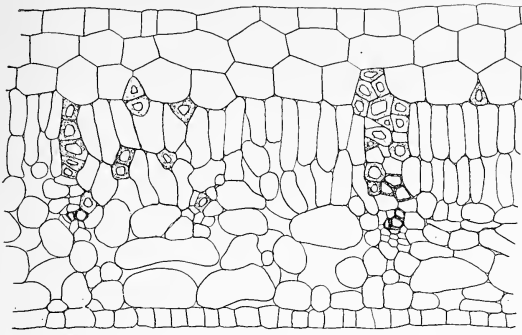


FIG. 6. Transverse section of mature lamina showing general leaf histology, $\times 200$. Tracheary elements indicated with black walls; sclerenchyma with stippled walls.

ONTOGENY OF THE VENATION

Throughout blade ontogeny a basipetal pattern of maturation prevails, both in the initiation of secondary veins and in the differentiation of the minor venation between the secondaries. When the intersecondary panels are first delimited the cells of the plate meristem which will produce the minor venation are essentially isodiametric (Figs. 8, 17). The insertion of new cell walls anticlinal to the surface during this phase is apparently random. In a panel of such isodiametric cells, localized, oriented divisions in a continuous series of cells produce the first procambial strands (tertiaries) (Fig. 9) in a manner similar to that described for *Liriodendron* (Pray, 1955a: 21). Concurrent with the differentiation of the tertiary procambial strands the nature of the intervening ground meristem becomes noticeably altered with the establishment of a general tendency for the cells to become markedly longer than wide (Figs. 7, 10, 13). This condition is due largely to repeated cytokinesis of a given meristem cell in the same plane producing small packets of similarly elongated cells (Figs. 10–14). Similar divisions in two or possibly three contiguous cells can produce the same effect. The latter apparently happens infrequently because there is a decided tendency for the planes of cell division in adjacent cells to be completely unrelated and, in fact, they are

rather frequently more or less perpendicular to one another. The tendency for small parallel groups of ground meristem cells to be formed, each independently oriented with respect to their neighbors, is characteristic of the ground meristem during the phases of leaf development concurrent with the formation of the minor venation as illustrated by examples in Figures 10–13. In a given section (Figs. 10–13) elongate cells are not evenly distributed. Sometimes small areas will display considerable regularity while others of the same leaf will have a rather sporadic expression of this tendency. It is from such parallel groups of cells that series of similarly oriented procambial strands are delimited (Fig. 16). Thus the essential nature of the minor venation of *Bobea* is determined by planes of cell division in the ground meristem immediately preceding procambial differentiation.

In the development of the minor venation (exclusive of obvious tertiaries) the delimitation of the procambium from the ground meristem appears to follow a rather orderly procedure when studied in paradermal section. A series of elongate cells derivable from subdivisions of a single cell or several adjacent cells is formed in this process. Most of these will subsequently redivide perpendicularly to the previously predominant plane of division, while one or sometimes several remain undivided. The elongate cells thus delimited are precursors of procambial strands. This series of steps can be illustrated by the following figures. In Figure 11 (top) there is a group of cells elongated perpendicularly to the course of the two procambial strands delimiting the areole. If, then, two or more of these cells remain undivided while the intervening ones further subdivide by a series of divisions at right angles to their long axes, the initials of procambial strands separated by a group of nearly isodiametric cells which are potentially ground tissue will be delimited. This apparently has occurred in Figures 12 (upper left) and 14 (upper right). This same

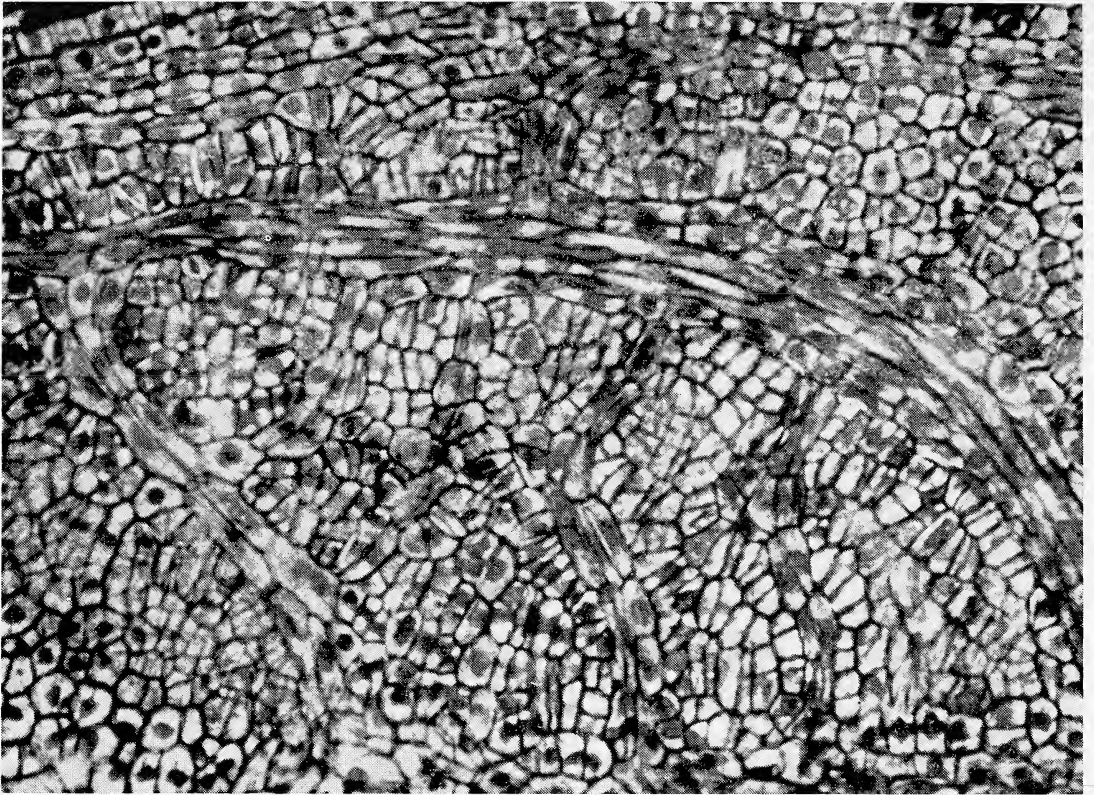


FIG. 7. Paradermal section of very young lamina showing about one half of an intersecondary panel with differentiating tertiaries, $\times 725$. Leaf midrib at lower edge; leaf margin at top. Prominent procambial strand extending from right to left is a secondary vein.

process has progressed farther in Figure 16. Thus areoles are produced which in the mature leaf often occur in more or less parallel series (see also Fig. 21).

During the differentiation of much of the minor venation, particularly below the quaternary category, there is a predominance of strands which are initially single celled (as seen in paradermal section). This is particularly true where a series of similar areoles have been delimited in a precise geometric manner

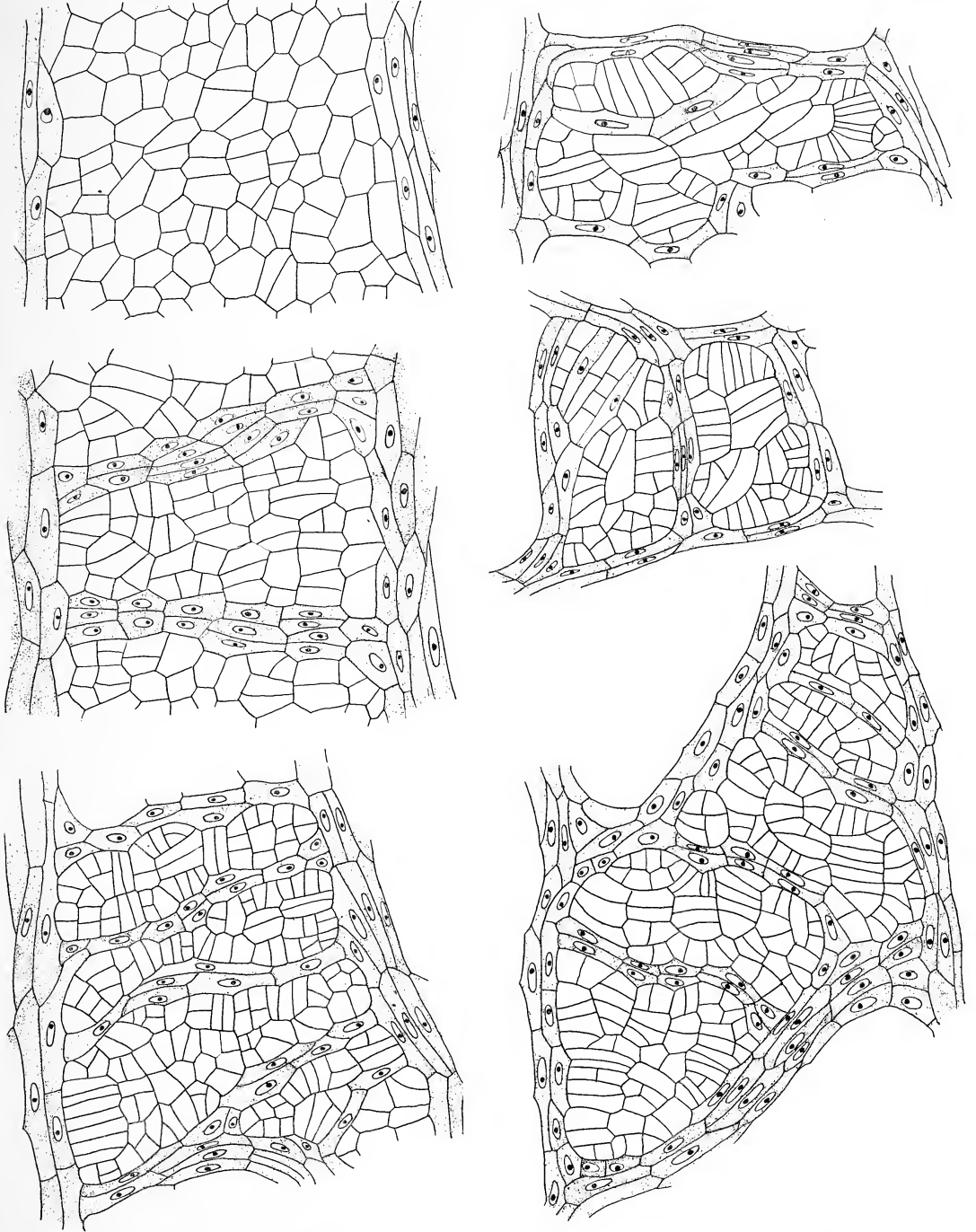
as described above (Figs. 13–15). Most often, on the other hand, strands which apparently were initially more than one cell in length are curved (Fig. 16). Also included in this category are those forked strands (Fig. 15, upper half) which delimited areoles of various irregular perimeters.

Much of the minor venation of *Bobea* shows less parallel orientation of veins than the preceding account suggests. This is directly attributable to the fact that much of the original

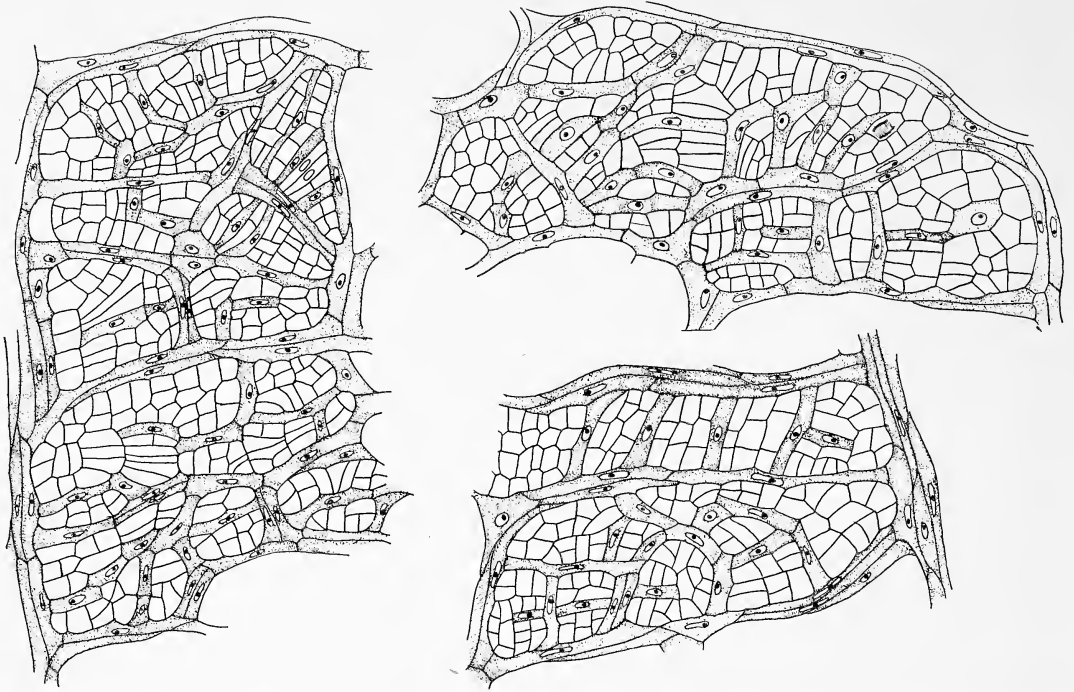
FIGS. 8–13. Portions of paradermal sections illustrating stages in the initiation and early ontogeny of the minor venation, $\times 700$ (except Fig. 8, $\times 1000$). Figure 8 (*upper left*): Intersecondary panel prior to appearance of any intersecondary procambium. Figure 9 (*middle left*): Similar panel with differentiated tertiary procambial strands. Note change in shape of ground meristem cells as compared with preceding figure. Figure 10 (*lower left*): Panel similar to Figure 9 in which subdivision of the ground meristem has proceeded further. Transverse procambial strands are tertiaries. Figures 11 (*upper right*) and 12 (*middle right*): Similar small areas illustrating the general nature of the ground meristem at the time quaternaries are being delimited. Figure 13 (*lower right*): Portion of intersecondary panel (midrib at left) with tertiary procambial strands. Another portion of the same panel is shown photographically by Figure 7.

ground meristem does not have the degree of precise parallel subdivision described in the foregoing ontogenetic series. However, the right-angled intersection of most veins and

the general rectangular nature of the ultimate areoles is related to the tendency for veins and intervening panels of mesophyll to be derived from rectangular initials. The appar-



FIGURES 8-13



FIGS. 14-16. Portions of paradermal sections in which ultimate areoles are probably being delimited (or have been delimited), $\times 500$. Figure 14' (*left*): Secondary vein at left margin; other large veins in these figures are tertiaries and quaternaries. (Fig. 15, *top right*; Fig. 16, *lower right*.)

ent random spatial relationship among various small groups of minor veins is a result of the apparent random planes of cytokinesis in each original ground meristem cell as compared with its neighbors.

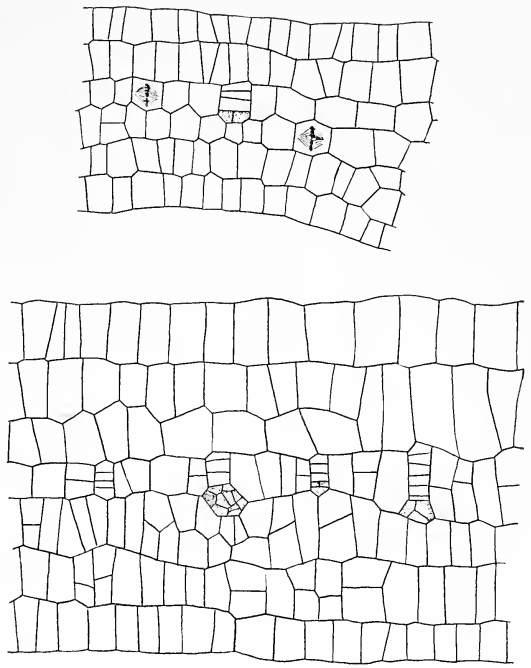
A comparison of transverse sections in successive stages of leaf ontogeny (Figs. 17, 18) demonstrates that the sclerenchyma and vascular tissues of a vein have a common origin from an original procambial initial by a series of longitudinal divisions periclinal to the leaf surface. The lowermost cell or several cells then subdivide in various longitudinal planes to produce a strand of narrow procambial cells. During the earlier phases of differentiation these two components of the fibrovascular system of the leaf are not readily distinguishable in paradermal section. Therefore, it is only in the later phases of leaf development that we can distinguish clearly the future sclerenchyma from the actual conductive tissues. Figures 19 and 20 show the

same area of a lamina at two levels; Figure 20 shows a section 12μ closer to the upper surface than Figure 19. In Figure 19 there are shown a number of probable ultimate areoles delimited by obvious procambial strands, forming a pattern characteristic of the mature venation of the species. At this level in the relatively immature lamina (15 mm. long) the plate meristem has apparently been fully segregated into procambium and fundamental tissue with a reversion to a completely random insertion of anticlinal walls producing groups of more or less isodiametric cells (*viz.*, Fig. 8). Apparently no more procambial strands are to be formed at this level. Just 12μ above the latter section we find the pattern much more intricate and apparently still in the process of differentiation. The cells delimited from the ground tissue in Figure 20 are the initials of the sclerenchyma. Careful examination of the figures under discussion reveals that in addition to a series of

initials being present above each procambial strand there are also at the higher level numerous additional anastomoses. The latter mature into sclerenchyma. Also noteworthy in Figure 20 are the several initials which end freely in the ground tissue. These are the precursors of the abundant fibers which extend into the mesophyll in the mature lamina. Quite infrequently idioblastic cells (Fig. 20) are encountered which are presumably the initials of the occasional idioblastic fibers or fibro-sclereids which occur in the leaf of *Bobea*. Finally it may be noted that the ground tissue at the level of Figure 20 appears to retain a greater predominance of rectangular cells, suggesting that cell division is still active with the possibility of further differentiation of sclerenchyma continuing later than at the level of the clearly distinguishable procambium. The continued meristematic activity of this region is understandable in view of the late maturation of the palisade typical of dicotyledonous leaves in general.

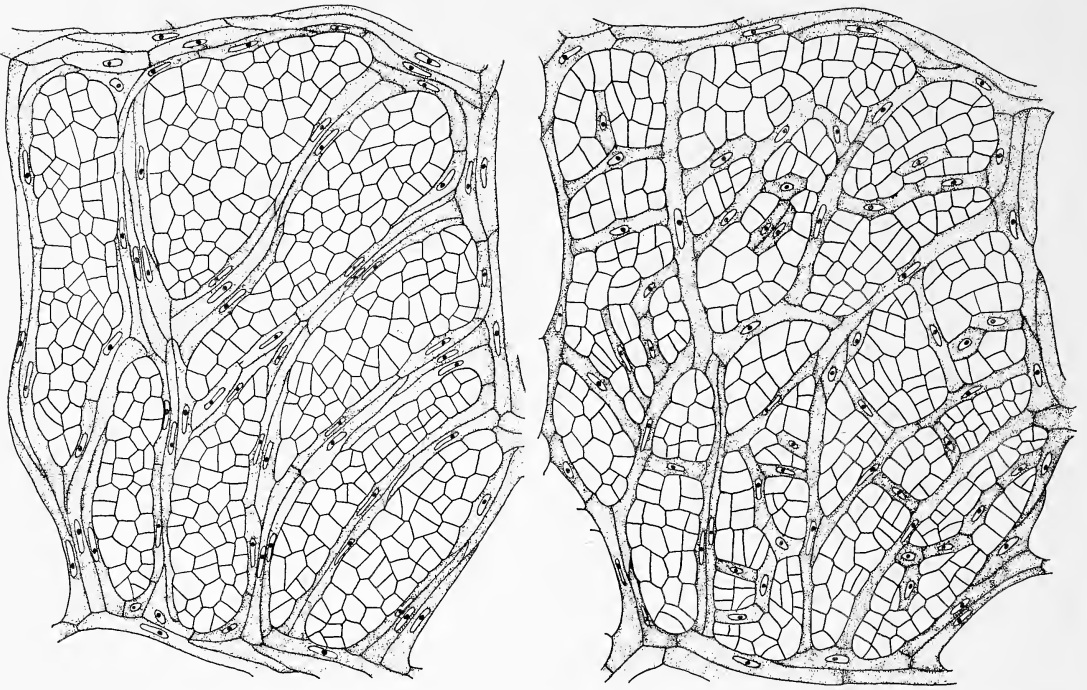
DISCUSSION

The older literature pertaining to the ontogenetic aspects of foliar venation and the modern histogenetic accounts have been reviewed and discussed by Foster (1952: 752–755) and Pray (1955c: 701–706). The present account of the leaf of *Bobea* appears to substantiate the ontogenetic pattern suggested in the latter paper. Namely, there is a definite correlation between the shape and arrangement of the plate meristem cells which give rise to the vein system and the venation pattern of the mature leaf. In fact, a remarkable similarity will be found when the pattern of cell shapes in the ground meristem (Fig. 13) is compared carefully with the pattern of areoles in the mature leaf (Figs. 2, 3). The pattern of polygonal areoles constituting the minor venation of the leaf, as exemplified by *Liriodendron*, is of very widespread distribution in angiosperms. It is assumed as a working hypothesis that such a pattern is a basic type from which the distinctive venation



FIGS. 17, 18. Transverse sections of laminae at two stages of development, $\times 500$. Figure 17 (*above*): Original 6-layered condition (between secondary veins) with differentiation of a tertiary in the third layer from the adaxial surface. Figure 18 (*below*): Several stages in the development of minor veins and the occurrence of periclinal divisions in the various subprotodermal layers. Stippling indicates provascular initials as distinguished from those cells directly above which will become the sclerenchymatous portion of the bundles.

types displayed by the Quinaceae and certain members of the Rubiaceae have evolved by parallel trends toward a lineolate disposition culminating in a lineolate orientation of the entire intercostal venation. The venation of *Bobea* may be considered to be typologically intermediate between that of *Liriodendron* and *Quina*. It is therefore interesting to note that the ontogeny of the foliar venation presented in this paper also may be regarded as intermediate between the two known extremes. In *Bobea* the first intercostal veins are delimited at a time when the insertion of anticlinal cell walls in the plate meristem which produces procambium for the minor venation is apparently random. The tertiaries and quaternaries thus delimited display a pattern in the



FIGS. 19, 20. Paradermal sections of the same area of a lamina at two levels after the ultimate areoles have been delimited, $\times 500$. Figure 19 (left) represents a section 12μ below that in Figure 20, showing a group of areoles enclosed by well-developed procambial strands. The panels of ground tissue will become mesophyll. Figure 20 (right): Same area 12μ higher showing pattern of superimposed sclerenchyma, much more intricate, still actively differentiating apparently.

mature lamina which is not basically different from that of *Liriodendron*. In the intervening areas of the plate meristem concerned there is, then, a decided tendency for groups of elongate cells to be produced by series of similarly oriented cell divisions. From these groups are finally differentiated parallel-oriented minor veins delimiting areoles which are markedly elongate with a tendency to be rectangular rather than polygonal. In this respect, *Bobea* to some extent resembles *Quiina*, in which the entire intercostal venation is derived from a plate of embryonic cells in which the general orientation of elongate cells clearly foreshadows the mature, highly lineolate venation. It is therefore concluded that the ontogenetic sequence in the development of the lamina of *Bobea* represents a divergence in its later aspects toward that of *Quiina* which

correlates with its difference in foliar venation pattern.

A critical evaluation of the above hypothesis must await the results from additional ontogenetic studies. Further investigations in the tribe Guettardeae would be highly rewarding, since in this apparently natural group there is such a wide variety of venation patterns. It is hoped that appropriate material of members of this group can be obtained to augment the present investigation. Similar studies should also be made of other representatives of the *Liriodendron* type of venation to test whether the postulated correlation here presented does indeed exist. In addition to intensive investigation of selected venation types there is also the need for more extensive surveys, such as have been initiated by the author in the Rubiaceae, to further our under-



FIG. 21. Illustrating the general nature in paradermal section of the ground meristem and procambial reticulum at a median phase of leaf development, $\times 600$. Secondary at extreme upper left.

SUMMARY

standing of variation in foliar venation and the significance of such variation in systematics.

The foliar venation of *Bobea elatior* has been described. The distinctive feature of the venation pattern is a minor vein system composed of elongate, similarly oriented areoles, usually lacking vein endings. Thus the minor veins produce in some areas of the lamina a lineolate effect. An ontogenetic investigation of the lamina showed that the elongate areoles making up the minor venation are derived by a fairly precise differentiation process from a plate-meristem of markedly elongate cells, whose arrangement clearly foreshadows the

vein pattern of the mature leaf. A comparison is made between the development of the venation of *Bobea* and that of other known types.

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Species of Zooplankton as a Means of Identifying Different Surface Waters and Demonstrating Their Movements and Mixing

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"IN AN AREA where several water bodies mix . . . the plankton animals alone can give the clue as to the water's origin unless the salinity differences are marked." Russell (1935) makes this statement during discussion of the indicator species *Sagitta elegans* Verril and *S. setosa* J. Müller from the English Channel and southern Irish Sea, and he has shown that when the two species occurred together, they were indicative of mixed waters. The remark suggests the possibility that more general use could be made of zooplankton organisms to indicate the origins of the waters in an area of mixing.

Russell's investigations concerned an area already comparatively well known faunistically and hydrologically, which is not true of the waters about New Zealand. A means has been needed whereby indicator species can be selected and utilized to demonstrate the sources, movements, and mixing of the waters for such little known areas. Two recent developments have assisted the realization of this. First, Miller (1950) used the temperature-salinity (T-S) diagram to show the origins and interrelationships of the several waters contributing to a mixture over an area of the continental shelf near Cape Cod. Second, Pickford (1946, 1952) has shown that the occurrences of the squid *Vampyroteuthis infernalis* Chun, when related (in the conventional T-S diagram) to the temperature and salinity at its points of capture, are confined in certain water masses. Similarly Haffner (1952) and David (1955) demonstrate environmental control over the distributions re-

spectively, of several species of the bathypelagic fish *Cbauliodus*, and of the chaetognath *Sagitta gazellae* Ritter-Zahony. An important corollary of this latter method is that representatives of the fauna of a water mass may be selected as indicators of the water through the relationships demonstrated to temperature and salinity.

The investigation by Miller concerned waters entering near-coastal areas; that of Pickford, and others, has been concerned with relating occurrences of species to particular oceanic water masses. By combining relevant procedures from the two techniques it would be reasonable to expect that the occurrences of zooplankton organisms could be viewed in relation to the waters entering, and in, a coastal area. Data from collections of plankton, temperatures, and salinities could then be evaluated in three general and related ways. From the combined diagrams it should be possible to identify a water body entering a particular locality, to select species which are representative of the fauna inhabiting that water, and to pursue the subsequent history of that water both from its own distribution and from the distributions of the selected species.

These several possibilities are investigated in the following account from data collected in oceanic and coastal waters, and their mixtures, about southern and eastern South Island, New Zealand. The collections are typical of those of many small scale surveys, but they were not intended for the present purpose and, therefore, are not ideal in certain respects. However, they do in fact demonstrate that the several possibilities may be realised.

The combined temperature-salinity and plankton (T-S-P) diagram is believed to con-

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tribute towards an objective determination of the indicator species in an area as comparatively little known as that about southern New Zealand. Further, the distribution of the species in the diagram can be used to confirm the distribution of the different waters. Salinity and temperature changes may take place over shorter, or longer distances, but may not be readily related to variation in the plankton occurrences. In the T-S-P diagram both physico-chemical changes in the environment, and the response to these of planktonic organisms, are demonstrable.

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MATERIALS AND METHODS

The collections of this study were made during surveying operations of H.M.N.Z.S.

"Lachlan" during January, February, and March, 1951. Stations were occupied between Wellington and the Auckland and Campbell islands (Figs. 1, 2), and data are from surface samples. Temperatures and salinities have been obtained for all stations; in addition, temperatures were usually taken at regular intervals between stations. Salinities and temperatures of subtropical water have been included from a cruise between Wellington and Auckland via the west coast of North Island (small, open circles in Fig. 3 and see pp. 21-23).

The temperature and salinity data from the above sources have been used to construct the T-S diagram (Fig. 3). All stations are included. Those for which only physico-chemical data are available are differentiated from those at which plankton tows were made as well.

Surface plankton collections were made at 65 of the stations (see Table 4). Hauls were of three minutes' duration, and procedure and gear were carefully standardised (Bary, in press). Samples have been analysed quantitatively and the order of abundance of the selected species has been entered on Figures 5 to 10. The quantitative treatment is of value, but its importance is reduced in the present study since samples were taken at varying times in the 24-hour period (see p. 19).

A scale of smaller increments than is usual in reporting on quantitative plankton analyses has been used in this study. They have been adopted because the short hauls frequently resulted in only small numbers of organisms being captured (see Table 4). It was necessary that occurrences of species in these small catches be adequately distinguished in order to detect whether there were reactions of species to changed environmental conditions and if these might be of ecological value.

Stations can be grouped conveniently into several series, as they were occupied during individual cruises (Series 4, 5, 6, and 7) or, failing this, in a particular area (Series 1, 2, and 3). In general, a series is spread over a

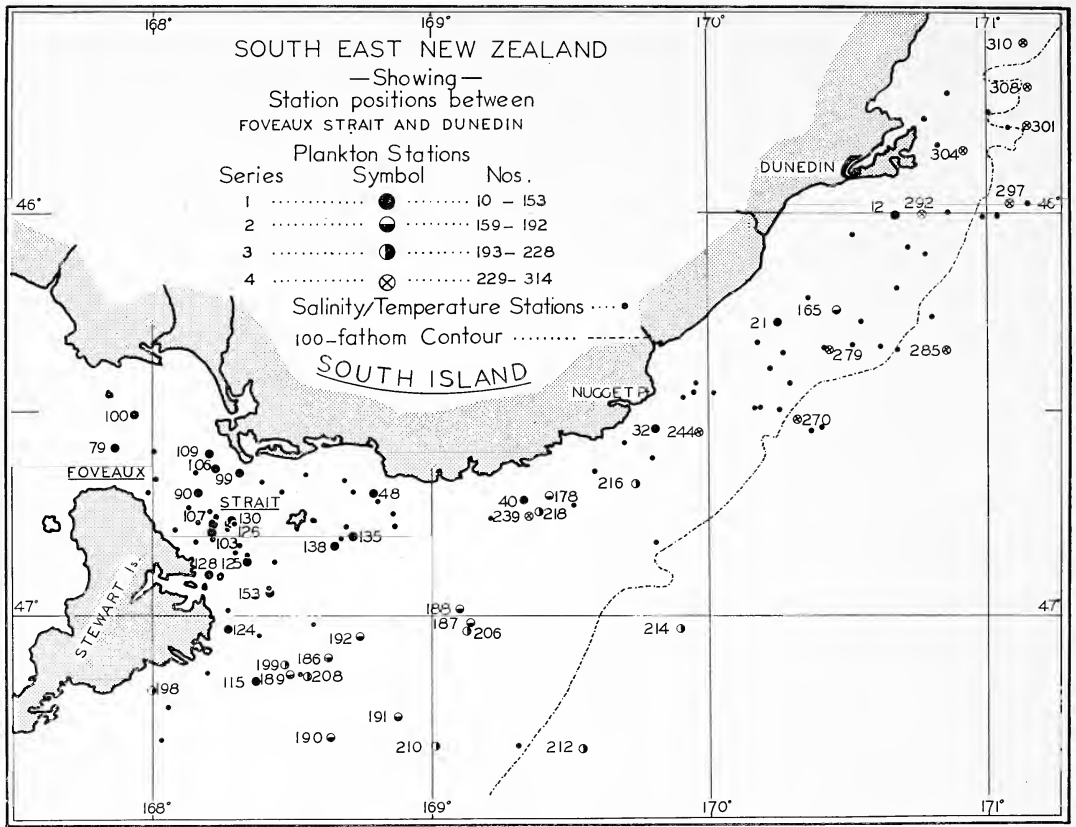


FIG. 1. Temperature/salinity and plankton stations in and about Foveaux Strait, southern New Zealand. Only plankton stations are numbered.

few days except for Series 1, in which stations accumulated irregularly over a period of 18 days; however, the stations are mostly from Foveaux Strait (Fig. 1). Information about the series is summarised in Table 1. In Figures 1, 2, and 3, each series of stations is symbolised separately; in subsequent figures this has not been practicable and for these it is necessary to locate stations in Figures 1, 2, or 3.

The method develops in two stages. In the first, each species is plotted, showing the order of its abundance, in the intercept of the salinity and temperature for all stations at which it was taken. In effect, species occurrences are superimposed on the T-S diagram to produce the temperature-salinity-plankton (T-S-P) diagrams (Figs. 5-10; note that the scale of Figs. 3 and 10 differs from that of

Figs. 5-9). The correlations of specie and water properties thus demonstrated, together with previous distributional records of the species, have enabled species to be selected which occur consistently within those ranges of properties typifying certain water bodies. These species are indicator species, and 25 have been selected. They form into four separate groups (Tables 3, 4), each of which is considered to represent the planktonic population normally associated with a particular range of environmental conditions. Figure 10 summarises the interrelationships of these four groups. In the second stage, the distribution of each group in the T-S-P diagrams is correlated with the geographic distributions of both the group and properties of the waters. In this way, those similarities and differences of the planktonic content between sta-

TABLE 1
THE STATION SERIES, THEIR LOCATION, AND PERIODS OF OPERATION

SERIES NO.	STATIONS NOS.	DATES	NO. OF DAYS	GENERAL LOCALITY OF STATIONS
1.....	10-153	5-6 to 24.I.51	18	} Foveaux Strait and southeastern New Zealand
2.....	159-192	29.I to 1.II.51	3	
3.....	193-228	5 to 13.II.51	8	
4.....	229-314	8 to 9.III.51	1	
5.....	1-6	3 to 4.I.51	1	} Between Wellington and Dunedin
6.....	320-343	21 to 22.III.51	1	
7.....	795, 826, 921	13 to 17.XI.51	4	Between southern New Zealand and Auckland-Campbell islands

tions or groups of stations in the T-S-P diagrams, are considered geographically in relation to the distribution of the water properties which result from the movements of water bodies relative to one another.

SOME GENERAL CONSIDERATIONS

Either the method proposed in this study, or that adopted by Pickford, may be used to select those species which are indicative of oceanic water masses. An alternative use of the present method is to select those species which are indicative of the environmental conditions in a particular, restricted, and little-known area. However, in a wider survey, one or more of these same species may be found in such a variety of conditions as to render them valueless as indicator species. Most of the indicator species in the present study are regarded as useful throughout the area considered, but it might well be necessary to select other indicators for a locality with hydrologic conditions dissimilar to those found in the eastern and southern waters of New Zealand.

The occurrences of two species in the present survey illustrate these remarks and, at the same time, demonstrate the feasibility of using species other than those which previous information would suggest as suitable indicators for the waters in the area. *Thysanoessa*

gregaria Sars is a tropical-subtropical-cool-temperate euphausiid which occasionally occurs in subantarctic waters (Sheard, 1953; Boden, 1954). However, it occurred as a breeding population in this survey, sometimes in high numbers, between the southern Auckland and Campbell islands and the subtropical convergence, i.e., in waters believed to be of subantarctic origin. *Cylopus magellanicus* (Amphipoda) and *Eucalanus acus* (Copepoda) have similar distributions and are typical subantarctic species (Barnard, 1930; Farran, 1929). *Paracalanus parvus* is a widespread copepod (Wilson, 1932; Vervoort, 1949). Brady (1915) recorded it as "fairly common" to 64° 34.5'S. (in 127° 08' E. long.) and at Auckland Island. In the present study, *P. parvus* occurred consistently, in large or very large numbers, in water believed to have originated in the subantarctic and become warmed in its progress northward. It was associated with *Euphausia lucens*, which is recognised as inhabiting warmer northern subantarctic waters (John, 1936), and with *Sagitta serratodentata* var. *tasmanica*, a "cold-tolerant" species (Thomson, 1947, and see p. 31). A few other species, e.g., among the Amphipoda, could be discussed similarly. These are species for which previous distributional records are at variance with the usage in this survey. However, it can be demon-

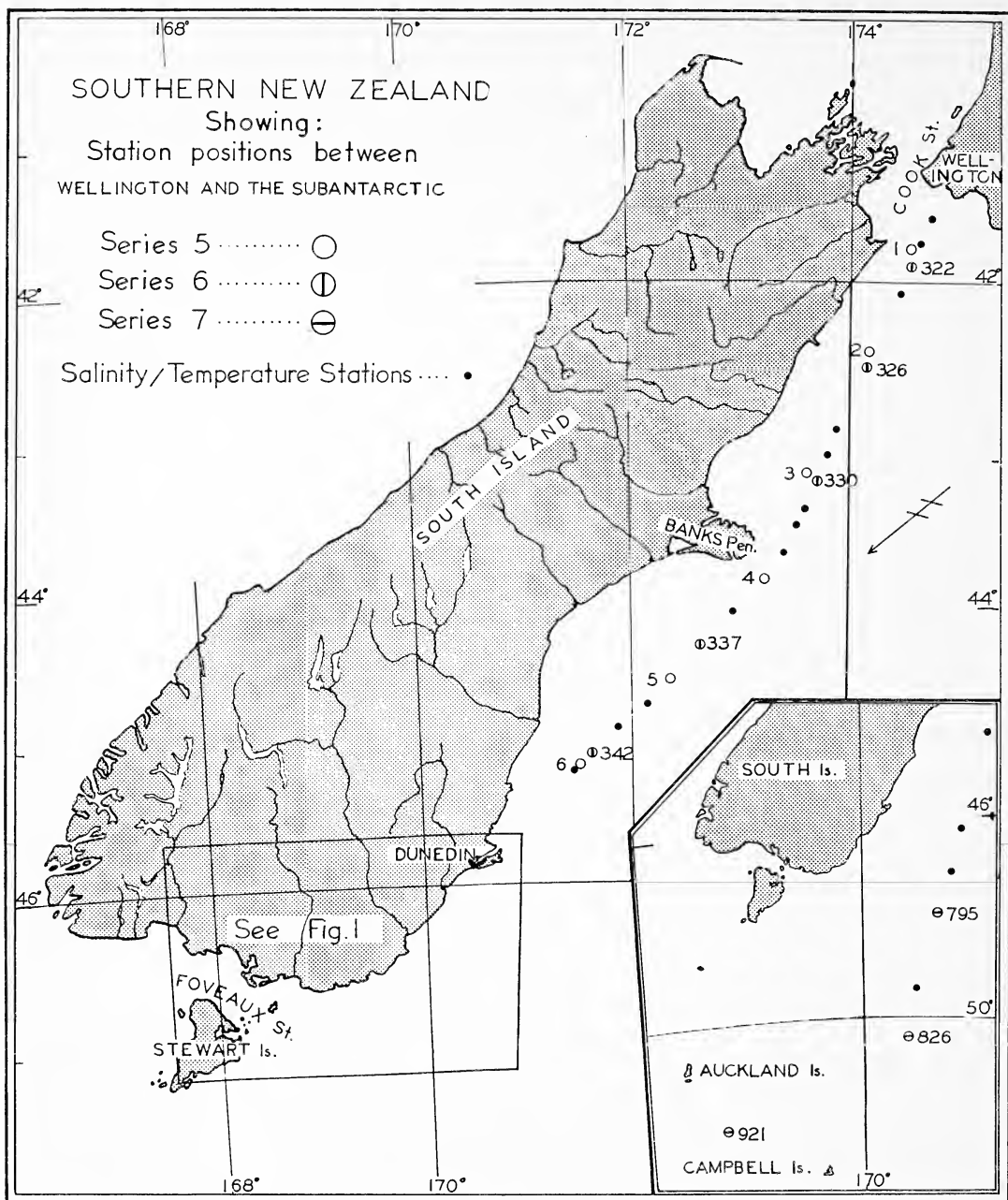


FIG. 2. Temperature/salinity, and plankton stations between Wellington and Dunedin in January (1-6), and March (320-343), 1951. The arrow shows the course of the ship which took the surface thermograph trace in Figure 4b. The approximate position of the subtropical convergence is shown by the two bars crossing the shaft.

INSET: Temperature/salinity and plankton stations between southern New Zealand and Auckland and Campbell islands, November 1951.

Only plankton stations are numbered.

TABLE 2
GENERAL PROPERTIES OF WATERS IN THE SUBANTARCTIC, AND OFF EASTERN AND SOUTHERN NEW ZEALAND*

WATER BODY	SALINITY, ‰	TEMPERATURE, °C.
Of Subantarctic Origin		
i. cold subantarctic.....	34.0 to 34.3	8.2 to 10.9
ii. warmed subantarctic.....	34.3 to 34.7	11 to 13.0
Of Subtropical Origin.....	35.0 to 35.5	13 to 17.5 plus
Coastal.....	— up to 35	13 to 16 plus

* The values listed are derived from the present sampling, but they approximate those given by Deacon (1937) for waters of subantarctic and subtropical origins.

strated that for the particular local conditions, each is largely confined within certain ranges of salinity and temperature (except possibly where mixing is taking place), and that each occurs in conjunction with species which can be stated as undoubtedly resident in the water characterised by those properties. They are thus useful indicator species under the local conditions.

To cover the conditions which may occur in mixed waters it is necessary that indicator species are selected as far as possible to include a range of adaptabilities. To this end more than one species is desirable from each water body. Further, several species may provide additional information through their variable reactions. For example, an adaptable species may maintain an association with a mixture of particular waters whereas a less adaptable one would not.

Frequent short plankton tows, with corresponding numbers of hydrographic samples, might well provide a better index to the overall surface conditions in an area than fewer hydrographic samples and fewer, but longer, tows. The latter may increase the quantity of a catch, but may decrease the relative accuracy with which the biologic sample can be related to the physico-chemical conditions. This would apply especially where steep gradients may exist, as for example in mixing waters. The geographic distributions of indicator species selected from the three-minute tows of this survey are found to closely coincide with the geographic distri-

butions of their respective waters. This general accord suggests that, although surface tows may vary quantitatively and qualitatively between one time and place and another, the present procedures have largely met the requirements for this type of study.

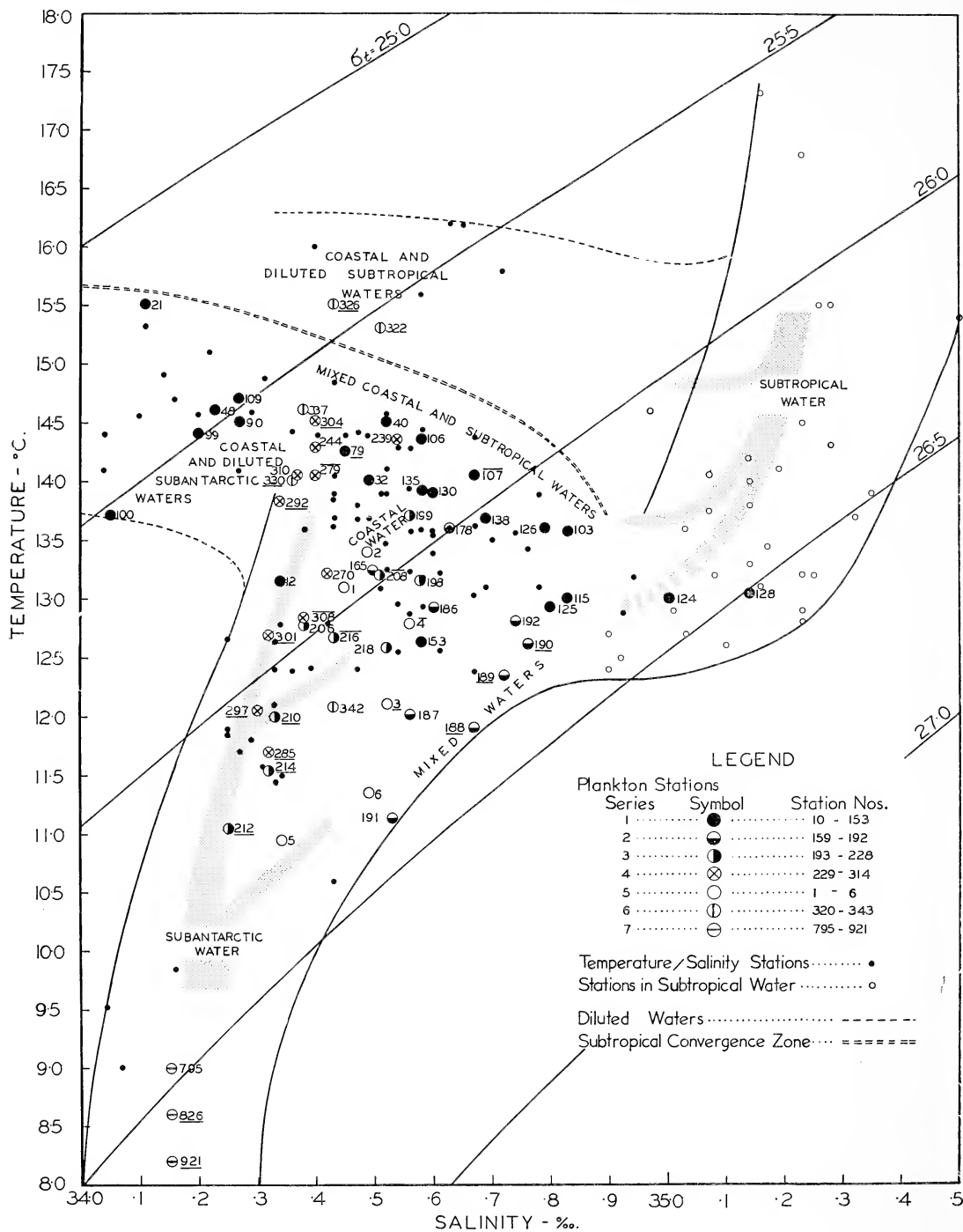
Collections were made as opportunity permitted. As a consequence two features possibly affect the distribution of species in the T-S-P diagrams, namely, diurnal migration of species and the asynoptic nature of the collections.

The effects of diurnal migration have been analysed in some detail. (Times of stations are given in Table 4. In this table, and in Fig. 3, stations are divided into those occupied during daylight, at night, and between dawn and sunrise, and between sunset and dark.) As would be expected, the numbers of species and of specimens captured increased at night (Table 4). It was thought that variations of this nature might render the T-S-P diagram of less value in the selection of indicator species, and, more especially, for reliably correlating their distributions with hydrological conditions. The fact that several species form an indicator group has some bearing. Thus, if the suspected adverse effects of diurnal migration on distribution were to be realised, all species of a group would have to react similarly at the one time. Occasions will arise when all species of a group could, for example, be absent from the surface at the same time. These occasions appear to affect group-distribution patterns in the diagrams

only in details, as discussed below.

The analysis has shown that all series of stations contained night tows and in all, except Series 1, at least some of these were con-

secutive. In addition, some species from the groups were captured in both day and night hauls. Two important facts were also demonstrated. First, fewer night than day tows are



needed to produce a T-S-P diagram from which the distribution of the species group can be related to the hydrological conditions. Second, and the more important, is that in the majority of instances, *those species which were taken in daylight occurred in similar conditions of temperature and salinity to the same species taken at night*. In other words, when a species was collected in day and night tows, it occurred almost only in the environmental conditions which were acceptable. This is reflected in the cohesion of the species' distributions in each of the groups in the T-S-P diagrams. Therefore, day tows serve to supplement night tows from a distributional point of view in the diagrams, and it is believed that data from both may justifiably be used in their construction. It has been found preferable to base interpretations of distributional relationships on the species' groups because diurnal migration may be affecting detail. To guard against the possible adverse effects which might accrue, it would be desirable to occupy future stations at comparable times, and preferably at night.

In T-S-P diagrams planktonic groups, or species, are shown independently of their times of capture. Therefore, occurrences of either individual species, or groups of species, can be directly related only to the environmental conditions in which they were captured, and to the species' composition at other stations. The species, and through them, the species' groups, will react to environmental changes (if of sufficient magnitude), but when these occur is not important in the T-S-P diagram. It is possible, therefore, to utilise asynchronously collected data in the T-S-P diagram. When species or groups of

species are considered in relation to the geographic distribution of the water properties then it becomes essential that as near synoptic series as possible are utilised. Nevertheless, it is believed that even for the T-S-P diagram, the nearer the approach is to synoptically made collections (as, for example, Series 4 to 6), the more reliable will be interpretations from the diagrams.

Pickford (1952: 209) has plotted the occurrences of *Vampyroteuthis infernalis* in relation to density as well as salinity and temperature. She quotes a suggestion that the distribution of this species is determined by its being "passively caught in a layer of constant density. . . ." Because of this suggestion, densities are plotted in Figures 3 and 10. It appears from Figure 10, however, that species may occur over a wide range of densities. It would appear, therefore, that this factor has little if any control over the distribution of surface zooplankton in the area of sampling.

WATERS INFLUENCING SOUTHERN AND EASTERN NEW ZEALAND

The surface waters are described as being of subtropical origin in the northern half and of subantarctic origin in the southern half of eastern New Zealand (Deacon, 1937; Garner, 1954). To the west, and lying north of an ill-defined subtropical convergence zone (Garner, *loc. cit.*) is Tasman Sea water. It is believed to move in an east-going drift towards New Zealand (Deacon, *loc. cit.*). On approaching the west coast of South Island the bulk of the water seems to be deflected northwards while some is thought to move southward and penetrate towards Foveaux Strait and Stewart Island (Deacon, Garner).

FIG. 3. T-S diagram of surface waters, southern and eastern New Zealand. Stations at which plankton was collected are differentiated from those where only salinities and temperatures were taken. Stippled arrows indicate the direction of water movements within the diagram, as deduced from the distribution of properties and the form of the water envelope (and as later confirmed by the plankton distribution). An underlined station number, e.g., 212, indicates a night tow; an overlined station number, e.g., 216, indicates a station occupied at dawn or dusk. An unmarked station is one occupied in daylight.

NOTE: The shape of this diagram superficially resembles that of the area in which samples were taken, but it is not a reproduction of the geographic area in another form.

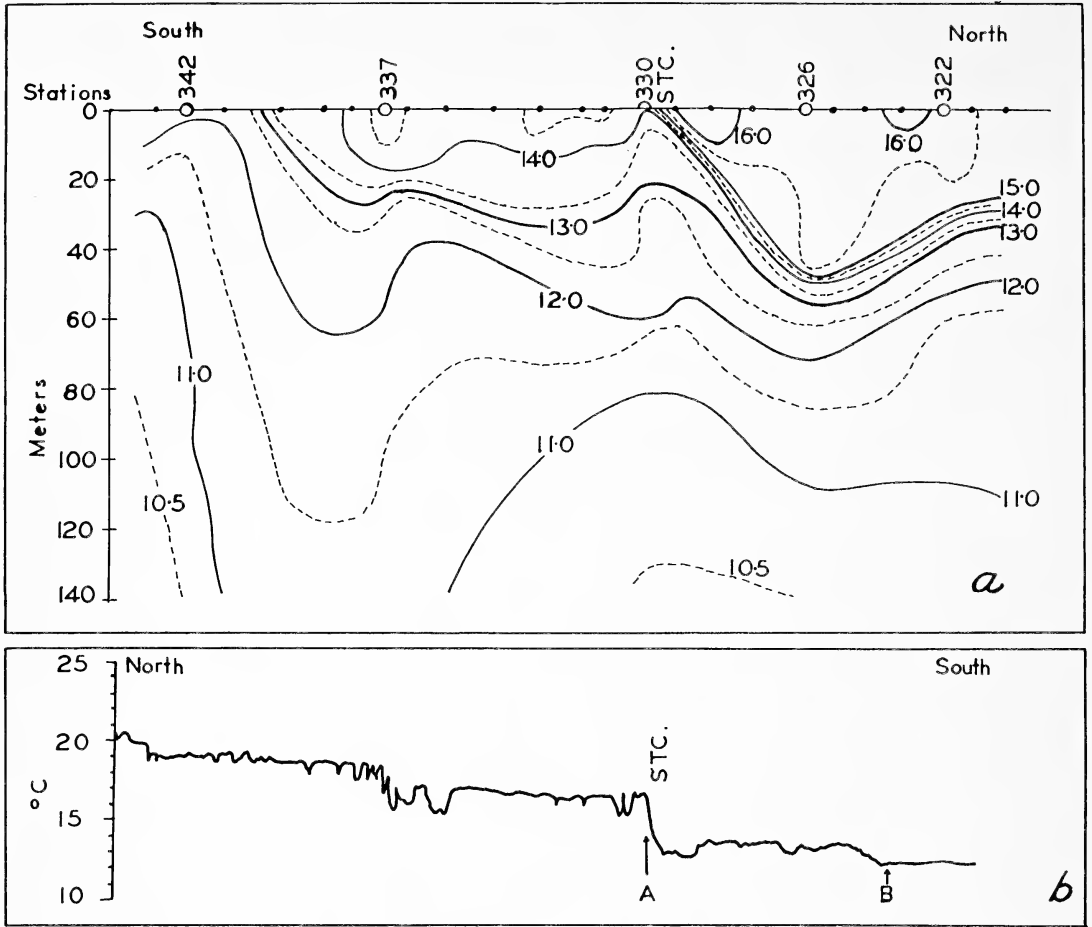


FIG. 4. *a.* Section to 140 m. between Wellington and Dunedin, March 21, 22, 1951. STC = position of subtropical convergence. Stations indicated by a circle are those at which bathythermograph casts were made; surface temperatures were taken at positions marked by dots.

b. Surface thermograph trace between $37^{\circ} 32' S.$ and $178^{\circ} 29' E.$ and Dunedin, mid-April, 1951. STC = position of subtropical convergence in $43^{\circ} 24' S.$ $174^{\circ} 34' E.$ (position A) distant 45 mi. and bearing approximately 96° from Station 330.

Few detailed data are available concerning the properties of the eastern central and southern Tasman Sea water.² That it is warmer and more saline than water of subantarctic origin is demonstrated by the temperatures and salinities of surface samples from the west of North Island between Wellington and North Cape (small open circles, Fig. 3). These data are of winter (July) conditions and consequently temperatures are low in comparison with the rest of the stations, which are summer stations. The temperature

ranges between 12.5° and $17.5^{\circ} C.$ and the salinity between 35.0 and 35.5‰ , values which are within those described for subtropical waters by Deacon (1937). For this

² Since this paper went to press, Rochford, D. J. (1957) has published an account of the waters of the Tasman Sea. He indicates that for the area west and south of South Island, New Zealand, subantarctic water exerts the main influence at all times. However, his data do not preclude the possibility that during spring and summer months some influence from warm Tasman Sea water (in part, my "water of subtropical origin") may penetrate southwards along the west coast towards Foveaux Strait. See his figure 25b.

TABLE 3
SPECIES' GROUPS, AS DETERMINED FROM THE
T-S-P DIAGRAMS, AND THE WATERS OF
WHICH THEY ARE INDICATORS

SPECIES' GROUP	WATER
Subantarctic	Water of Subantarctic origin
i. Southern Subantarctic species	from 8°C.
ii. Northern Subantarctic species	11°C. and higher
Subtropical Species	From, or due to, the influence of subtropical water
Coastal Species	Coastal water—an admixture of subantarctic, subtropical and fresh waters

reason, and for lack of any published evidence to the contrary, the Tasman Sea water and the waters northward of the subtropical convergence to the east of New Zealand are considered together as "water of subtropical origin" in this study. Whether in fact the physical and faunistic properties of the two areas will prove to be identical, or nearly so, has yet to be demonstrated. For the purpose of the present investigation the T-S characteristics of this water are included in Figure 3 for two reasons. First, they provide a contrast across the subtropical convergence with the water originating in the subantarctic; second, they delineate the mass from which the warm saline water (and a warm-water fauna) that influences southern and north-eastern South Island is being derived.

Subantarctic (West Wind Drift) water moves mostly toward the east, but with a northerly component. It has a strong influence on the waters of southern and eastern South Island (Garner, 1954) and perhaps also in some measure on those of the west coast. Some is also believed to pass into Foveaux Strait from the west. The temperature at Station 921 (Fig. 2) was 8.2°C., and it increases northwards to about 13°C. at the convergence. Salinity ranged between 34.0 and 34.3 ‰ in the colder waters and 34.3 and 34.7 ‰ in the warmer (northern) waters.

Such values are within those described for subantarctic water by Deacon (1937). The properties of these waters are summarised in Table 2 and their relationships illustrated in the T-S diagram, Figure 3.

Waters of subtropical and subantarctic origins meet in the subtropical convergence, a zone usually described as of variable width which is believed to migrate northwards in winter, southwards in summer. The existence of the convergence eastwards of New Zealand is undoubted, from evidence discussed by Deacon (1937) and Garner (1954). Evidence from the present survey indicates that it was crossed twice, with biological and hydrological samples being obtained during the first traverse. Data from surface waters from the cruise of March 21–22, 1951 (see Series 6, pp. 47, 48, and Figs. 4*a*, 19*b*, 20*b*), show that near Station 330 there was an abrupt increase northwards of 2°C. and of 0.3 to 0.4 ‰ salinity (over subantarctic salinities as at Stations 341, 342). The section constructed on the basis of bathythermograph records to 450 feet (approximately 138 m.) from between Wellington and Dunedin (Fig. 4*a*) shows that towards the north cool water was submerged beneath a layer 35 to 60 m. deep of warmer water. Immediately north of Station 330 this cool water reaches the surface. South of Station 330, and including Station 337, is a second body of warm water which is of coastal origin (Figs. 19*b*, 20*b*) and which overlies, and is mixing with, subantarctic water. On the second crossing on April 18, a surface thermograph trace (Fig. 4*b*) recorded a temperature drop from 16.8° to 12.8°C. in a position approximately 45 miles seaward on a bearing of 96° from Station 330 (Fig. 19*b*). These data are typical of those associated with a convergence of warm and cold waters, and it is believed they are attributable to the subtropical convergence. This would fit in with Garner's interpretation of these and other data, and, if so, the crossings herein discussed were of the southern extremity of a south-going tongue of subtropical water which was

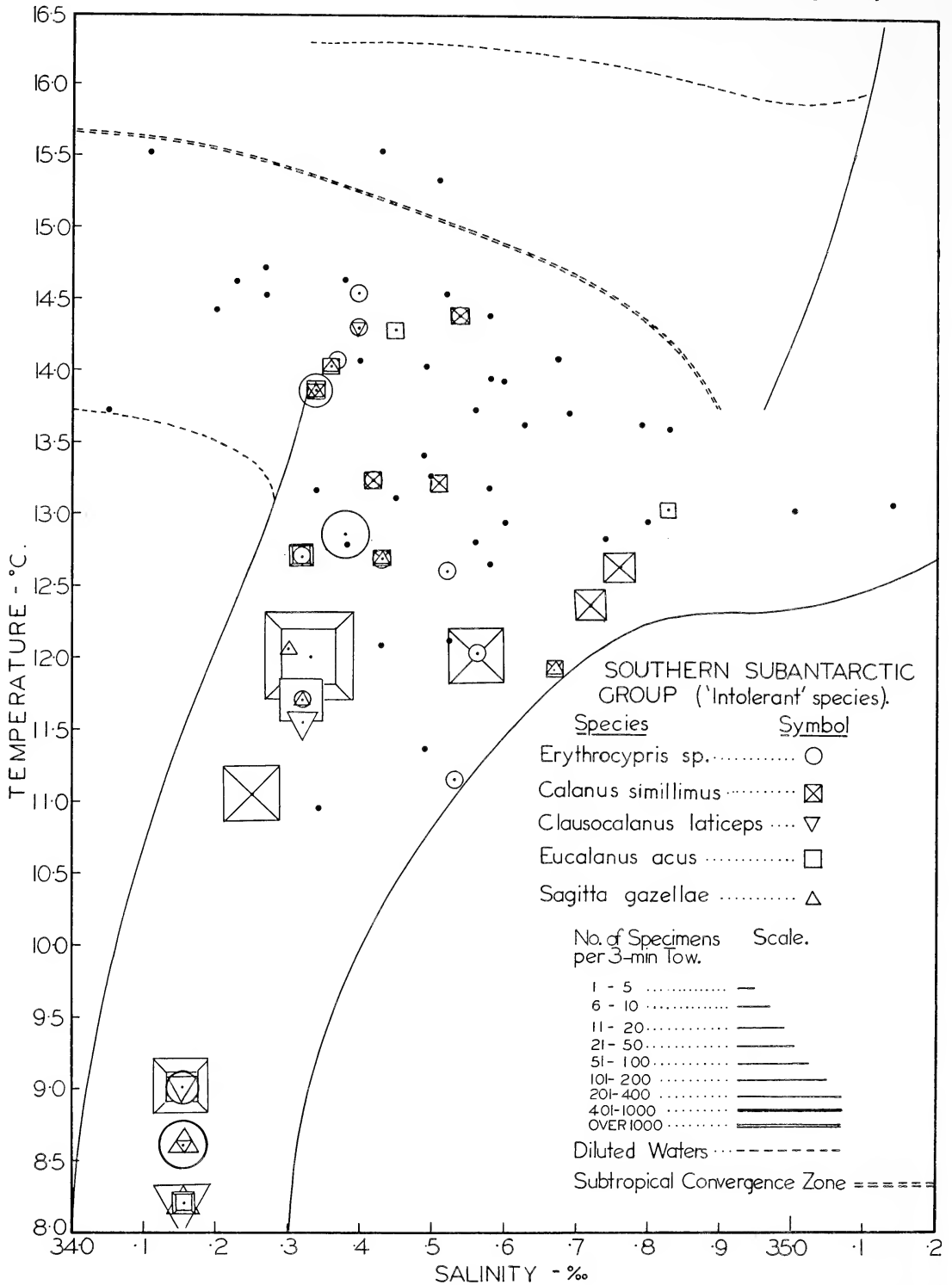


FIG. 5. The distribution in the temperature-salinity-plankton (T-S-P) diagram of Southern Subantarctic species which show a lack of adaptability toward coastal water through a marked reduction in the numbers taken from it. Water envelope as in Figure 3. Plankton stations at which no specimens were collected are shown by ●

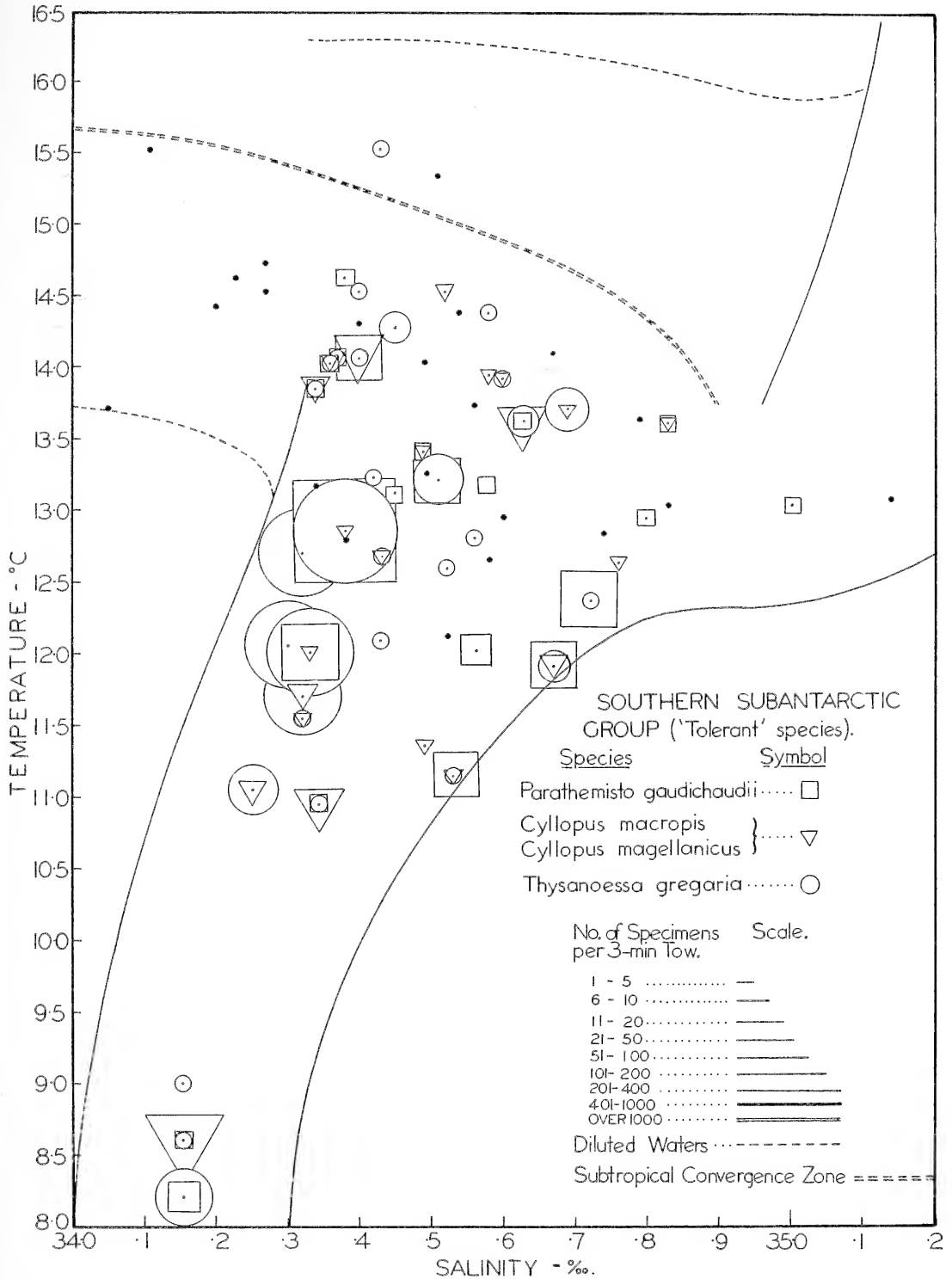


FIG. 6. The distribution in the T-S-P diagram of Southern Subantarctic species which are comparatively more widespread in (i.e., more "tolerant" of) coastal water. The numbers taken are higher in the coastal water than for the "Intolerant" species shown in Figure 5. Plankton stations at which no specimens of the group were taken are shown by ●

penetrating down the east coast—an extension of the East Cape Current (see Garner 1954, also his fig. 4*a*). That the data are in fact attributable to crossing the convergence is borne out to a considerable degree by the biological evidence.

Coastal water appears from Figure 3 to be an admixture of fresh water runoff and water of subtropical and subantarctic origins. Subantarctic water is of lower salinity than the water of subtropical origin and will dilute it; both of these waters and their mixtures will be diluted by fresh water. The salinity of coastal waters ranged from less than 34 ‰ (not shown in Fig. 3) up to about 35 ‰, and depends in part on which oceanic water predominates at a station, and on the proportion of fresh water in the coastal water mixture. The temperature ranged between 13° and 16°C., which is intermediate between those of waters of subtropical and subantarctic origins.

In the T-S diagram (Fig. 3) the water envelopes have been drawn arbitrarily to include all points entered. Solid lines indicate those water masses identifiable from the present data; dashed lines are indicative of dilution of the waters from these masses. The double dashed line signifies the subtropical convergence and separates all stations occupied to the south of it from those to the north. The proper extent of the convergence cannot be shown because the low winter temperatures of the water of subtropical origin permit the coolest samples from this water to be located in the summer temperature range of the coastal-subtropical mixture. Because of this, and because no stations crossed the convergence clear of the influence of coastal water, no position for the subtropical convergence between uncontaminated waters is shown in the diagram.

From the distribution of properties in the T-S diagram and from its form, general movements of both subtropical and subantarctic waters towards coastal water can be deduced. There will be mixing between these (and with fresh water) and this is represented in the

region of extreme salinity variation in the temperature range of about 13° to 15.5°C. Confirmatory evidence on water movements and especially those concerning mixing areas is to be derived from the distribution and interrelationships of the several groups of indicator species. In Figure 3, the stippled arrows show the general water movements as deduced from the T-S diagram, while in Figure 10 the movements as demonstrated by the planktonic distribution are illustrated. There is a general similarity.

SPECIES' GROUPS IN RELATION TO WATERS IN THE AREA

Four groups of species have been selected as representative of the zooplankton resident in the waters of the area of sampling (Tables 3, 4). There is one group from each of the coastal and subtropical waters, and two from water originating in the subantarctic. One of the subantarctic groups represents those species occurring predominantly in the colder waters and for convenience called the "Southern" Subantarctic Group; the other has been selected from those species occurring in water of subantarctic origin which has been warmed in its progress northward, namely, the "Northern" Subantarctic Group (see pp. 31-33).

The species and the species' groups are listed in Table 4, together with the numbers of specimens captured and the stations at which they were taken.

The degree to which the association of species in each of the groups is maintained in their normal environment, and when they are carried into abnormal conditions, is summarised in Figures 5 to 9 and is discussed below.

Southern Subantarctic Group

Stations 795, 826, and 921 (Fig. 2) lie within the field of cold subantarctic water as defined earlier, and appear to be removed from the influence of water of subtropical

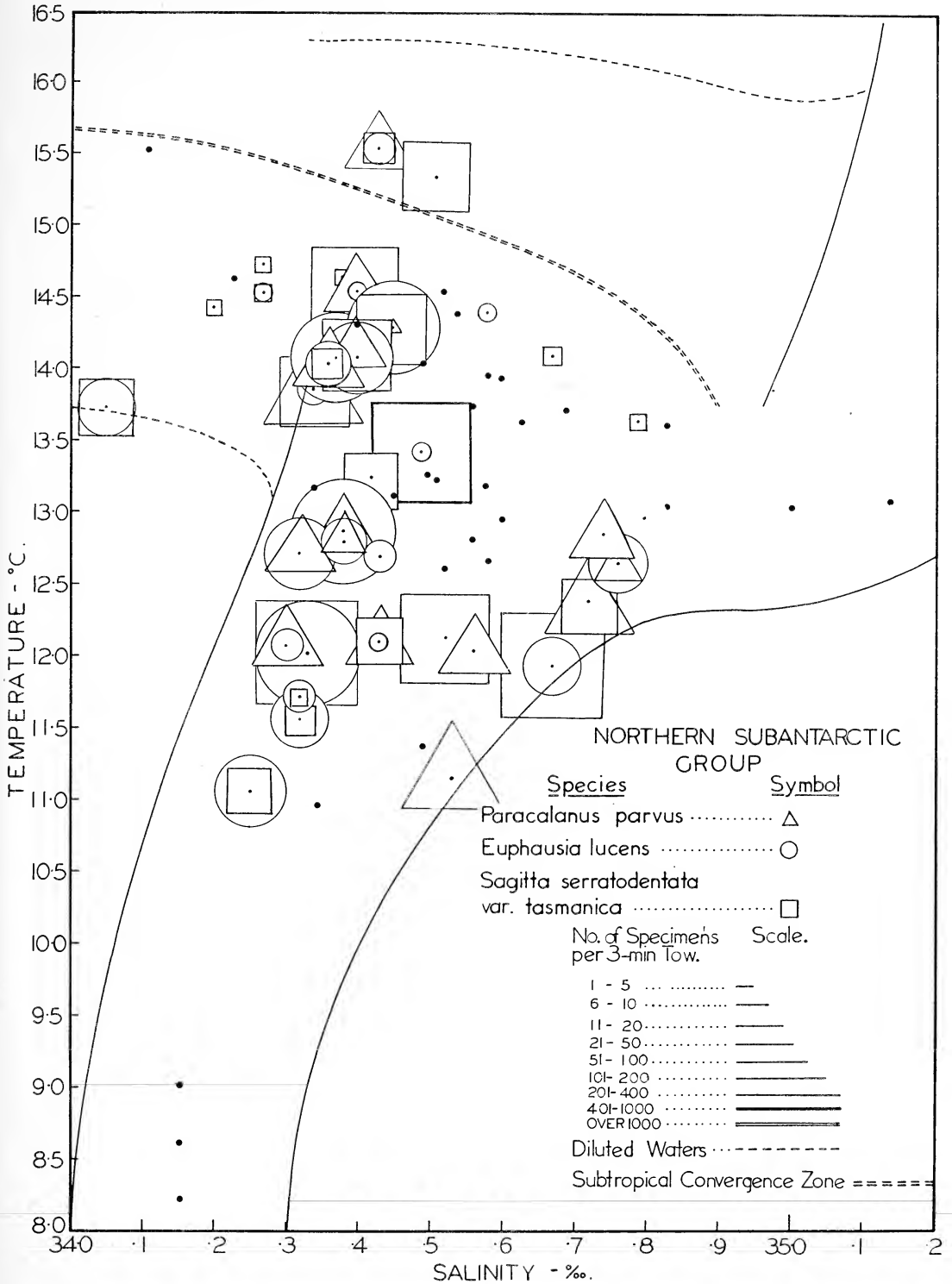


FIG. 7. The distribution of Northern Subantarctic species in the T-S-P diagram. Large numbers were taken. The species are confined to the northern, warmed subantarctic water, but extend into coastal water in strength in two areas where the subantarctic water is intruding into and mixing with, coastal water. Plankton stations at which no specimens of the group were taken are shown by ●

TABLE 4 Continued
THE PLANKTON STATIONS, THEIR TIMES AND DATES, AND THE SPECIES AND GROUPS COLLECTED AT EACH

STATION NO.	TIME OF DAY† (HOURS)	SERIES	SOUTHERN SUBANTARCTIC										NORTHERN SUBANTARCTIC	SUBTROPICAL				COASTAL							
			"Intolerant"					"Tolerant"						Paracalanus parvus	Euphausia lucens	Sagitta s. tasmanica	Sapphirina spp.	Hyperoche mediterranea	Iblea magallanica*	Thalia democratica*	Tengomyxis macropsis	Tengomyxis tenuipes	Parabemisto parvipes	Parabemisto australis	Nyciphanes australis
Dates	No.	Eurybrogypris sp.	Clansocalanus laticeps	Eucalanus acus	Calanus simillimus	Sagitta gazellae	Parabemisto gaudichaudii	Cylopus magellanicus	Cylopus macropsis	Thysanoessa gregaria	Paracalanus parvus	Euphausia lucens	Sagitta s. tasmanica												
285	2200.N		2	16		3	1	8	67	6	5														
292	0015.N	8-9.III.51	7	2	1	1	1	10	3	8	55										1				
297	0205.N					3			200	7															
301	0315.N		1	1	1				119	87															
304	0423.N		1						1	3	104														
308	0550.O		14						496	236											10	24			
310	0630.D		3						5	115											1	15	3		
322	1630.D																								
326	2035.N																								
330	0030.N	21-22.III.51		1				1	3	1															
337	0715.D																								
342	1217.D																								
795	1900.D		8	9	23																				
826	0300.N	13-17.XI.51	12	3	3																				
921	0300.N		40	3	3																				

* Combined totals of solitary and aggregate forms shown separately in Figure 8.

† D = daylight stations; N = stations at night; O = stations from dawn to sunrise, or sunset to dusk.

+ Signifies larger numbers of specimens than were counted.

origin. Species taken at these stations may be regarded as resident in such subantarctic water. Accordingly the species of the Southern Subantarctic Group have been selected from those collected at these stations.

Nine species have been selected. *Erythrocypris* sp., *Clausocalanus laticeps* Farran, and *Sagitta gazellae* Ritter-Zahony were present in small numbers, *Eucalanus acus* Farran in moderate numbers, and *Calanus simillimus* Giesbrecht was often very common, preponderantly as a Stage V copepodite. *Clausocalanus laticeps* and *E. acus* are both described as typically cold-water species (Farran, 1929; Hardy and Gunther, 1935) and stocks of *S. gazellae* are demonstrated as residing in antarctic and subantarctic waters by David (1955). *Calanus simillimus* is only to be captured from the southern waters (Vervoort, 1951). The numbers of these five species were noticeably reduced in coastal and mixed waters, which possibly indicates a lack of adaptability to the changed conditions. Consequently they have been distinguished as "Intolerant" species (Fig. 5). *Parathemisto* (*Euthemisto*) *gaudichaudii* (Guer.) and *Thysanoessa gregaria* Sars occurred commonly, but *Cyllopus macropis* (Bovallius) and *C. magellanicus* Dana were present in smaller numbers. *Thysanoessa gregaria* was discussed on page 17. *P. gaudichaudii* is a fairly widespread species in the colder waters of northern and southern hemispheres, while *Cyllopus* spp. have been recorded only from the colder southern waters (Stebbing, 1888; Barnard, 1930; Hurley, 1955; Hardy and Gunther, 1935). Larger numbers of these species penetrate into coastal waters, which suggests a greater tolerance towards altered conditions than was apparent among the "Intolerant" species; they are accordingly distinguished as "Tolerant" species (Fig. 6). Both "Tolerant" and "Intolerant" species belong in the Southern Group.

In the T-S-P diagrams Southern Subantarctic species are in continuous distribution, in moderate to high numbers, throughout water of subantarctic origin. All of the species

occur as well in coastal water, but the numbers of specimens collected decrease with modification of the environmental conditions as mixing progresses between the subantarctic and coastal waters. This is especially so of the "Intolerant" species. Dilution by fresh water (Stations 99, 90, 48, 109) and, to a lesser degree, increase in salinity (Stations 126, 103, 124) appear to restrict the "lateral" spread of species in the diagrams although much of their apparent effects may be due to the stations having been occupied in daylight. Rising temperatures are less restrictive. Most of the species were taken throughout the range sampled, but much less commonly at the higher temperatures, even in hauls made at night.

Transfers of species from subantarctic to coastal waters were largely concentrated about three groups of stations, namely 292, 330, 310, 304, 79, 40, and 189, 190, 125. Subantarctic species also extend, in small numbers, through Stations 218, 4, 198, 208, to 178, 138, and 130. The stations of these three aggregations will be referred to subsequently when it will be found that they were situated in mixing waters (see Figs. 3, 10).

Northern Subantarctic Group

The species selected for the Northern Subantarctic Group were confined to that warmer water (i.e., 11°C. and higher) which is believed to have originated in the higher latitudes of the subantarctic. None was present in the colder waters at Stations 795, 826, or 921 (Fig. 2). Three species have been selected, namely, *Sagitta serratodentata* Krohn var. *tasmanica* J. M. Thomson, *Paracalanus parvus* (Claus), and *Euphausia lucens* Hansen.

Sagitta serratodentata has been described as "cold tolerant," while the variety *tasmanica* is reported to inhabit waters of 11° to 17°C. (Thomson, 1947). John (1936) describes *E. lucens* as predominantly a northern subantarctic species occurring most frequently between 12° and 14°C., which confirms Tattersall's

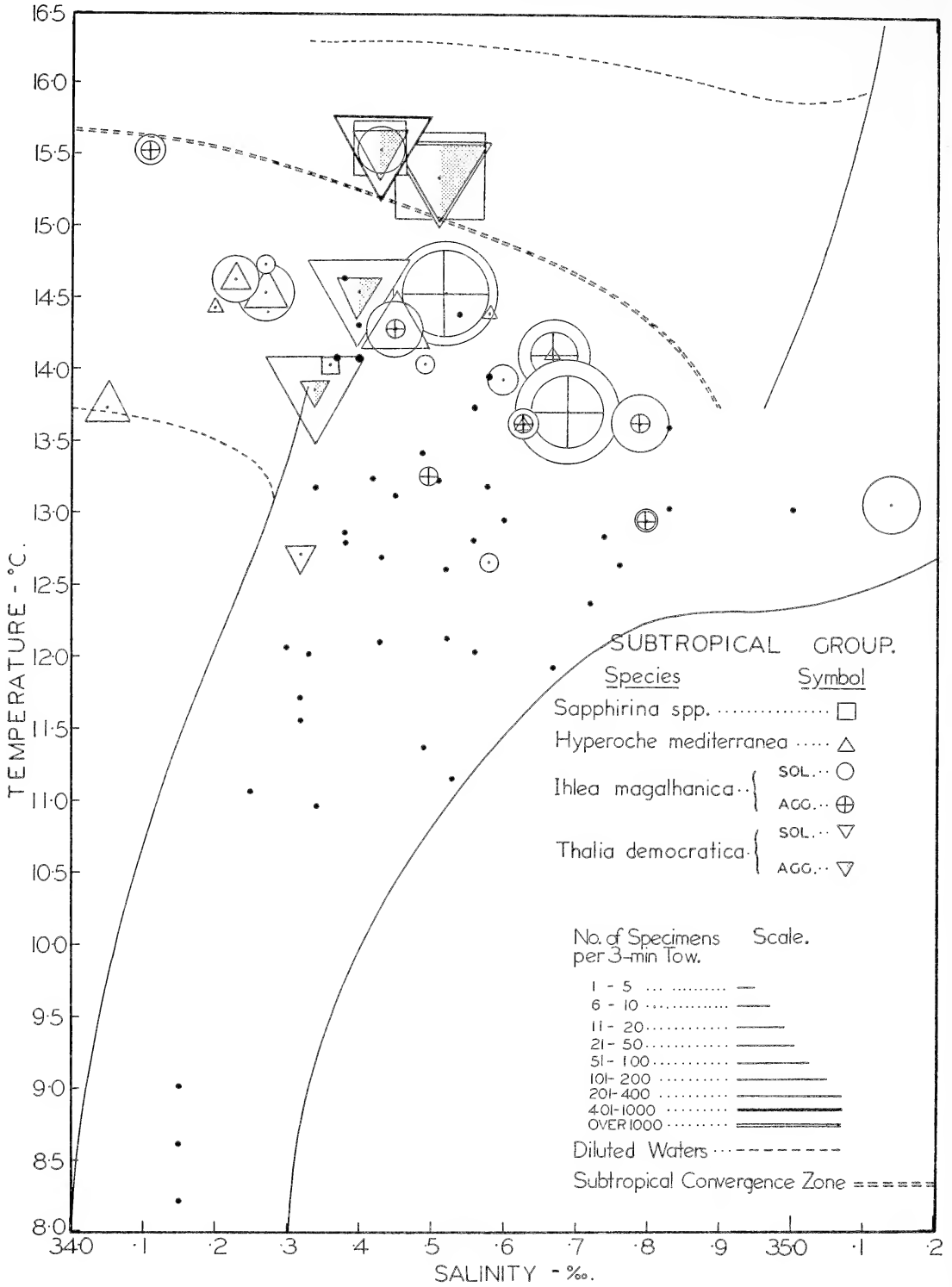


FIG. 8. The distribution of Subtropical species in the T-S-P diagram. Species are almost confined in the warmest water. Plankton stations at which no specimens of the group were taken are shown by ●

(1924) appreciation of its distribution. Thus the distribution of these species as shown in the T-S-P diagram (Fig. 7) agrees with previous accounts. The distribution of *P. parvus* is restricted to that recorded previously (see p. 17).

The distributions of the species and the numbers captured relative to temperatures and salinities are shown in Figure 7. It is evident that the numbers taken were often large. All species were strongly represented at Stations 292, 330, 310, 79, etc., and 189, 190, (referred to as being in mixed waters in the discussion of the Southern Subantarctic Group), but are present only as rarities, or are absent from collections at other stations in coastal-subtropical waters. Reduced numbers were taken at Stations 212 and 214 in colder waters. As these were night stations this reduction may be a reflection of the effects of the lower temperatures. At some other stations in these colder waters, e.g., Stations 5, 191, 6, specimens were absent or rare, but this may be a result of the stations being occupied in daylight.

Not only do the Northern Subantarctic species inhabit the comparatively warmer water of subantarctic origin, but they can penetrate into warm mixed waters in larger numbers than any of the Southern Group of species. This may be consequent on their adaptation to higher temperatures in their more usual habitat. According to John (1936), there is a gradual amelioration of conditions, with changes in the composition of the planktonic fauna to correspond, as one proceeds from colder to warmer northern waters in the subantarctic. Therefore the abrupt transition suggested by the convenient subdivision of the species into Northern and Southern Subantarctic Groups probably over simplifies the faunal distribution. Further sampling at temperatures lower than 11°C. may demonstrate a gradual decrease in the frequency of occurrences and in the number of species taken of the Northern Subantarctic Group—a decrease which would accord with John's views. How-

ever, such would not necessarily detract from either the Southern or Northern groups of species as indicators of the particular conditions for which they have been selected.

Subtropical Group

The species of the Subtropical Group have been selected on the basis of their previous distributional records. Although detailed sampling is required in those New Zealand waters which are beyond doubt of subtropical origin in order to demonstrate that the species originated there, it is believed that they are typically of the subtropical population. The species selected are *Sapphirina* sp., *S. angusta* Dana, *S. gemma* Dana, *S. sali* Farran, and *S. pyrosomatis* Giesbrecht (see Wilson, 1932), *Iblea magalbanica* Apstein, *Thalia democratica* Forskal (see Thompson, 1942, 1948), and *Hyperoche mediterranea* Senna (Stephensen, 1924, Hurley, 1955). Of these, *H. mediterranea* did not occur at Stations 322 and 326, and *Sapphirina* spp. were taken only at these stations.

The wide range of salinities (Fig. 8) over which these species are taken points to their tolerance in this regard. On the other hand, the species maintain a close association with the warmest water and only exceptionally are specimens taken outside of it. The group thus strongly contrasts with the two Subantarctic groups.

The species of this group are normally associated with subtropical water. In this survey they occur largely in the warmest water (Fig. 8), and therefore it is suggested that this water is of, or is being influenced by, water of subtropical origin. Except for Stations 322 and 326, the majority of the collections of the Subtropical species were from stations of Series 1 (see Figs. 1, 3), mostly within Foveaux Strait, i.e., within the area expected to be most strongly influenced by any eastward flow of water from subtropical sources. The few other occurrences of the species usually are associated with coastwise extensions of the subtropical influence.

It may be coincidental that the Subtropical species have proved adequate to indicate the waters of subtropical origin from both east and west of New Zealand. If further investigation shows that the faunas are dissimilar, separate indicator groups would probably need to be established for the waters of each of these areas.

Coastal Group

Species indigenous to coastal waters must necessarily be tolerant of the considerable fluctuations in temperature and salinity which may occur in these waters. The species of the Coastal Group are distinguished from the Subtropical Group by occurring over a much wider range of temperatures (Figs. 8, 9). Six species have been selected, namely *Tenagomysis macropsis* Tattersall, *T. tenuipes* Tattersall, *Parathemisto (Euthemisto) gracilipes* Norman, *P. (E.) australis* Stebbing, *Nyctiphanes australis* Sars, and *Oikopleura dioica* Fol. *Nyctiphanes australis* is a recognised coastal species (Sheard, 1953), as is *O. dioica* (Thompson, 1948). *Tenagomysis* spp. have been confined almost completely to neritic conditions (Tattersall, 1918, 1923; Bary, 1956). *Parathemisto australis* has been collected previously only in coastal areas (Stebbing, 1888; Barnard, 1930), which is true of the present material (Hurley, 1955). *Parathemisto gracilipes* occurred in similar localities to, and was often captured with, *P. australis*, although the literature describes it as an oceanic species. Of these species only one specimen of *N. australis* was captured in water of unquestioned subantarctic origin (Station 212, Fig. 9), presumably as a stray. On the other hand, all species were present very commonly at stations where subantarctic water is believed to have been mixing with coastal water (Stations 292, 310, 330, etc., and Stations 189, 190, 125). A few specimens of *Parathemisto* spp. were taken at Station 322—suggestive of coastal water at the station. The occurrences of Coastal species at Stations 124 and 128 are not incon-

sistent. These stations lie in highly saline water which appears to be originating in a large shallow inlet on the north coast of Stewart Island (Patterson Inlet, Figs. 1, 12), and it is this water which locates the stations in the part of the diagram representing subtropical water (Fig. 3).

There is a general, but patchy, distribution of Coastal species throughout the coastal water, from high to low salinities and up to the highest temperatures. Nevertheless, they are almost completely absent from subantarctic water, even when it is contiguous with coastal water. It is believed that the species either are unable to survive being transferred from the coastal into subantarctic water, or that some physical process at the boundary between the waters prevents such a transfer (see pp. 48-49).

INTERRELATIONSHIPS BETWEEN SPECIES' GROUPS, AND TEMPERATURES AND SALINITIES

The interrelationships of the species' groups and their correlation with temperatures and salinities are shown in Figure 10. The groups are distinguished in the figure by hatching, and a subjective estimate of the abundance of each is indicated. The "area of chief concentration" is demarcated by lining-in and represents that portion of the diagram in which the bulk of each of the groups was captured.

As particular organisms are undoubtedly characteristic of particular waters, those instances where species from several waters are found together are believed to represent areas of mixing waters. Figure 10 illustrates that there are aggregations of stations (already referred to) from which large mixed catches were consistently made. Stations 292, 330, 310, 279, 304, 40, and 79 (refer also to Fig. 3) form one aggregation and Stations 189, 190, and 125 another. All four species' groups were present at most stations of the first aggregate, which indicates that the collections are from a mixture of the three waters. Subtropical species were absent from stations of the second

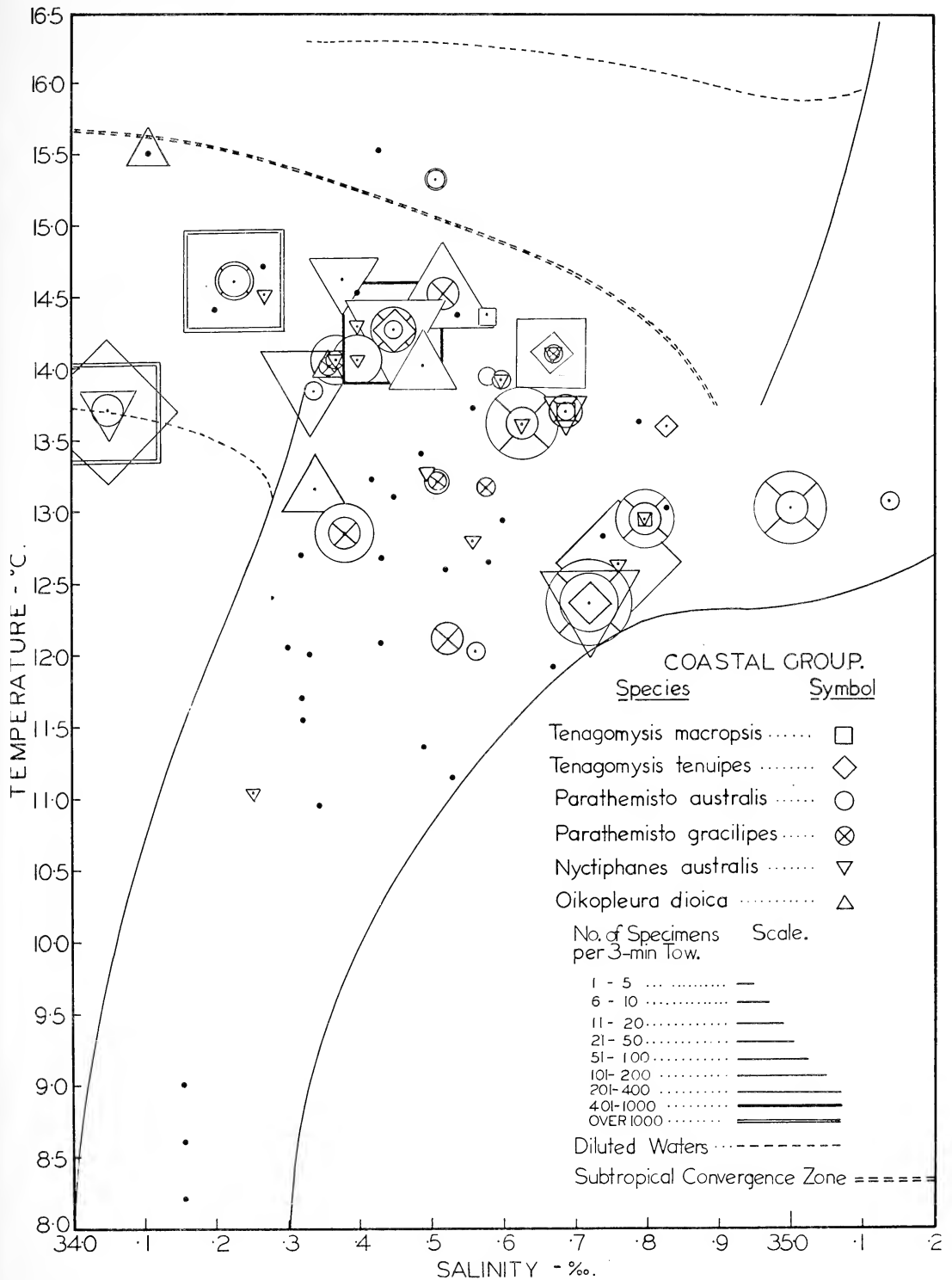


FIG. 9. The distribution of Coastal species in the T-S-P diagram. These species occur commonly over comparatively wide salinity and temperature ranges. They do not occur in subantarctic water except where it is intruding into, and mixing with, the coastal water. Plankton stations at which no specimens of the group were taken are shown by ●

aggregation (except Station 125), suggesting little or no influence from water of subtropical origin. A third group of stations yielded comparatively small mixed catches of Coastal, Subtropical, and "Tolerant" Southern Subantarctic species, which indicates that mixing was also taking place. This mixing may have been on a minor scale or the small catches may be due to the tows being made in daylight. The stations form a discontinuous series extending more or less vertically through the diagram to terminate at Stations 130 and 138.

The distributions of the groups in Figure 10 are brought about by movements of the waters of which they are indicators. Therefore, the general courses of such movements should be traceable from these distributions. The fact that subtropical oceanic species are present in the coastal water indicates that water of subtropical origin is moving into the coastal water. Similarly the distribution of the Subantarctic species shows they also are being carried into the coastal water. These movements are shown by stippled arrows in Figure 10. Those portions of the T-S-P diagram which are illustrative of intensive mixing of plankton and waters suggest that, as well as these general movements, there are others in which there is a more vigorous, localised penetration shorewards. It would seem that these are predominantly of water of subantarctic origin, intruding into coastal water.

A number of the stations of each of the regions of mixed waters in Figure 10 are widely distributed geographically and in time. Nevertheless, where similar environmental properties have ensued on the mixing of the waters, the group composition of the plankton hauls, and often the quantity collected, are comparable. Thus in this T-S-P diagram, the selected representatives of the zooplankton emphasise and enable the identification of those stations at which mixing of waters is inducing similarities in the environmental conditions. Conversely, the diagram shows for those stations at which one group of spe-

cies is present, or predominates, that the water is entirely or predominantly of that mass for which the species constitute an indicator group.

It can be argued with respect to the "faunal island" about Stations 322 and 326 (Fig. 10) that more frequent sampling would have revealed a continuity in the species distribution between these and other stations of the series (Fig. 2). In all, seven salinity-temperature and plankton stations were occupied near to and north of what is believed to be the subtropical convergence (Figs. 4*a*, 19*b*), and all are located in the T-S diagram (Fig. 3) in water of subtropical origin.

Waters of mixed properties undoubtedly occur about the convergence. However, should water of either subtropical or subantarctic origin be present in slightly greater quantity, stations would tend to aggregate in the one or the other in the T-S diagram. The predominating water would be reflected in the species which were present. On the other hand, if samples are from truly intermediate conditions, an intermediate position would be occupied in the diagrams; but if the transition zone is narrow (as in the present traverse, see Fig. 4*a*), such samples would be rare. The subtropical group of species predominated at Stations 322 and 326, which agrees with the stations being north of the convergence and in water largely of subtropical origin (some Subantarctic species were taken, but they are believed to have originated in the subsurface subantarctic water, see p. 47). In the circumstances, therefore, it seems reasonable to separate Stations 322 and 326 from the remainder.

GEOGRAPHICAL DISTRIBUTIONS OF TEMPERATURES, SALINITIES, AND SELECTED SPECIES, AND CORRELATION OF THESE WITH THEIR DISTRIBUTIONS IN T-S-P DIAGRAMS

A sequence of geographical charts incorporating synoptic or quasi-synoptic collections of temperatures and salinities should demonstrate cyclical or other changes in the distri-

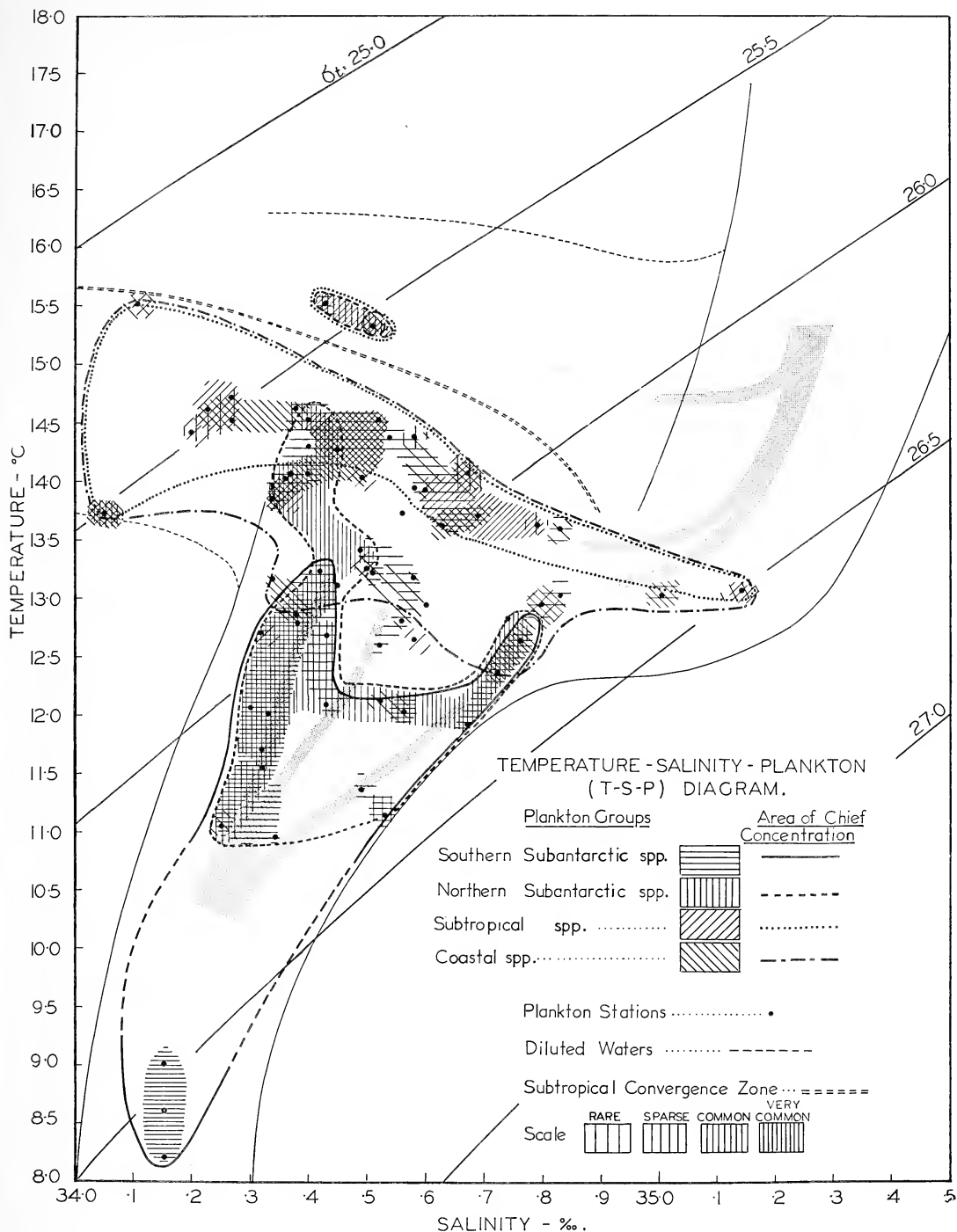
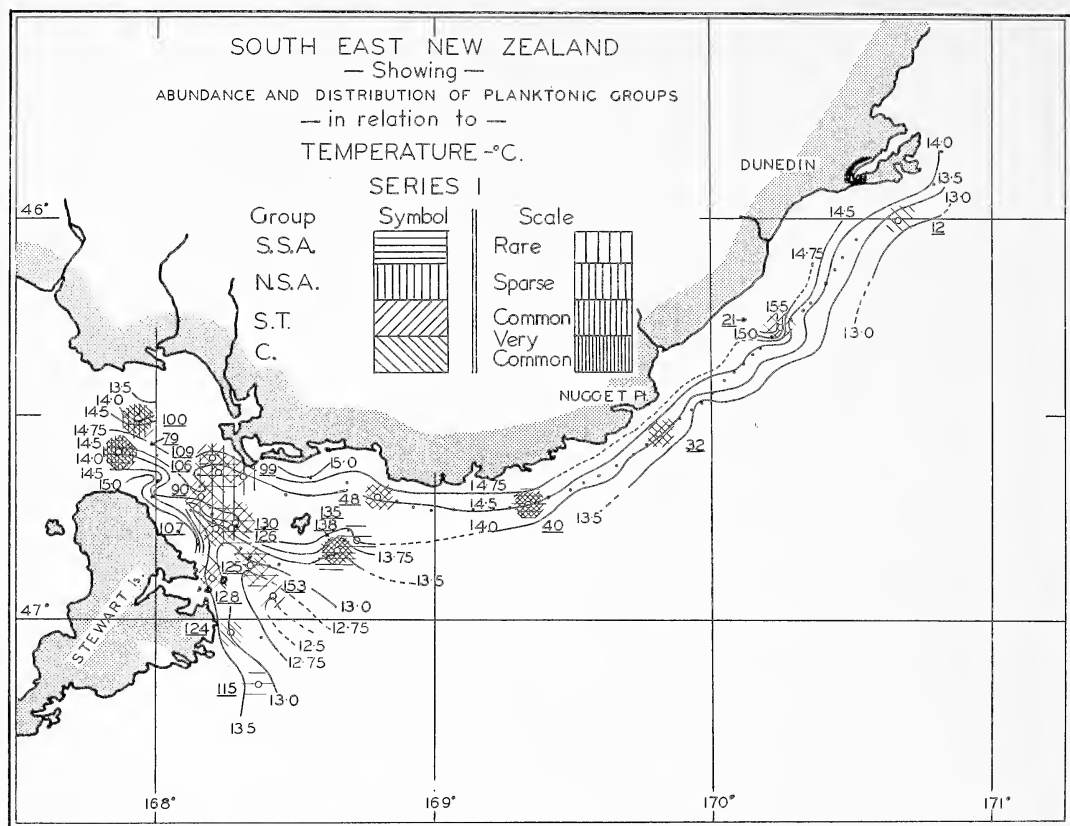


FIG. 10. A generalised T-S-P diagram in which the distributions and interrelationships of the four planktonic groups from the waters about southern New Zealand are shown. Note the three areas where mixed plankton catches indicate that mixing of waters is taking place. The water envelope is as in Figure 3; only plankton stations are entered.



FIGS. 11, 12. Series 1, Stations 10–153, January 6–24, 1951. The distribution of Southern and Northern Subantarctic, Subtropical, and Coastal species in relation to Figure 11, Temperature, °C.; and Figure 12, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperatures or salinities additional to those taken at plankton stations •; plankton station numbers are underlined.

butions of the properties of an area. In turn such changes may be correlated with variations in the geographic distribution of the plankton to yield information showing the causes and effects of water movements on species distribution. Accordingly the geographical distributions of water properties and of plankton groups are discussed for the stations of Series 1 to 7. The relationships thus disclosed are considered with reference to the distributions in the T–S–P diagrams.

Series 1. Stations 10 to 153; 6 to 24.I.51

The stations of Series 1 were accumulated over a period of 18 days. Of these, Stations

10 to 48 were occupied during January 5 to 6, 1951. Charts of the distributions of temperatures and salinities (Figs. 11, 12) illustrate an average of conditions because of the length of time involved.

Warm, comparatively highly saline water extends from the western and central Straits along the South Island coast, and has probably originated in that Tasman Sea water which has been deflected to the southward along the west coast of South Island. It is being diluted by fresh water. Other highly saline water appears to be entering from Patterson Inlet, and spreads thence south-eastwards along the coast of the island. Cooler water (Fig. 11) is present as a tongue-like intrusion

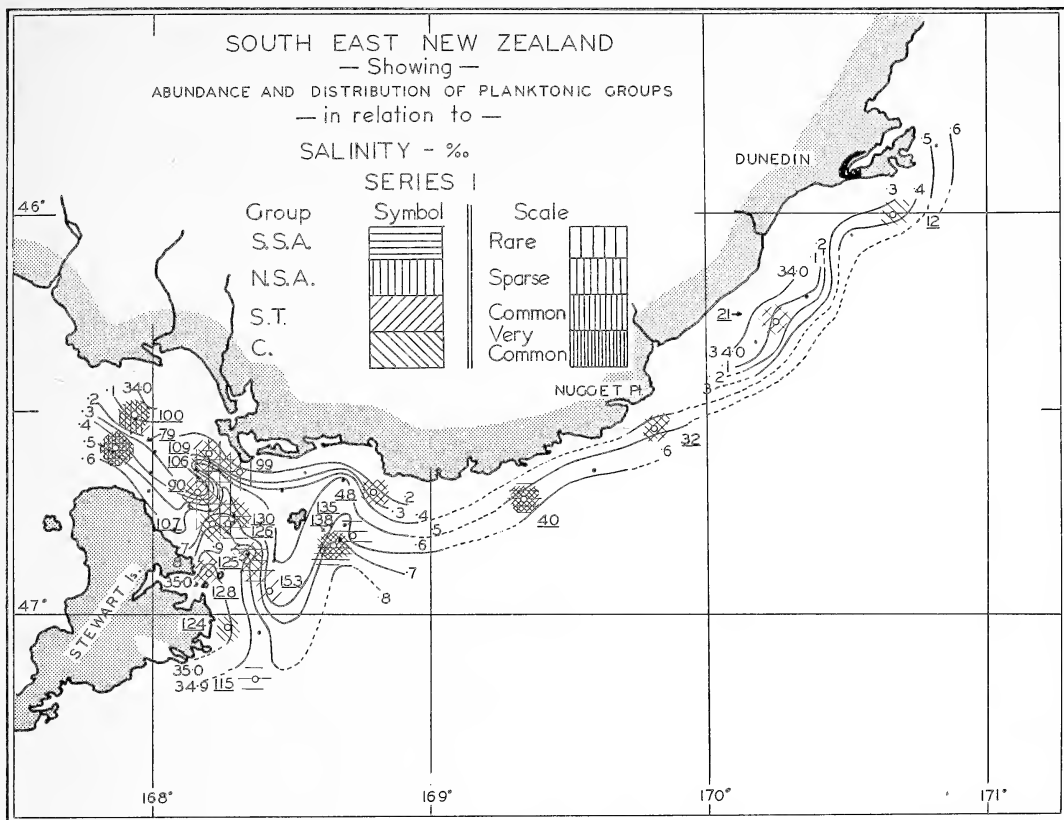


FIG. 12. See legend for Figure 11.

from the southeast. However, the distribution of salinities suggests that highly saline water has spread throughout the area.

Only some general features of the plankton distribution in relation to that of the water properties will be discussed. From the T-S diagram (Fig. 3) it is apparent that the stations of Series 1 lie predominantly in the warmest waters, only a few being slightly influenced by the cool water from the south-east—a condition conforming more to that indicated by the distribution of salinities (Fig. 12). However, the T-S-P diagrams (e.g., Figs. 6, 10) demonstrate that Subantarctic species were present, in small numbers, at several of the stations. Thus indications are that water of subantarctic origin is entering Foveaux Strait, some of it probably from the south-east, as is suggested by the conformation of the isotherms (Fig. 11).

Station 79, and the geographically close Station 100, both possess a strong representation of Subantarctic species. In the T-S-P diagram (Fig. 10) Station 79 forms one of that group of stations at which occurrences of all plankton groups are suggestive of a mixture of all waters. It is likely, therefore, that subantarctic water is present, entering probably from the west, along with mixed coastal-subtropical waters. That the influence of this subantarctic water is weak is suggested by both the positions of Stations 79 and 100 in the T-S diagram (Fig. 3), and the lack of any indication of the water about them in the relevant geographic charts (Figs. 11, 12). Station 138 is in that part of the T-S-P diagram (Fig. 10) representative of mixing on a minor scale, and Subantarctic, Coastal, and Subtropical species were collected. The configurations of the isolines indicate a small-

scale intrusion of water of subantarctic origin into coastal-subtropical waters at Station 138. Thus the planktonic occurrences accord with the influences bearing at that point.

Occurrences of zooplankton at other stations could be individually discussed, and rational explanations of the presence or absence of groups can be advanced for many of them, but the detailed picture that results is a confused one. The waters are very mixed. The distributions of the species' groups are to an extent reflecting this state, which is aggravated by the long period over which sampling continued.

It is reasonable to deduce, from the physical data presented in Figures 11 and 12, that there is some influence from water of subtropical origin in Foveaux Strait. The presence of typically Subtropical species is supporting evidence. More conclusive evidence for the influence is demonstrated, however, from the distributions of the Subtropical species in the T-S-P diagrams (Figs. 8, 10, in particular). The occurrences of these species coincide with the distribution of the warmest waters which are in such a position as to be contributed to directly from the subtropical mass (Figs. 3, 10). Subtropical species were collected also at stations in later series (Stations 178, 199, 239, 292, 304); these occurrences are indicative of coastwise extension of the subtropical influence.

Series 2, Stations 159 to 192; 29.I.51 to 1.II.51

The stations of Series 2 (excepting along the coast of South Island) are eastward of, and a little further to seaward than, those in Series 1 (Figs. 1, 13). Cooler temperatures than those in Series 1 prevail along the coast of South Island, and there is a broad intrusion of cool water (Fig. 13) from the south and east. There is, too, an admixture of high salinity water throughout the sampled area (Fig. 14). A northwest to southeast displacement of the isolines about Stations 189 and 190, eastward of Steward Island, suggests that

warm, high salinity water is present, possibly from Foveaux Strait.

Very common occurrences of Northern and Southern Subantarctic groups of species at Stations 187, 188, 189, 190, and 192 are believed to be indicative of a strong influence from water of subantarctic origin (Figs. 7, 10). Common occurrences of Coastal species at Stations 189 and 190 point as well to mixing between the coastal and subantarctic waters about these stations, and also suggest that the high salinity water extending from Patterson Inlet does in fact originate there, and is not an intrusion from other oceanic sources. The occurrences of the planktonic groups in relation to the geographic distributions of water properties (Figs. 13, 14) provide a similar picture. Stations 189 and 190 lie on the southwest side of the intruding low-temperature water. Mixing is undoubtedly taking place about these stations between this and the warm, saline Straits water. The collections of mixed planktonic groups confirm this. Stations 187, 188, 191, and 192 are closely associated with the intruding cool water (Fig. 13), which the predominance of Subantarctic species indicates is of subantarctic origin.

Stations 178 and 165 lie in high salinity, warm inshore water (Figs. 13, 14), and the Coastal and Subtropical species at both stations are in agreement with this. In addition, mixing with subantarctic water is indicated for Station 178 by the Subantarctic species occurring there. The regularity of the isolines in the vicinity of the station denotes that the waters are mixed, which agrees with Station 178 being (together with Stations 138, 135, and 130, Series 1) in that portion of the T-S-P diagram (Fig. 10) representing mixing of waters on a minor scale.

Stations 187 to 192 are moderately separated geographically, but their grouping in the T-S-P diagram demonstrates a certain homogeneity of environmental conditions. The diagram heightens the effect that coastal water has on the composition of the plankton

at Stations 189 and 190, but at the same time demonstrates an overall influence from Subantarctic species which are being introduced by water of subantarctic origin.

Subantarctic species, and water of subantarctic origin, are more in evidence at stations of Series 2 than at those of Series 1 (for which Subtropical species indicate that at least some of the water has originated in the subtropical mass). The differences between the series are concisely illustrated by the T-S-P diagrams (Figs. 7, 8, 10).

Series 3. Stations 193 to 228; 5 to 13.II.51

The beginning of Series 3 is separated by four days from the end of Series 2. In Series 2, lower temperatures than in Series 1 pointed to an increased subantarctic influence off the coast of South Island. In Series 3, cool, low-salinity water has intruded strongly towards the coast, centred a little to the west of Stations 216 and 218 (Figs. 15, 16). This intrusion appears to be acting as a barrier to an east-going coastwise movement of warm, high-salinity water, causing it to spread in a fanlike manner towards the southeast. High salinities and temperatures to the east of Stewart Island suggest that some of this water may be escaping in a narrow zone along the coast of the island. The isohalines and, to a lesser extent, the isotherms indicate that the influence of the cool, low-salinity water extends well in towards the Strait.

Apart from an exceptional occurrence of a Coastal species at Station 212, the plankton taken at Stations 210, 212, 214, 216, 218, and 206 is entirely of Southern and Northern Subantarctic groups (Figs. 10, 5, 6, 7). The water at these stations, therefore, is regarded as being of subantarctic origin. The stations are moderately separated geographically (Figs. 1, 15). However, their aggregation in the T-S and T-S-P diagrams (Figs. 3, 10) emphasises an essential homogeneity of the water which the occurrences of the subantarctic species confirm.

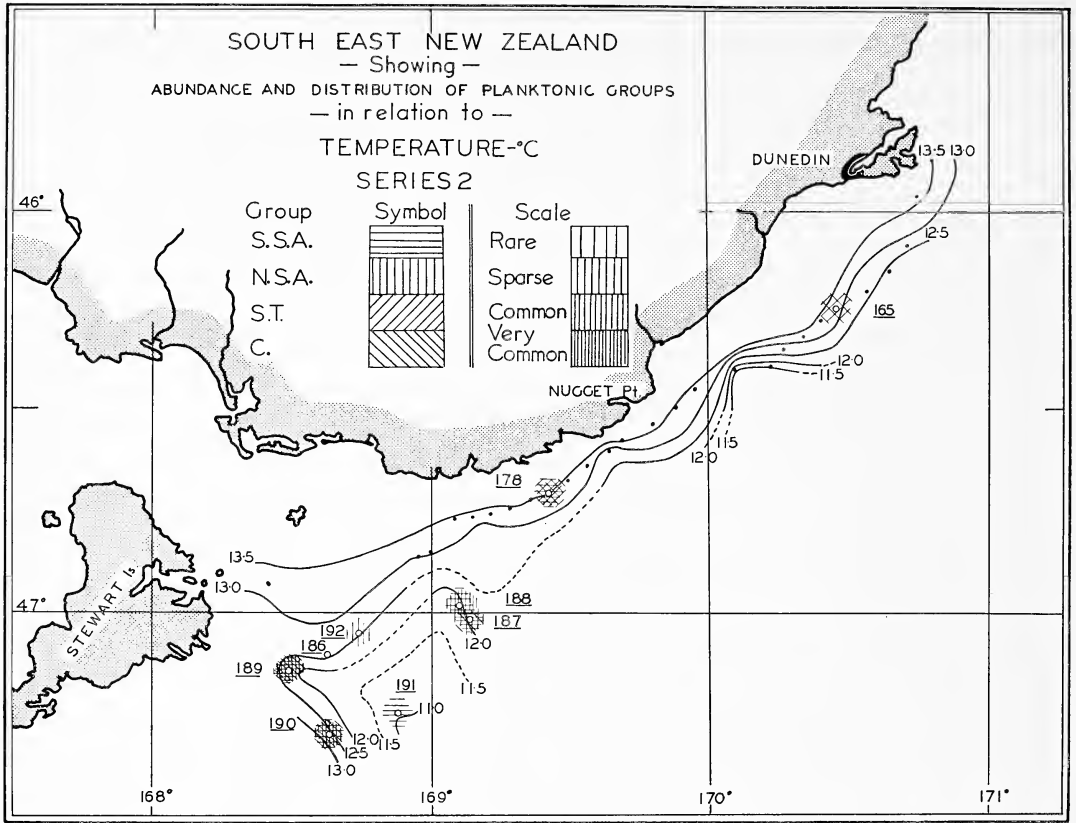
Four stations, namely 218, 208, 198, and 199 are located in water of slightly higher salinity (Fig. 10) than the other stations of the Series, possibly as the result of coastal water mixing with that from the subantarctic. Occurrences of Coastal plankton at 208 and 198 support this view; the subantarctic influence is evident from the Southern Subantarctic species captured at 218 and 198, and Northern and Southern Subantarctic species at 208. (No selected species were taken at Station 199.) From the geographic charts Station 218 appears from its temperature (Fig. 15) to be influenced by subantarctic water; on the other hand, the comparatively high salinity suggests some influence from coastal-subtropical water. As Southern Subantarctic species only were taken, the latter influence was not confirmed by the plankton haul. The temperature and salinity at Station 208 indicate that it is located in mixed waters and its plankton content supports this.

It is of interest that the distribution of the selected Subantarctic species of Series 3 indicates that uncontaminated water of subantarctic origin has a restricted salinity range of between about 34.2 and 34.45 ‰ (Figs. 3, 10).

There are distinctive characteristics to the species composition of stations in this, as compared with the previous two series, which are readily seen from the T-S-P diagrams. They are believed to be directly attributable to the different properties which are evident between the waters of the three series. Unlike Series 1 and 2, water of subantarctic origin is dominant in Series 3, and the occurrences of the Subantarctic species coincide with and, in fact, delineate its extent in the diagrams (Figs. 5, 6, 7, 10).

Series 4. Stations 229 to 314; 8 to 9.III.51

The collections of this, and the subsequent, series are as nearly synoptic as is possible from a single ship. Stations of Series 4 were occupied approximately one month later than those of Series 3.



FIGS. 13, 14. Series 2, Stations 159–192, January 29–February 1, 1951. The distribution of the four planktonic groups in relation to Figure 13, Temperature, °C.; and Figure 14, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperatures or salinities additional to those taken at plankton stations •; plankton station numbers are underlined.

When compared with Series 3, higher temperatures near the coast of South Island (Fig. 17) point to a restoration of the influence of mixed coastal–subtropical waters, originating probably in the west. A slight influence from water of subantarctic origin is indicated by the shoreward deflections of isotherms south of Nugget Point. The pronounced shoreward bulges of isotherms and isohalines at a number of other localities are suggestive of stronger influences from the same source (Figs. 17, 18). The conformation of these isolines may suggest as well an offshore movement of coastal water in adjacent areas. Steep temperature gradients between the warm saline coastal and the cool, less saline

oceanic waters are suggestive of mixing, over short distances. There is an area of more general mixing extending from shortly south, to north, of Dunedin.

In the T–S diagram (Fig. 3) the plankton stations of Series 4 lie in a group between 11.75° and 14.5°C., and (all but Station 239), between 34.3 and 34.4 ‰ salinity. Thus they are closely associated with Stations 212, 214, etc., of Series 3. At each of Stations 270, 285, 297, 301, and 308 there is a strong representation of Northern and Southern Subantarctic planktonic groups (Fig. 10). Therefore, the position of the stations in the T–S diagram, and their plankton content, associate them with the water of subantarctic origin. The

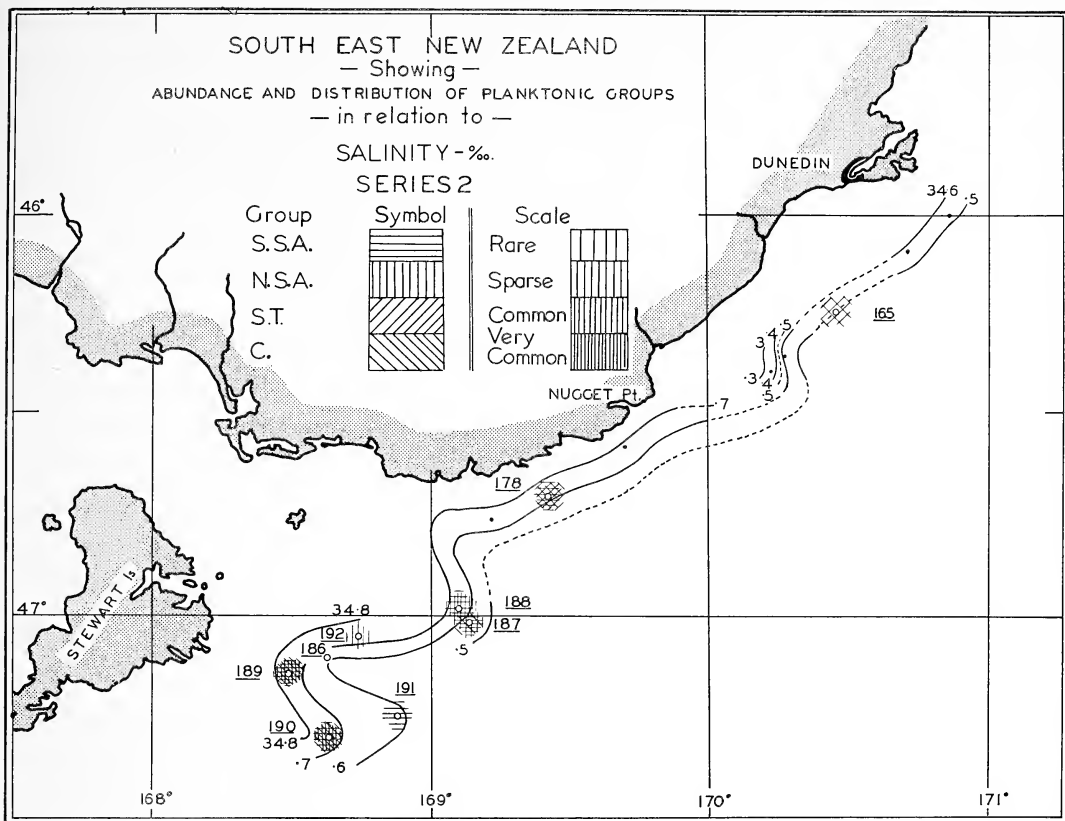


FIG. 14. See legend for Figure 13.

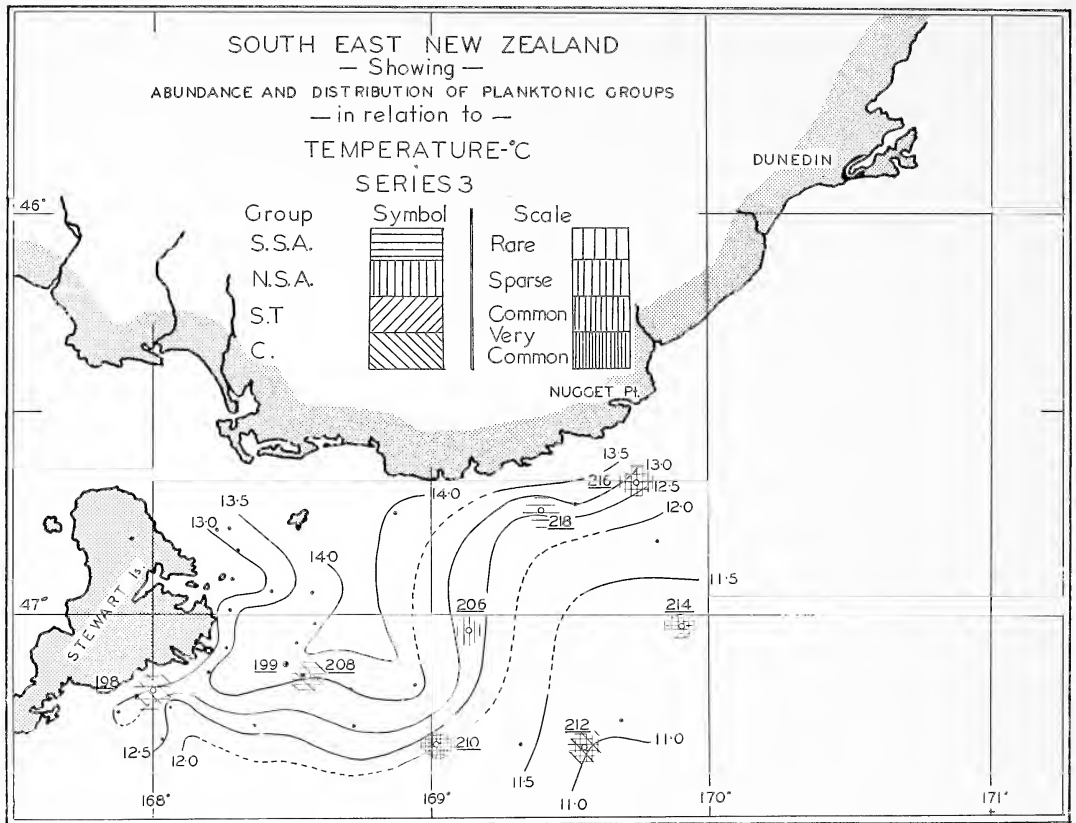
subantarctic influence is confirmed by the geographical distribution of temperatures at Stations 285 and 297 (Fig. 17), and salinities at 270, 301, and 308 (Fig. 18).

Of the remaining stations in Series 4 (Stations 292, 310, 279, 244, 304, and 239), Station 239 lies in coastal water (Fig. 10), but exceptionally contained a rare representation of the Southern Subantarctic Group; this group was present also at Station 244. Temperatures indicate that subantarctic water may be influencing these two stations (Fig. 17) which possibly explains the plankton occurrences. Nevertheless Coastal and Subtropical planktonic groups would have been more appropriate, especially at Station 239.

Stations 292, 310, 279, 304, and 244 are grouped together in the T-S-P diagram and

the mixed Coastal, Subtropical, and Subantarctic (mostly Northern) plankton at most of them denotes they are sampling in a mixture of subantarctic and coastal-subtropical waters. Isotherm configuration (Fig. 17) indicates that, following an initial mixing between water of subantarctic origin (as is present at Stations 285, 297, and 308) and coastal water, the influence of the subantarctic water continues shorewards towards Stations 279, 292, and, to a lesser degree, 310. Isohalines (Fig. 18) point to Station 304 being influenced by water of subantarctic origin as well.

Series 4 is important for two reasons. First, Stations 292, 310, 279, 304, and 244 form a compact group in the T-S-P diagram (Fig. 10). These are geographically isolated sta-



FIGS. 15, 16. Series 3, Stations 193–228, February 5–13, 1951. The distribution of the four planktonic groups in relation to Figure 15, Temperature, °C.; and Figure 16, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperature, salinity additional to those taken at plankton stations •; plankton station numbers are underlined.

tions, but they are aggregated because of similarities of hydrological and biological properties, which are the result of invasions into coastal water, at several localities, of water of subantarctic origin. Second, coastal and subantarctic waters in the T-S and T-S-P diagrams are linked through a continuous series of stations. Such a linkage demonstrates beyond reasonable doubt that the Subantarctic plankton collected in the coastal area originates, and is transported, in water of subantarctic origin which is penetrating shorewards (and at the same time is being warmed). These two facts thus contribute evidence in support of an earlier statement that planktonic content of mixing waters may be utilised to indicate the sources of the waters being

mixed.

The T-S-P diagram (Fig. 10) emphasises the similarities in planktonic content and hydrologic conditions between Series 3 and 4, even though they are separated geographically by at least 60 miles, and by almost a month in time. Of interest also, is that while subantarctic groups penetrated into warmer waters at Stations 279, 292, 304, and 310, coastal species did not penetrate to Stations 285 and 297, lying predominantly in subantarctic water. Coastal and Subtropical species rarely were taken in subantarctic water, even when, as at these stations, the collections were made at the extremities of what may be regarded as offshore directed movements of coastal water.

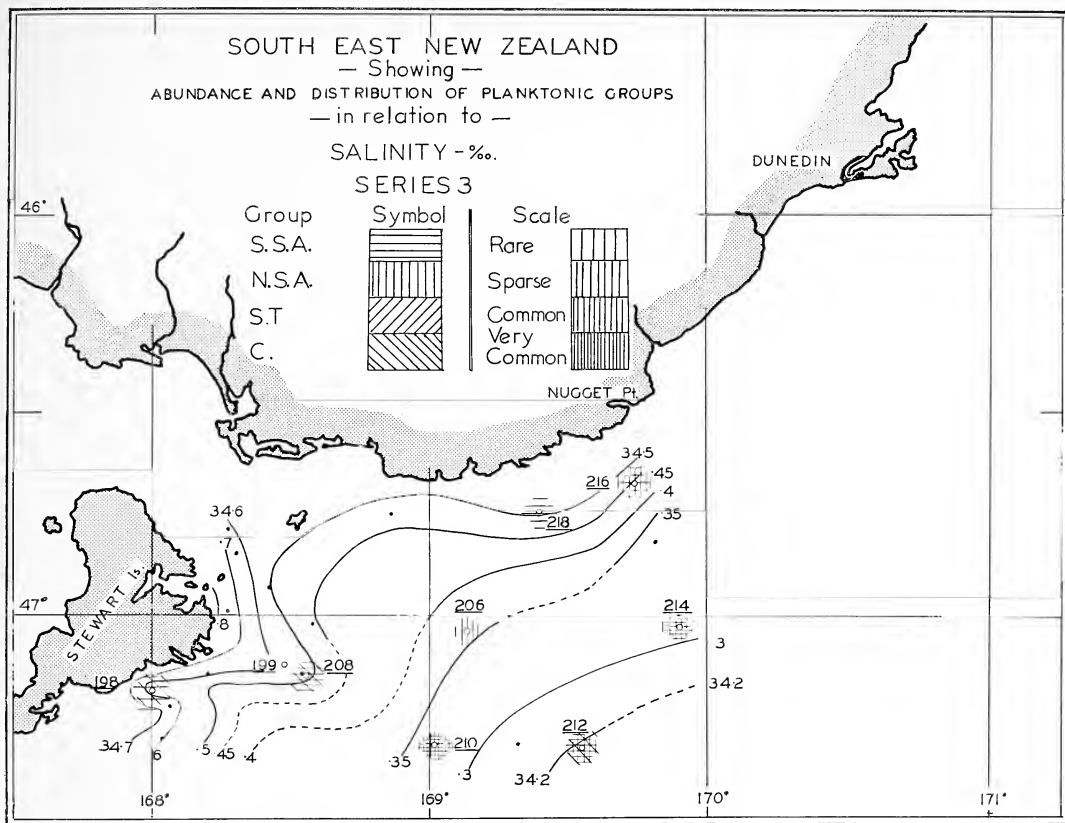


FIG. 16. See legend for Figure 15.

Series 5. Stations 1 to 6; 3 to 4.I.51

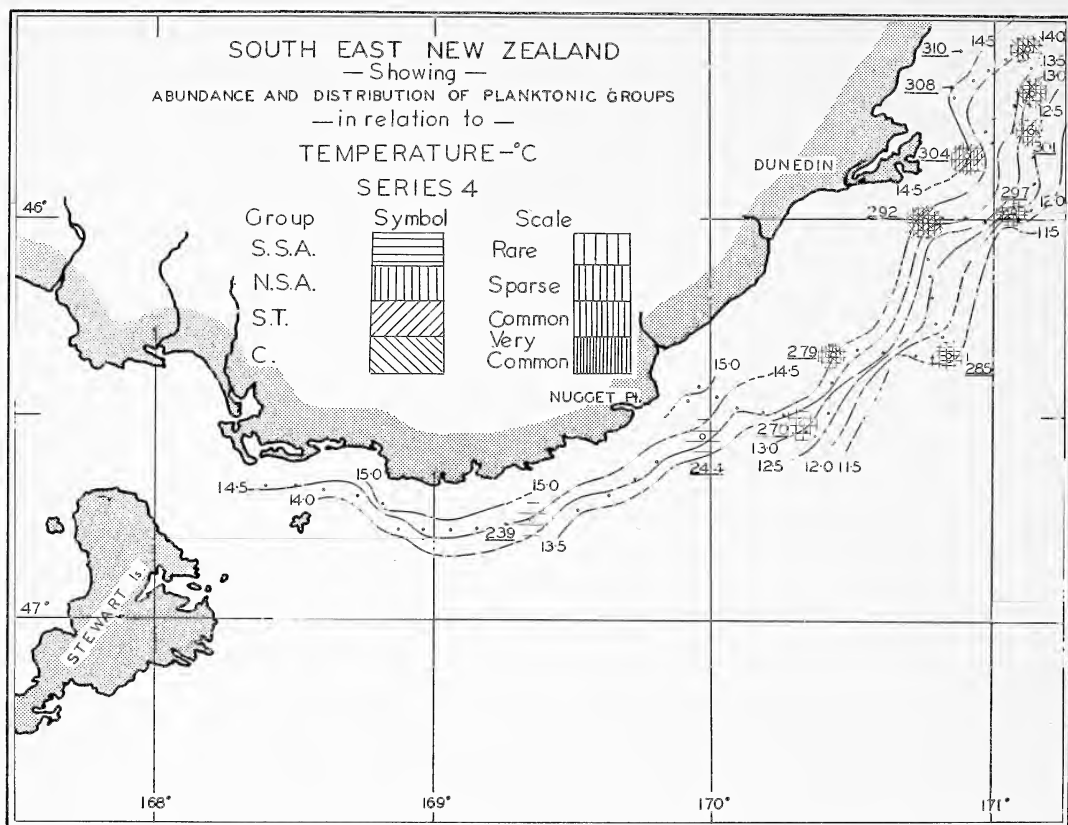
Stations of Series 5 and 6 were occupied during cruises between Wellington and Dunedin in January and March, respectively. Stations of Series 5 precede those of Series 1 by three days, but their discussion has been deferred for convenience of comparison with those of Series 6.

The stations of Series 5 are believed to sample either from water of subantarctic origin, or from a mixture of this and high-salinity, but *cool*, coastal water. The temperature and salinity at Station 5 (Figs. 19*a*, 20*a*) indicate the presence of water of subantarctic origin only. At Station 6 this water is predominant, but the slightly increased salinity points also to coastal water being incorporated. Higher salinities again at Stations 1 to

4, indicate an increased admixture of the coastal water. The steady rise in temperature northwards along the coast probably reflects a latitudinal increase. However, the distributions of temperatures and salinities demonstrate that the water is essentially homogeneous and predominantly of subantarctic origin. Supporting evidence comes from the planktonic occurrences.

Either or both Northern and Southern Subantarctic groups occur at Stations 2 to 6 (none of the species captured at Station 1 was among those selected). Coastal species were present at Stations 4 and 3, but they do not occur elsewhere. These distributions indicate the influence of subantarctic water at all stations, together with that of coastal water at Stations 3 and 4.

In the T-S diagram (Fig. 3) Stations 5, 1,



FIGS. 17, 18. Series 4, Stations 229-314, March 8-9, 1951. The distribution of the four planktonic groups in relation to Figure 17, Temperature, °C.; Figure 18, Salinity, ‰. S.S.A. (Southern Subantarctic group); N.S.A. (Northern Subantarctic group); S.T. (Subtropical group); C. (Coastal group). Temperature or salinities additional to those taken at plankton stations •; plankton station numbers are underlined.

and 2 lie within the narrow salinity range which appears to typify water of subantarctic origin. That only Subantarctic species occur at Stations 5 and 2 confirms this (Fig. 10). Stations 6, 3, and 4 occur over much the same temperature range, but at higher salinities. The occurrences of Subantarctic species testify to the influence of subantarctic water at these stations.

Although there are Coastal species at Stations 3 and 4, neither T-S nor T-S-P diagrams demonstrate a source for the water which transports the species. Nor do these diagrams show whence comes the more saline, cool water responsible for separating Stations 3, 4, and 6 from Stations 1, 2, and 5. The geo-

graphical distributions of salinities, temperatures, and plankton (Figs. 19a, 20a) demonstrate the probability that this water is coastal in origin. Seasonal temperature changes take effect more slowly in water than in air, and air temperatures, at the time of sampling, had not reached summer maximum. Therefore it is reasonable to expect comparatively cool coastal waters. The separation of the two lots of stations arises when this high-salinity, but cool, inshore water mixes with, but does not warm, the more offshore subantarctic water. In Series 6, on the other hand, the coastal water has a much higher temperature (Figs. 4a, 19b) and therefore raises the temperature of the subantarctic water with which it mixes;

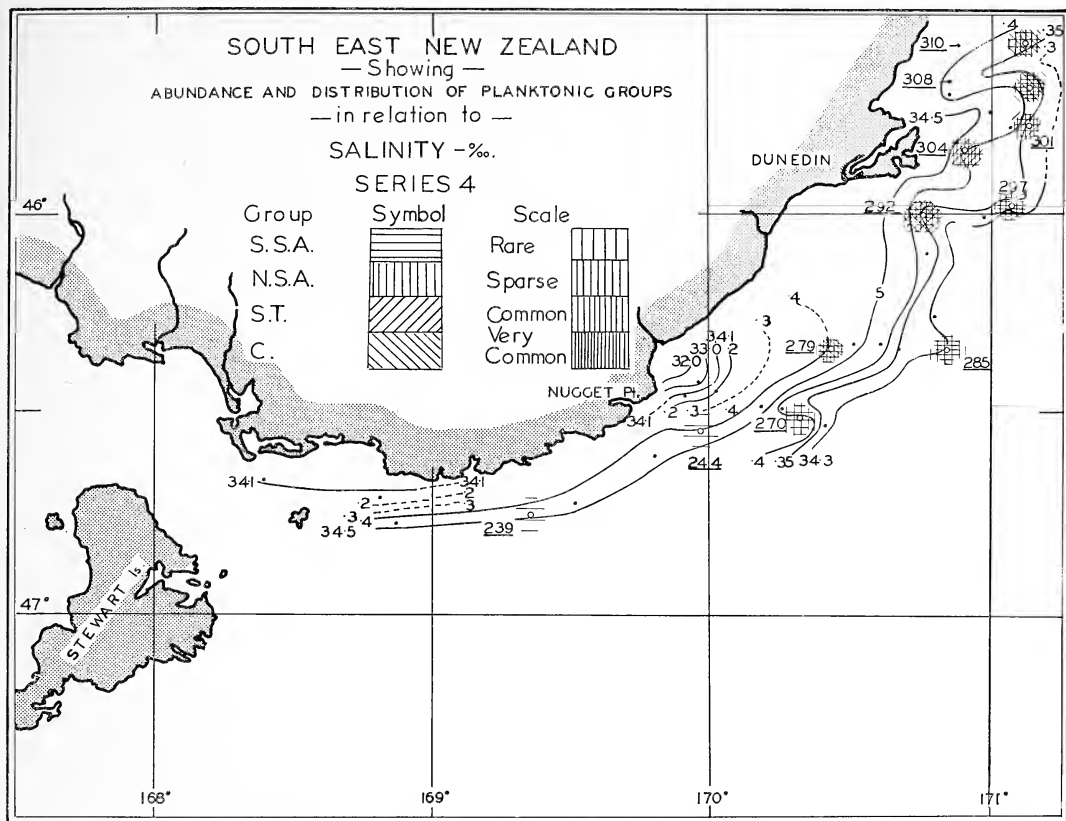


FIG. 18. See legend for Figure 17.

and, incidentally, makes for readier identification (in the T-S-P diagram) of the mixed sample.

Series 6. Stations 320 to 343; 21 to 22.III.51

These stations were occupied in March, and the shoreward extremity of the subtropical convergence now transects the series (see p. 22). Stations 320 to 328 are north of the convergence, 331 to 343 to the south of it; Stations 329 and 330 are near to the meeting zone of the subtropical and subantarctic waters (Figs. 4a, 19b, 20b).

Subantarctic water is strongly evident, through low temperatures and salinities, only at Stations 341 to 343. Northwards towards the convergence there is a pronounced coastal influence shown by high temperatures and

also by increased salinities (salinities decrease farther inshore as a result of dilution with fresh water). North of the convergence, the salinities at some stations approach those of open ocean subtropical water (about 35 ‰), but dilution is apparent and to a considerable degree at Stations 322 and 326.

Southern and Northern Subantarctic species occurred at Station 326, and Northern species at 322. They are probably to be accounted for by upward migration of the organisms from the subsurface subantarctic water.

The occurrences otherwise of the several planktonic groups conform to the distribution of the waters. Station 342 has only Subantarctic groups present, but at Station 337 these groups are rare and the Coastal Group predominates. At Station 330 there is a mix-

ture of the four groups, but at 326 and 322 the Subtropical Group is dominant.

The T-S-P diagram (Fig. 10) illustrates the general correlation between the occurrences of planktonic groups and the distribution of the water properties shown in the geographical charts. Station 342 is the only one clearly in subantarctic water and its fauna is entirely of Subantarctic groups. Station 330 is situated in the portion of the T-S-P diagram representative of water of subantarctic origin intruding into, and mixing with, coastal-subtropical waters. The four planktonic groups are present, which is consistent. However, both its position in the T-S-P diagram, and the predominance of Subantarctic species indicate that the subantarctic influence is strongest. Station 337 lies just outside the larger of the subantarctic intrusions in the T-S-P diagram. Isotherms and isohalines (Figs. 19*b*, 20*b*) suggest a strong coastal influence, which is confirmed by the predominance of Coastal species. Stations 326 and 322 are separated from all other plankton stations by the subtropical convergence. Both occur in water of subtropical origin, somewhat diluted by lower salinity coastal water, and Subtropical species predominated in the plankton.

It is important that the species' occurrences of Series 6 indicate the approximate position of the subtropical convergence. A comparison of faunal distributions, as well as physical data, of Series 5 and 6 show that the convergence has moved southwards during the three months separating the series.

Series 7. Stations 795 to 921; 13 to 17.XI.51

The stations of this series have enabled the source of the Southern Subantarctic species to be demonstrated, and have distinguished them through their origin in cold water from the Northern Subantarctic group. The temperatures and salinities of the stations are within those given for subantarctic water by Deacon (1937). Because water samples were lost, the salinities of the three plankton stations 795, 826, and 921 have been arbitrarily

chosen from within the range indicated by other stations in the series. The north-going component in the West Wind Drift, ensures that the influence of water in the latitudes of Stations 826 and 921 eventually will be felt about southern New Zealand. Through its agency, the more adaptable of Southern Subantarctic species will be transported to the nearshore waters. The temperature at Station 795 was 2°C. lower than any from which the Northern Subantarctic Group was taken. It would appear that this difference may be adequate as a barrier to these species in view of the geographical proximity of the station to Foveaux Strait (Fig. 2).

DISCUSSION

The selection of those species which are most representative of the faunas of particular waters can be made from the species' distributions in relation to temperature and salinity with the aid of the T-S-P diagrams. In turn, the extent of the influence of water bodies entering an area can be assessed through the distribution of the species in the T-S-P diagram, as well as by the temperatures and salinities of the waters. Species selected as representative of the fauna of one water may occur in other waters, often at groups of stations for which there are similar properties of temperature and salinity. The stations of such a group may be widely scattered in time and place, but affinity between them is demonstrable by means of their species' content. Thus the species relate the waters at the stations to their sources, and at the same time demonstrate the direction and extent of the water movements which have brought about the planktonic distribution. Because the species of a group indicate the presence (and source) of a water body, therefore the distribution of this water in another with which it is mixing can be traced in the T-S-P diagram through the distribution of these species.

The study raises problems relating to the transfer of organisms between one body of water (or range of conditions) and another.

Physiological adaptability probably plays a major part in deciding whether a species will survive such a transfer. For example, "Intolerant" species, because they were appar-

ently unable to adapt readily, show sharp reductions in numbers as coastal water is reached, while the more adaptable "Tolerant" species penetrated into it more freely (Figs.

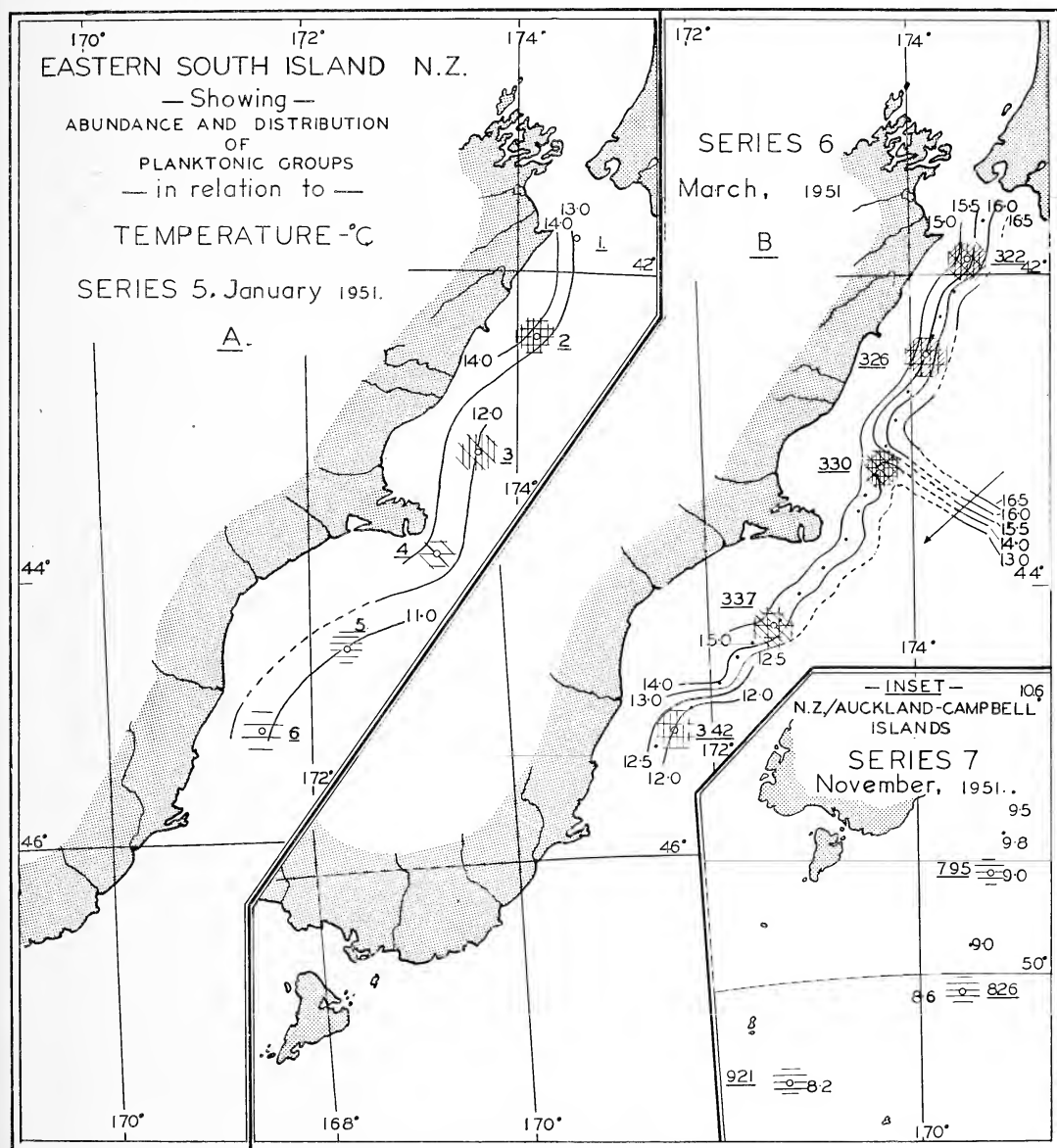


FIG. 19A, B. The distribution of the four planktonic groups in relation to temperature for A. January 1951; Stations 1-6. B. March 1951; Stations 320-343.

INSET: November 1951; Stations 795-921.

The break in temperatures across the subtropical convergence in B are drawn in conjunction with data from the surface thermograph trace, Figure 4b. The symbols for the planktonic groups, and the scale of abundance, are as in Figures 10-21.

5, 6). On the other hand, it has been remarked that Coastal species have not penetrated into water of subantarctic origin. A possible explanation of these facts is that some cold-adapted Subantarctic species can survive the increase in temperatures between cold subantarctic and warm coastal waters, but that coastal species are unable to adapt to lower temperatures. It is difficult to see that this explanation is totally adequate. A preponderant one-way movement of Subantarctic species into coastal areas is demonstrated in the T-S-P diagram (Fig. 10), and is also apparent from analysis of the plankton catches at stations of Series 4 for example (Figs. 17, 18). When oceanic waters move into coastal water, compensatory movements out of the area should ensue. At least some of the low-density inshore water might escape by overriding denser subantarctic water, in which case coastal species would be carried offshore and their numbers gradually decrease as environmental conditions become adversely modified. The opposite appears to be true in most instances. The numbers of the Coastal group of species captured decrease abruptly between 12.5 and 13.0°C. (Fig. 9), as the oceanic water is reached, e.g., as at Stations 285, 297, Series 4. It seems unreasonable to suppose that the abruptly effected absence of the Coastal species results from a sudden application of some physiological factor, and it is suggested that there may be reasons involving hydrological phenomena.

It is possible that the northeast moving current along the coast sets up a superficial transverse circulation (Sverdrup *et al.*, 1942: 676-677) which passes surface oceanic water shorewards. It is conceivable that offshore, surface transport of organisms could be prevented by the development of such a circulation. This mechanism would tend to accumulate less dense water to the left of the direction of flow, i.e., along the coast. In turn, this would facilitate a lateral, offshore transfer of water, and the contained organisms, at deeper horizons. However, such would not be re-

vealed by the surface sampling of this survey.

A second possibility is that the transfer between the coastal and subantarctic waters proceeds through the agency of discrete pockets of water, formed on a small scale but in an analogous manner, to those between the Gulf Stream and neighboring waters (Iselin and Fuglister, 1948; Ford and Miller, 1952). Isoline configurations in several of the Figures 11-20 suggest the development of pockets on the shoreward side of the north-going oceanic waters. If the transfer of surface water were largely shorewards, as seems possible, it would assist in explaining the abrupt cessation of the offshore occurrences of Coastal species.

The method of the T-S-P diagram is suitable for determining the tolerances of species to temperature and salinity in that it demonstrates their reactions to changes in environmental conditions. The fact that data are collected in the field is advantageous and especially so when considered in conjunction with experimental evidence, for example of the long or short term temperature adaptability of species. Sheard (1953: 21, and personal communication) indicates that temperature tolerances may vary according to the range to which the local stock of a species has become adapted; the occurrences of *Thysanoessa gregaria* in the present survey appear to be a case in point. In general, *Th. gregaria* is rarely captured in subantarctic waters (Sheard, 1953; Boden, 1954). But it was consistently taken as a Southern Subantarctic species during the present survey. It reacted to increasing temperatures (Fig. 6) by a reduction in numbers in a manner similar to other species of the Southern Subantarctic Group. It is possible that this may be a stock of *Th. gregaria* which is adapted to cold water. If so, considerable interest would accrue at this stage in comparing upper and lower temperature tolerances of this and Subtropical stocks, both by experiments and through field data by means of the T-S-P diagram.

The technique of the T-S-P diagram has

been confined to surface waters in this study. It is applicable, however, to determining relationships between plankton and water masses in a vertical direction. David (1955), and others, have been concerned with the

vertical distribution of species on an ocean-wide scale, but the method equally applies to much more limited areas. It should prove of value also in studies of plankton-water relationships near convergences, areas of up-

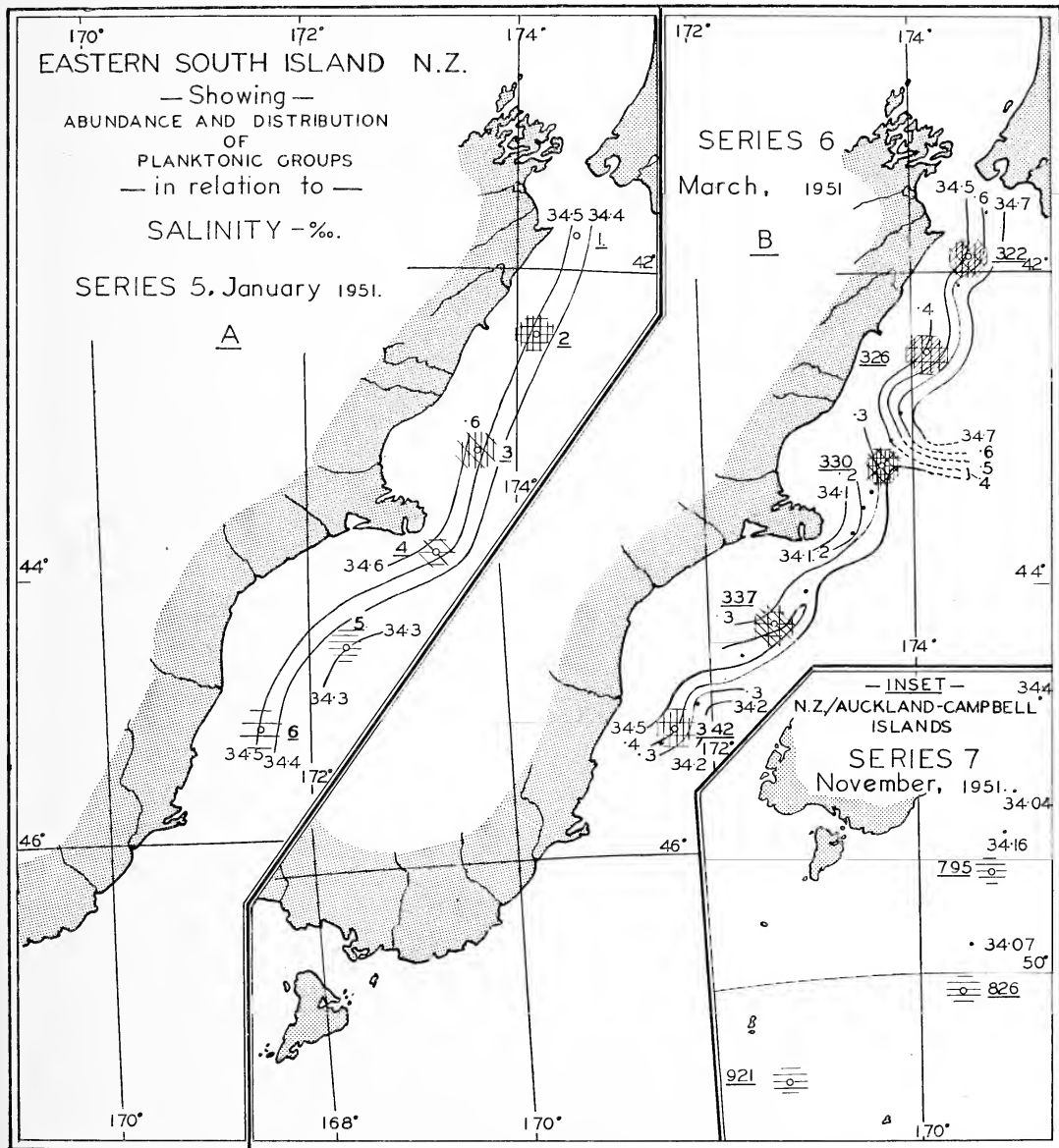


FIG. 20A, B. The distribution of the four planktonic groups in relation to salinity for A. January 1951; Stations 1-6. B. March 1951; Stations 320-343. INSET: November 1951; Stations 795-921.

The position of the subtropical convergence in B is suggested by the dashed isohalines near Station 330. The symbols for the planktonic groups, and the scale of abundance, are as in Figures 10-21.

welling, in water masses surrounding small islands, and it may be of considerable value in the study of patchiness in the distribution of organisms, e.g., of aggregation in the statistical sense. There is little doubt that a comparable technique may be used to determine the effects on organisms of other pairs of environmental factors and in this connection the use by Moore (1950, 1952) and Moore, Owre, Jones, and Dow (1953) of the light and temperature relationships of euphausiids and other zooplankton should not be overlooked. Last, a convenient, three-dimensional picture of the distribution of a species would be presented if a T-S-P diagram, constructed from data from vertical series of samples, were allied with the geographical distribution of the species.

SUMMARY

1. Two principles concerning plankton distribution have been established by earlier workers. First, bodies of water with distinct properties possess distinctive planktonic faunas. Second, when one of these bodies of water mixes with another, the faunas are mixed. In this present study, species have been selected as indicators of the constituent waters of an area about southern New Zealand where waters of subtropical and subantarctic origins are mixing together, and with coastal water. The surface waters entering the area are identified by their temperature-salinity relationships.

2. All occurrences of a number of selected species of the plankton have been superimposed on the T-S diagram of surface waters in the area to produce the temperature-salinity-plankton (T-S-P) diagram. It is found that the distribution of each of the several waters coincides with the distribution of its indigenous species. Further, where one of the waters penetrates into, and mixes with another, it is demonstrated that the species of the one are transported into the other and a mixed fauna results.

3. Examples are discussed in which stations (isolated geographically and in time) aggregate in the T-S diagram. The similar environmental conditions which exist at these stations are the result of several intrusions at different localities of subantarctic into coastal water. The individual intrusions have been demonstrated by considering the geographic distribution of water properties in near-synoptic series of stations. The close affinity between the stations of each aggregate is demonstrated in the T-S-P diagram by means of the similarity of the plankton captured at the stations.

4. Plankton distribution in the T-S-P diagram, allied with that shown by the geographical distribution of the species, has demonstrated a southward migration of the subtropical convergence during the summer.

5. Temperature and salinity tolerances of species and the reactions of species, or groups of species, to changes in temperature and salinity, are readily observable in the T-S-P diagram.

6. The T-S-P diagram is potentially useful in studies of distribution about convergences, small islands, near areas of upwelling, and for studying patchiness of plankton.

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The Structure and Reproduction of *Gulsonia annulata* Harvey (Rhodophyta)

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Gulsonia HARVEY is a little-known monotypic genus of red algae which has been variously placed in the Cryptonemiaceae (Harvey, 1855, 1860), close to *Crouania* (J. G. Agardh, 1876; Schmitz, 1889) and to *Wrangelia* (J. G. Agardh, 1894, 1897), and in the Nemalionales near *Batrachospermum* (Schmitz and Hauptfleisch, 1897; Fritsch, 1945).

Gulsonia annulata was originally described by Harvey (1855) from Phillip Island, Western Port, Victoria and later (Harvey, 1860) recorded from Georgetown, Tasmania. Harvey's collections were apparently sterile, but later J. G. Agardh (1894, 1897), and Schmitz and Hauptfleisch (1897) described carpogones, tetraspores, and monospores without indicating the source of their material. Only in recent years has the alga again been recorded (Womersley, 1948, 1950).

During February, 1956, abundant drift material was collected at Pennington Bay, Kangaroo Island, by the authors. Some 90 specimens were collected as they were washed in over the reef, comprising 51 tetrasporic, 24 female and cystocarpic, 3 male, and 12 sterile plants.

Gulsonia annulata is also known from Sturt Bay on Yorke Peninsula and from Eucla, near the South Australian—Western Australian border. Apparently it is comparatively rare, only being found in drift material from well below low tide level; the plants decompose fairly rapidly when cast ashore.

The following account is based on the rich Kangaroo Island collection of February, 1956.

Shortly before this paper was submitted for publication, Kylin's (1956) account of the

Rhodophyta became available. Here Kylin also recognises the identity of *Gulsonia* Harvey and *Crouaniopsis* J. and G. Feldmann, and transfers *C. annulata* (Berthold) J. and G. Feldmann to *Gulsonia* as *G. mediterranea* Kylin nom. nov. The same epithet had also been adopted for the Mediterranean species by the present authors. Kylin, however, gives little more than a formal generic description of *Gulsonia*, and his comments are apparently entirely based on the Mediterranean species.

VEGETATIVE FEATURES

The plants ranged up to 30 cm. in height with an average of 18 cm., and a main axis diameter of 2 mm. The thallus axis and branches are terete, uniaxial, and articulate, with each axial cell bearing from its upper end a whorl of four short branches of limited growth. These whorled lateral branches form nodal bands, less distinct in the youngest parts, where they almost completely cover the axis, and most prominent over the rest of the plant, except in the oldest parts of the main axis and branches where they become obscured (Fig. 1). This is due to the development of 1–3 descending corticating filaments from the basal cell of each short branch, which cover the axis and in the oldest parts of the plant form a dense, tough, and feltlike covering over the whorled laterals as well as the axis. The corticating filaments are simple or sparingly branched, of 7–10 elongate cells averaging 250–300 μ long, by 25–30 μ broad. The axial cells of the thallus are approximately twice as long as wide, reaching dimensions of 1300 μ by 700 μ at the base of the plant. The intercellular connection between cells shows a prominent, thickened platelike structure (Fig. 2c, d).

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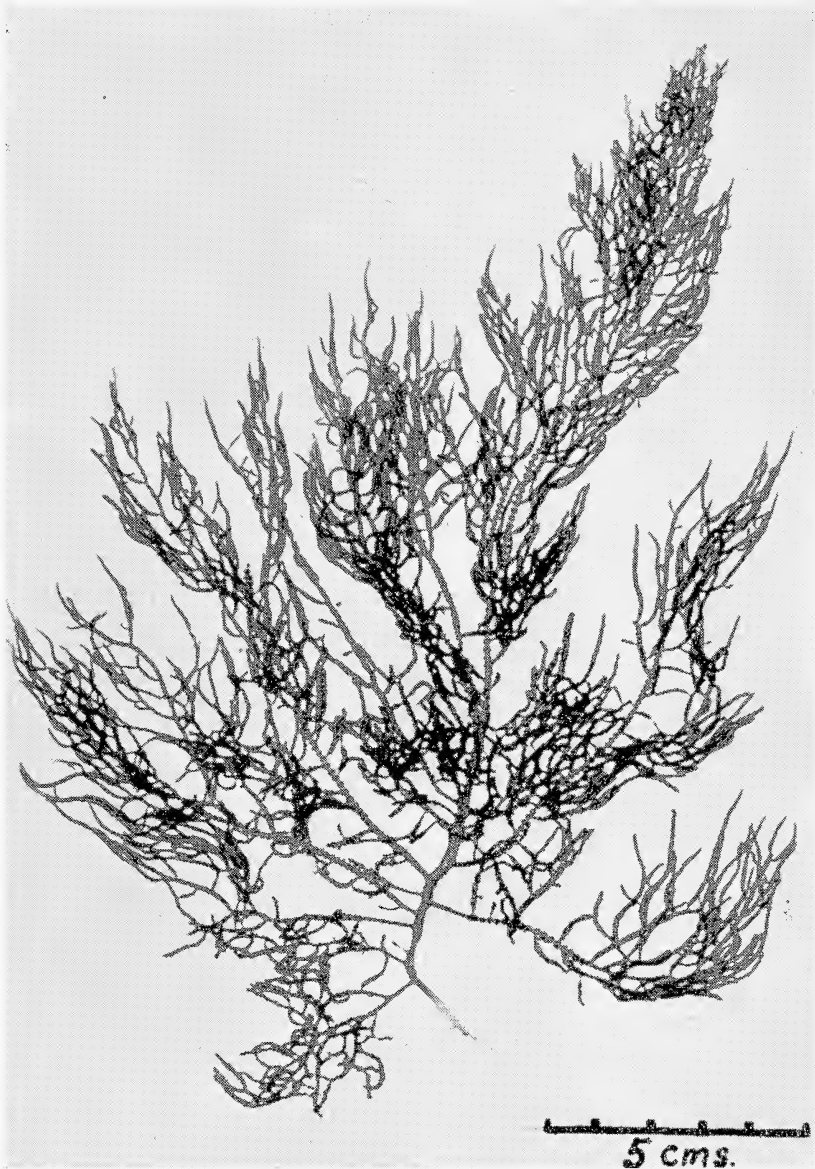


FIG. 1. *Gulsonia annulata* Harvey. Habit of plant showing nodal formation except at base and tips of branches.

The lateral whorled branches consist of 5-7 orders of cells. Cells of the second order are formed dichotomously on the basal cell, thence each cell of successive orders produces a whorl of three cells except the outermost which are borne either in two's or three's. Occasionally the normal terminal cells are transversely divided (Fig. 2b). Cells of each order are progressively smaller, the terminal

ones averaging 20μ long by 6μ broad. Hairs about 300μ long, with a swollen tip, are frequently formed from the terminal cells (Fig. 2b). Reproductive organs, young vegetative branches and gland cells are borne on the lateral branch whorls.

Branching of the thallus is irregular, and young vegetative branches may occur on any, except the oldest, parts of the plant. Each

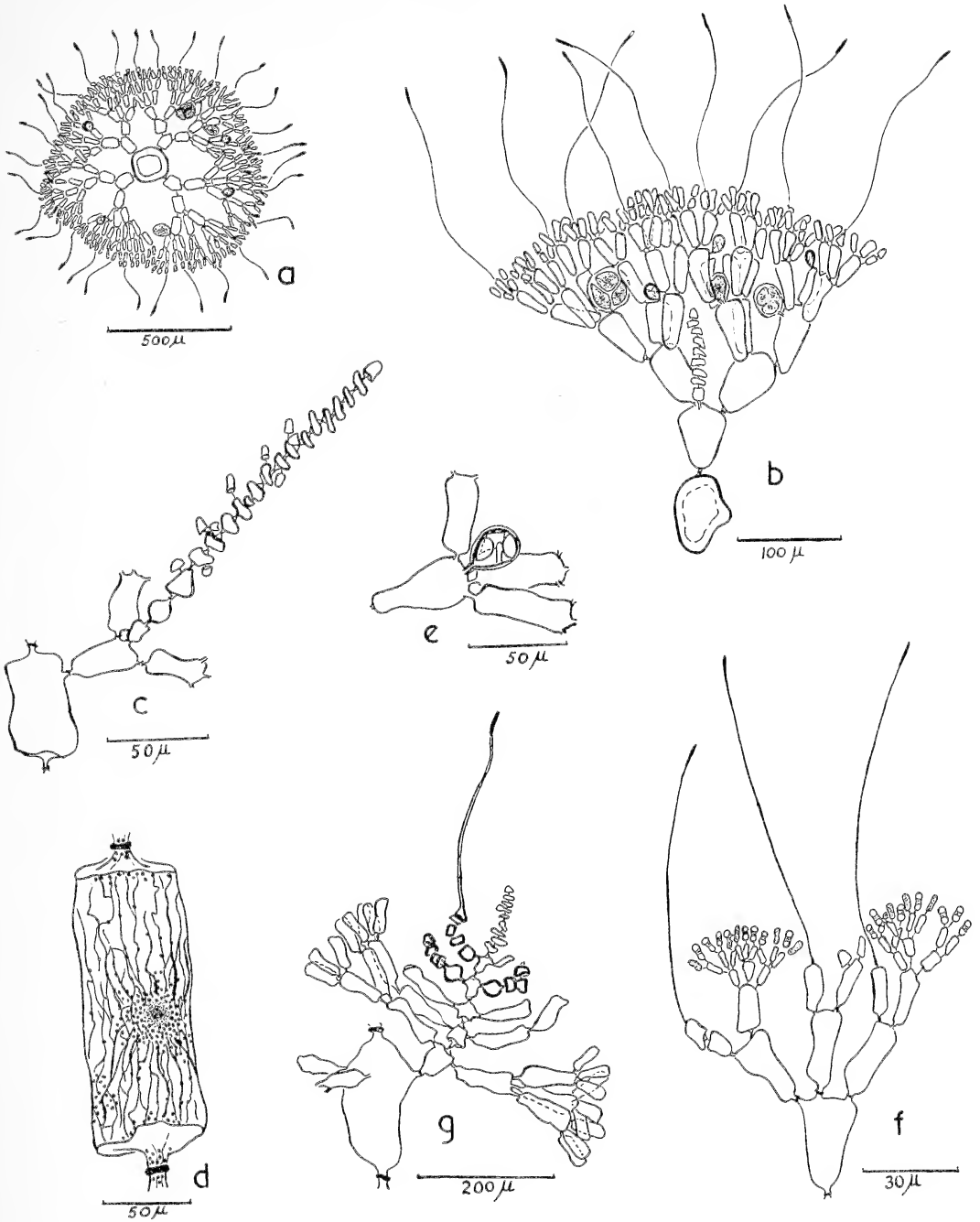


FIG. 2. a, Transverse section of thallus of tetraspotic plant of *Gulsonia annulata* Harvey showing whorl of four lateral short branches arising from axial cell and by three from each subsequent cell; b, short lateral branch of *Gulsonia annulata* Harvey showing branching by two from basal cell and by three from each subsequent cell, young lateral branch, stages in development of tetraspores, scattered "gland" cells and terminal hairs from some cells; c, development of first lateral cells in young vegetative branch of *Gulsonia annulata* Harvey; d, mature axial cell of *Gulsonia annulata* Harvey showing chromatophore pattern, nucleus, and small granular inclusions; e, "gland" cell of *Gulsonia annulata* Harvey with inclusions; f, terminal spermatangia of *Gulsonia annulata* Harvey with median nucleus; g, fertile branch of *Gulsonia annulata* Harvey borne on basal cell of short lateral branch and bearing two carpogonial branches on the third axial cell and one on the fourth.

branch develops from the outer end of the basal cell of a lateral whorl member (Fig. 2b, c). The initial of the new branch divides transversely, forming a chain of 16–20 cells before cells in the central part of this chain divide laterally to cut off basal cells of the new whorl (Fig. 2c). These basal cells are arranged roughly in an anticlinal spiral, and divide rapidly to form the whorled laterals when the new branch emerges from within the old branch.

All cells are uninucleate, with a large, dense nucleus usually in the mid-part of the cell near the periphery. The chromatophores vary greatly in form, but are constant in any one type of cell. In the outer cells of the whorled laterals they are irregularly platelike, covering almost the whole periphery of the cell. As the cells increase in size the chromatophores change through an irregular anastomosing stage to branched, linear shapes in the larger cells of the main axes. These linear chromatophores tend to converge towards the nucleus (Fig. 2d). Carpospores and tetraspores contain chromatophores which form an irregular, granular network. The nodal or banded appearance of the thallus is accentuated by the denser chromatophores in the small outer cells of the whorled laterals, giving a deeper colour to the nodal bands. In older axial cells, covered by corticating filaments, the chromatophores are greatly reduced. Most cells contain numerous cytoplasmic granules, often concentrated around the nucleus, and at the cell junctions (Fig. 2d).

Pyriform "gland" cells, with a thick mucilaginous wall, occur on cells of the whorled laterals (Fig. 2b, e) in all plants. These cells average about $30\ \mu$ in length and each contains several larger inclusions of varying but definite form (Fig. 2e). These may be the "monospores" referred to by Schmitz and Hauptfleisch (1897), but are probably comparable to the gland cells of other genera of Ceramiaceae.

The whole thallus is enveloped in a mucilaginous matrix, making it quite slimy.

TETRASPORANGIA

Tetrasporangia are produced in the upper parts of the thallus, on the outer end of cells of the third order of the whorled laterals. Only one tetrasporangium develops on a single cell (Fig. 2a, b). The sporangium is at first spherical, uninucleate, and sessile, attached by a thin cytoplasmic connection. It reaches $70\text{--}80\ \mu$ in diameter before division commences. The nucleus divides twice, and with four nuclei present the protoplast division commences at the periphery and proceeds inwards, giving four uninucleate tetrahedrally arranged spores (Fig. 2b). Meiotic figures were not seen in the material available. Accumulation of Floridean starch is indicated by red staining with iodine in tetrasporangia over about $50\ \mu$ in diameter, the staining becoming deeper in mature spores. Mature tetrasporangia are about $80\text{--}90\ \mu$ in diameter.

SPERMATANGIA

Male plants bearing spermatangia are not easily distinguished from sterile plants, but are slightly paler in colour and "rougher" in appearance. This is due to the spermatangia which are formed from the majority of the terminal cells of the whorled laterals. Each normal terminal cell bears a further two or three whorls of small cells, the outermost being the spermatangia. These spermatangia are $8\text{--}9\ \mu$ long, constricted in the centre, with a median nucleus and two prominent vacuoles (Fig. 2f). Spermatangia are not formed from the occasional terminal cells which divide transversely. Spermatangia are $3.5\text{--}4\ \mu$ in diameter.

FEMALE PLANT AND CARPOSPOROPHYTE

In female plants, special branches, initially similar to young vegetative branches, occur at short intervals along the axis of main branches. However, normal vegetative growth ceases with the development of carpogonial branches, which are produced either singly or in opposite pairs. Most commonly the third

or fourth axial cell (from the base) of the fertile branch bears two carpogonial branches, while the cell above it (fourth or fifth) bears one (Fig. 2g). Carpogonial branches have, however, been found on axial cells up to the seventh, and occasionally four or five on one fertile branch. Only one carpogonial branch on each fertile branch ultimately gives rise to a mature carposporophyte; in fact, not more than one mature carpogonial branch with a trichogyne was ever observed on a single fertile branch.

An axial cell cuts off laterally a supporting cell of similar size (though later the axial cell is usually larger), which in turn gives rise to the first three cells of the carpogonial branch. At this stage the supporting cell and carpogonial branch are together about 50 μ long. The third cell of the carpogonial branch cuts off a fourth, the carpogonium which develops the elongate trichogyne (Fig. 3a, b). The trichogyne projects through the whorled laterals of the thallus, reaching a length of up to 350 μ (Fig. 3c).

Several spermatia may adhere to one trichogyne, but only one develops a connection through the trichogyne wall. Very soon after fertilisation the trichogyne disintegrates, leaving the four-celled carpogonial branch.

On the upper side of the supporting cell a rounded auxiliary cell is cut off, and almost simultaneously the fertilised carpogonium divides transversely to form a small superior cell and larger inferior cell (Fig. 3d). From the lower part of the latter a small cell ("connecting cell") is cut off which enlarges and grows out towards the auxiliary cell. The auxiliary cell elongates to meet the connecting cell and ultimately fuses with it (Fig. 3e-g). The zygote nucleus presumably is left in the inferior cell when the carpogonium divides and transferred via the connecting cell to the auxiliary cell. The other cells of the old carpogonial branch commonly contain more than one nucleus at this stage. The first, and less frequently the second and third, cells of the carpogonial branch may cut off one

(rarely two) small cells which do not appear to have any function (Fig. 3e, f, h).

Comparatively few stages of actual fusion between carpogonium and auxiliary cell were found in comparison to large numbers of stages just before and shortly after, indicating that this transference of the diploid nucleus to the auxiliary cell is a rapid one.

The old carpogonial branch slowly disintegrates while the auxiliary (fusion) cell develops rapidly. Fusions between the auxiliary cell and other cells do not occur, but the auxiliary cell divides into a lower foot cell and upper central cell (Fig. 3h). The central cell buds off successive gonimolobes, each cutting off cells which divide to produce rounded groups of carpospores (Fig. 3i-l, Fig. 4). Only one fairly mature group of carpospores is present at any one time, with one or two younger groups developing. Mature carpospores average 75-80 μ wide by 100-120 μ long.

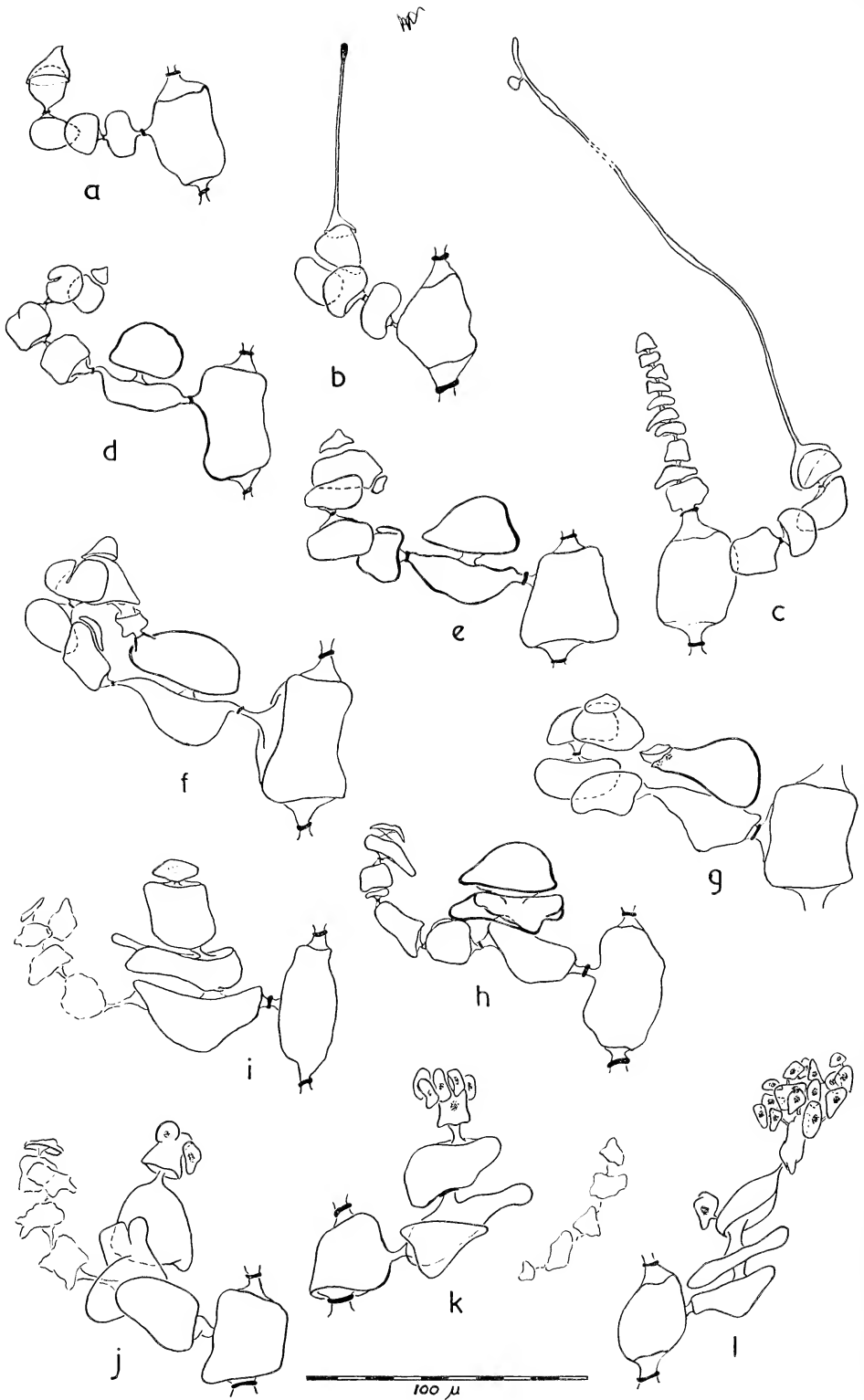
Two or three of the axial cells directly below those bearing carpogonial branches each bear a whorl of di- or trichotomously branched sterile filaments, which form a short, loose involucre around the carpospores (Fig. 4).

The mature carpospore groups are visible as small protrusions scattered irregularly over the thallus. The age of the carposporophytes shows a steady progression from the younger to the older parts of the thallus. On any one plant, however, there is not a very great difference between the oldest and youngest stages present.

SYSTEMATIC POSITION

As indicated in the introduction, *Gulsonia annulata* has been variously classified in the Cryptonemiales, Nemalionales, and Ceramiaceae by different authors. Previous accounts of the genus were all limited by inadequate material for study.

This investigation shows that *Gulsonia* is closely allied to *Crouania*, and belongs in the tribe Crouanieae of the Ceramiaceae. The



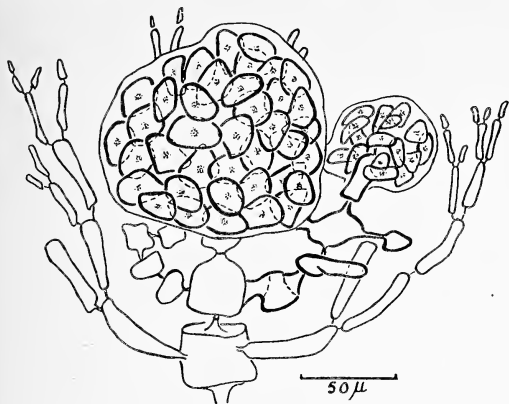


FIG. 4. Three stages in carpospore development. Sterile filaments from the axial cell immediately below the fertile axial cell form a loose involucre around the carpospore mass.

thallus construction, method of reproduction, and arrangement of the carpogonial branches are typical of the group. However, *Gulsonia* does differ from *Crouania* in two important features:

1. The carpogonial branches are borne on special fertile branches, whereas they are borne on the main axis in *Crouania*.

2. Lateral branches of unlimited growth are formed from the basal cell of a lateral whorl of limited growth, whereas in *Crouania* they develop directly from cells of the main axis.

These differences clearly indicate that *Gulsonia* is generically distinct from *Crouania*.

In 1940 J. and G. Feldmann separated *Crouania annulata* Berthold (a Mediterranean species) as a new genus *Crouaniopsis*, distinguished from *Crouania* by the same two fea-

tures as distinguish *Gulsonia*. This separation, and J. and G. Feldmann's account of *Crouaniopsis* (see also Feldmann-Mazoyer, 1940) indicate that *Crouaniopsis* is generically identical with *Gulsonia* as has been recognised by Kylin (1956). In describing *Crouaniopsis*, Feldmann-Mazoyer (1940: 279) compares it with *Gulsonia*, noting the vegetative similarity of the two genera, but follows the description given by J. G. Agardh (1894) of the reproduction of *Gulsonia* and assumes the two to be generically as well as specifically distinct. Agardh's description is quite inadequate to indicate whether or not the two are generically distinct. The main features of *Gulsonia* (including *Crouaniopsis*) may be summarised as follows:

1. Thallus of uniaxial construction with short branches of limited growth in whorls of four from the upper part of each cell of the central axis, giving a noded appearance.

2. The development of young lateral branches of unlimited growth from the basal cells of the whorled laterals.

3. Four-celled carpogonial branches produced on special lateral branches which cease further development.

4. A short, loose involucre of filaments produced from axial cells at the base of the carposporophyte.

5. A loose cortication of the lower parts of the plant by filaments produced from the basal cells of the whorled laterals.

Gulsonia annulata Harvey and *Crouaniopsis annulata* (Berthold) J. and G. Feldmann are remarkably similar in form and appearance, but (judged from Feldmann-Mazoyer's figures and description) differ as follows:

FIG. 3. *Gulsonia annulata*. Stages in the development of the carposporophyte: a, Young four-celled carpogonial branch and supporting cell borne on axial cell of a fertile branch; b, trichogyne developing from the fourth (carpogonial) cell of the carpogonial branch; c, fusion of spermatia with fully developed trichogyne; d, stage after fertilization. Carpogonial cell divided and auxiliary cell cut off from upper face of the supporting cell; e, small connecting cell cut off from inferior carpogonial cell and elongation of auxiliary cell towards it; f, connecting cell fused with auxiliary cell while still attached to the inferior carpogonial cell; g, further fusion of connecting cell with auxiliary cell now completely separated from carpogonial cell; h, fusion cell (old auxiliary cell plus connecting cell) divided transversely to give an inferior foot cell and a superior central cell; i, first gonimolobe developed from central cell; j, first divisions in carpospore development from gonimolobe; k, further development of carpospores from gonimolobe; l, a second gonimolobe bud developing from central cell, while first bud continues further carpospore development.

1. The ultimate cells of the whorled laterals in *Crouaniopsis* are more elongate than in *Gulsonia annulata*.

2. *Gulsonia annulata* forms "gland" cells; *Crouaniopsis* apparently does not.

3. Tetrasporangia of *Gulsonia annulata* are formed on cells of the third order of the whorled laterals; in *Crouaniopsis* on cells of the second order.

4. In *Crouaniopsis* the spermatangia have an apical nucleus (Feldmann-Mazoyer 1940: 166), while in *Gulsonia annulata* the nucleus is median.

Direct comparison with preserved material of *Crouaniopsis* may show other differences, but they are clearly specifically distinct. Owing to the identity of the specific names, Kylin (1956) renamed the later species of Berthold. The genus *Gulsonia* thus comprises two species:

GULSONIA Harvey 1855

Gulsonia annulata Harvey (1855 : 334; 1860: 320, pl. 193A; 1863 : synop. 614). J. G. Agardh (1876 : 88; 1894 : 122, pl. II, f. 13; 1897 : 56). Kuetzing (1866 : pl. 66 c - e). De Toni (1897 : 66; 1924 : 151). Schmitz (1889: 435-456). Schmitz and Hauptfleisch (1897 : 329 - 331). Womersley (1948 : 161; 1950 : 178). Feldmann-Mazoyer (1940 : 279). Kylin (1956: 373).

DISTRIBUTION: Eucla, Western Australia to Georgetown, Tasmania.

Gulsonia mediterranea Kylin (1956: 373).

SYNONYMY: *Crouania annulata* Berthold (1882:518); *Crouaniopsis annulata* (Berthold) J. and G. Feldmann (1940: 181).

DISTRIBUTION: Western Mediterranean.

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A Mechanism of Color Variation Operating in the West Coast Sea Hare, *Aplysia californica* Cooper

LINDSAY R. WINKLER¹

THE WIDE VARIATION in the coloration of different specimens of *Aplysia californica* Cooper, which inhabits the algal zones from Monterey Bay on the central California coast to the Gulf of California, has been the source of considerable question as to the specific homogeneity of the species. Cockerell (1901) based a new species name, *A. ritteri*, on an especially brightly colored variety. Garstang (1890) experimented with the European *Aplysia* and showed that there was a definite connection between diet and coloration. He believed that the veliger larvae settled in deep water and then migrated from deep water through the red, brown, and green algal zones, taking in turn the color of each.

MacMunn (1899) and Schreiber (1932) have indicated that the normal skin pigment is basically made up of degradation products of the tetrapyrrole molecule of chlorophyll. These are partly porphyrins, which are cyclic tetrapyrrole compounds, and bilins, which are linear chains of pyrrole molecules resulting from a break in the cyclic tetrapyrrole ring. The color and consequent absorption spectrum of these products varies as their structure is changed. Thus bilins from degraded green chlorophyll can produce a variety of blues, browns, greens, yellows, and reds which are all characteristic colors of the bilin compounds.

Many marine algae possess a high concentration of nonchlorophyllic pigments. Among these are the plant bilins or phycobilins, such as red phycoerythrin and the blue-green phycocyanin.

The colors most often seen in the skin of *A. californica* are brown, green, red, and purple, all of which are characteristic bilin colors. The purple pigments are concentrated in the branchial region and are seldom if ever seen elsewhere externally. The basic external body colors are brown, dark green, and grey, with various gradations between them. The red coloration is usually observed in larger specimens from deeper water and is the color most readily proved to be a result of food consumption.

In an effort to determine the relation of color to food, three approaches to the problem were used: (1) the comparison of color pattern and food, as shown by fecal pellet analysis; (2) controlled feeding experiments; and (3) observations on the absorption spectrum characteristics of the pigments.

MATERIALS AND METHODS

Juvenile specimens of *Aplysia californica*, ranging from 4 to 5 inches in length, were captured in the central shore area of Lunada Bay, Palos Verdes, California, and placed in individual pint fruit jars. As soon as a specimen passed a fecal pellet the pellet was collected in a vial and the animal was released in an area far enough removed so as not to be recollected. In this manner a total of 25 individuals was sampled. Pellets were also taken

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from large adult specimens from deeper water in Lunada Bay and off Palos Verdes Point, $\frac{1}{4}$ mile to the north. The pellets were collected in small, screen-capped vials, and were kept in refrigeration until they could be examined and tabulated.

Numerous specimens of *Aplysia californica* of various color combinations were kept from one to three months in 5-gallon pyrex cylinders supplied with aeration and glass wool-charcoal filters. The sea water was changed as pollution made necessary. These animals were fed on special diets to determine associated color relationships.

Hemolymph was drawn from the hemocoel after the animals had been cooled to refrigerator temperature to render them inactive. This prevented the release of the contaminating purple ink. The blood was centrifuged to remove the cellular elements, and the spectra were run on a Beckman model DU spectrophotometer. Extracts of the pigment of *Plocamium pacificum* were made by grinding the seaweed in a mortar with centrifuged sea hare hemolymph to duplicate the ionic conditions of the purple hemolymph occurring in certain specimens.

Extractions of certain dermal pigments were made with weak hydrochloric acid. Usually 10 per cent v/v was used, although one drop of concentrated hydrochloric acid in 10 cc. of distilled water would dissolve the pigment. The areas of the animal surface from which it was desired to extract pigment were cut off with scissors and placed in the dissolving solutions. These were then studied spectrophotometrically.

EXPERIMENTAL DATA

Fecal Pellets Analysis

The diet of the young specimens of dark green and grey coloration consisted of a wide variety of algae, but the dominant representatives were *Ceramium eitonianum* and *Gigartina canaliculata*. In no case was *Plocamium pacificum* present in noticeable quantity. All of the older specimens had red body streaks and

a characteristic purple foot. In every case a varying but very noticeably dominant representation of *Plocamium pacificum* was found to be present. Other greener seaweeds were also present in small quantities.

Controlled Feeding Experiments

Specimens of *Aplysia californica* in all of the available color patterns were kept in the aquaria from one to three months and fed on a diet of parsley leaves and celery tops. These specimens all acquired a uniform pigmentation characterized by a light-brown base color and small dark-brown spots. One large feeding of *Plocamium pacificum* fed to these specimens produced a decidedly pink cast to the base color. This, however, was only temporary.

Two small red animals (2-3 inch) from the *Plocamium* beds north of Palos Verdes Point, apparently similar to the animals mentioned by Berry (1907), were kept in tanks in the laboratory. When captured, these young sea hares were a uniform light pink without markings, although one had a very few pinpoint dots of brown. These animals thus bore no color resemblance to the greenish-brown or red-streaked *Aplysia*. It appeared at first that they constituted a new species, but after two weeks of feeding on parsley leaves they developed the coloration characteristic of *A. californica*. These two animals, fed on parsley leaves, grew to be 4 to 5 inches in length and so closely resembled other animals of similar size and experimental diet but of different initial coloration that it became impossible to differentiate them.

Observations on the Pigments

The blood, or hemolymph, of *Aplysia* is normally a clear fluid without noticeable coloration. However, it was found that specimens feeding principally on *Plocamium pacificum* possessed blood with a strong purple coloration. Spectrophotometric curves were run on the blood and compared with extracts of *Plocamium*; however, while the curves themselves proved interesting, they did not show common absorption maxima with those found

in extracts of *Plocamium pacificum* nor did they show a relationship with *Aplysia* purple.

It was also noted that several hours after removing a dead *A. californica* from sea water, the brown epidermal layer of the skin can be rubbed off. In the red-streaked, *Plocamium*-feeding animals it was found that beneath this layer, on the surface of the unpigmented dermal layer, were broad, purplish red streaks of deposited material. In life these streak marks appear red, as the result of the filtering action of the thin epidermal layer. These streaks interconnect to form a reticulum which is most pronounced on the sides, especially near the margin of the foot.

The streaks were rapidly dissolved in dilute hydrochloric acid, dilute acetic acid, and 70 per cent alcohol, the latter changing the gross color to yellow. The acid extract consistently gave a strong absorption peak at 548 m μ (Fig. 1C) with an irregularity in the curve at 490 m μ . The nature of this irregularity suggested to the writer that the curve might be a composite. The streaks were differentially ex-

tracted with distilled water and dilute hydrochloric acid. In the former the streak-coated tissue was soaked overnight. The resultant extract was a light yellow and the gross color of the streaks had changed somewhat. The streaks were then completely dissolved in dilute hydrochloric acid in a few minutes.

The water extract showed peaks at 548 and 490 m μ (Fig. 1B). The acid solvent contained a component with absorption maxima at 503, 520, and 548 m μ , the one at 548 being broad, the other sharp (Fig. 1A). No attempt was made to employ quantitative techniques so the relative height of curves A and B are probably not correctly portrayed. When the two are dissolved together the additive effect produced the curve in Figure 1C.

Upon neutralizing the composite extract of the streaks, the color completely disappeared. Upon reacidification the color was reconstituted without significant spectral change, but if made strongly alkaline, a jell-like precipitate formed.

DISCUSSION AND CONCLUSIONS

The reversion of specimens of all available color patterns to a common pigmentation when fed a common diet demonstrated the dependence of these animals on food pigments for their coloration. The land plants which supplied principally chlorophyll as a pigment lacked the special pigments which are normally obtained by these animals from their algal diet. It seemed logical to search for the cause of the red streaks from among these special algal pigments.

The consistence with which *Plocamium pacificum* was found in the fecal pellets of the red-streaked animals led to experiments with that algal form. Feeding experiments involving *Plocamium* over the extended period necessary to produce red streaks were impractical because of the perishable nature of the sea weed. However, single large feedings produced a pinkish cast on the bodies of parsley-fed experimental animals, caused by the blood's becoming temporarily purple.

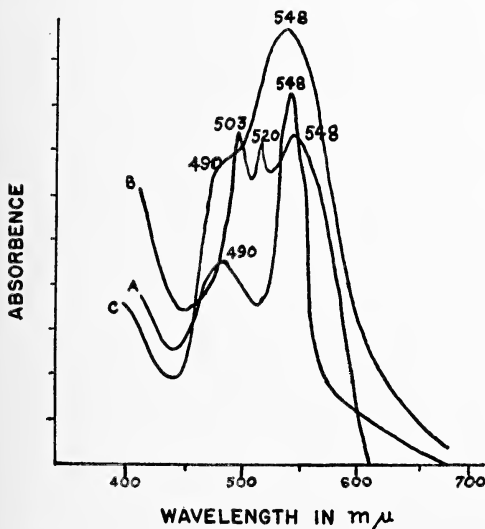


FIG. 1. The curve shown in A is produced by the water soluble fraction of the subcutaneous purple streaks, while that in B is produced by a subsequent acid extraction. The total spectrum of the two components is shown in C. No attempt was made to make the several extracts quantitative.

The lack of common absorption maxima between the extracts of *Plocamium pacificum* and the purple-colored blood is doubtless the result of digestive changes. The significant fact, however, remains that animals feeding on the pinkish purple, phycobilin-pigmented *Plocamium pacificum* develop purple hemolymph. The fact that these purple-blooded specimens also lay down a subcutaneous purple reticulum is very significant, showing the manner in which this particular pigment is transferred from plant to animal pigmentation. It has been demonstrated that the portion of the streaks insoluble in water was soluble in hydrochloric acid. This solubility characteristic suggests the presence of a nitrogen base, perhaps an amine.

SUMMARY

1. Fecal pellet analysis indicated that *Plocamium pacificum* is the major dietary component of red-streaked *A. californica*.
2. The coloration of the widely different color variants could be changed to a homogeneous, indistinguishable pattern by feeding them a diet of parsley and celery leaves.
3. The absorbed pigment from the digested *Plocamium* colors the blood of the sea hare purple.

4. A pigmented compound may then be deposited in a subcutaneous, purple reticulum, having the gross effect of red streaks due to the filtering action of the brown cutaneous layer.

5. Though all the pigments in the chain are of a red to purple color, they have been so changed in the body of the sea hare as not to have common absorption maxima. Their spectra show no affinity with *Aplysia* purple.

6. The streak deposit is composed of not less than two component pigments.

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Four New Species, a New Genus, and a New Suborder of Hawaiian Fishes¹

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THE DESCRIPTION of new taxa in a "Handbook of Hawaiian Fishes" recently submitted for publication was considered inadvisable. Certain of these are grouped together here, i. e., three new species of Gobiidae (*Quisquilius aureoviridis*, *Q. limbatosquamis*, and *Hazeus unisquamis*), a new genus and species of Callionymidae (*Pogonymus pogognathus*), and a new suborder of Perciformes (Schindlerioidei) erected for the fishes of the genus *Schindleria*.

Family GOBIIDAE, Genus QUISQUILIUS

The two new species of *Quisquilius* described below can be assigned to that genus with considerable assurance, as the type species, *Q. eugenius*, is another Hawaiian form of which numerous specimens are available. The characteristics listed in the following paragraph are held in common by the two new species and *Q. eugenius*.

No hairlike or flaplike appendages on the head or shoulder girdle. No serrations or spines on the preopercle. Maxillary not prolonged posteriorly. No V-shaped notch in the tip of the lower jaw. No teeth on the vomer. Teeth in both jaws in several rows, those of the outer and inner rows enlarged and spaced at intervals. One or two fanglike teeth in the outer row at each anterolateral angle of the lower jaw. Tongue usually with a slight to broad notch in the tip. Cleft of the mouth more or less oblique. Both nostrils in tubes, the anterior at least twice as far from the posterior as from the groove behind the upper lip. No pores on the head. The rows of

papillae (not shown in Fig. 2) are in very uniform alignment. There is one pair on the posterior portion of the interorbital and two rows of about 5 papillae each on the flesh covering the premaxillary pedicels. A series of about 5 large, widely spaced papillae borders the orbit below. A row or pair of rows runs backward from the eye just above the upper border of the opercle. Two horizontal rows on cheek, the upper sometimes extending all the way across but the lower ending on middle of cheek. A verticle row down front of operculum with two branches running back or down and back from it. One or two rows along the lower border of the preopercle. One row of papillae above and two below enclose the corner of the mouth. Two rows on the gular membrane, one on each side. Gill openings extending down to below the preopercular border, the distance between their lower ends equal to or less than an eye diameter. Ten or more developed gill rakers on the lower limb of the outer arch. Scales ctenoid, those on the body not especially enlarged posteriorly. Scales on top of head extending forward nearly to eyes, but no enlarged scales just behind eyes. First dorsal fin with 6 spines. First spine in both dorsal fins with a flexible tip. Caudal rounded, not longer than the head length. Pectoral without silky rays above. The united pelvics without a basal frenum, the membranes uniting the inner rays easily torn (as it apparently was in the holotype of *Q. eugenius*).

Examination of numerous specimens of *Q. eugenius*, 15 to 45 mm. in standard length, indicates no great sexual dimorphism. Over the available size range there is also no great differentiation in sensory papilla pattern. However, the cheek squamation does not appear until well after all of the other scales have formed.

¹ Contribution No. 112 of the Hawaii Marine Laboratory in cooperation with the University of Hawaii, Department of Zoology and Entomology. Manuscript received December 18, 1957.

² Department of Zoology and Entomology, University of Hawaii.

Among Hawaiian gobies *Zonogobius* (as represented by *Z. farcimen*) seems to be the closest relative. These two genera are set off from other Hawaiian gobies by the following features: no pelvic frenum; two longitudinal series of papillae on the flesh covering the premaxillary pedicels; and 10 or more developed gill rakers.

Of the three Hawaiian species of *Quisquilius*, *Q. eugenius* is an abundant shallow-water fish inhabiting areas of dead coral. It seems to be restricted to depths of less than 15 feet. The other two species are in general deeper-water forms, though the type of *Q. aureoviridis* was collected in a tide pool with a maximum depth of 7 feet.

Quisquilius aureoviridis sp. nov.

Fig. 1, Table 1

HOLOTYPE: USNM 175013, 37.1 mm. in standard length taken in a rotenone station at Pupukea, Oahu, Territory of Hawaii by Gosline, *et al.*, Dec. 23, 1949.

PARATYPES: USNM 175014, 1 specimen. 36.2 mm., about 1 mi. north of Kailua, Hawaii, T. H., Gosline, *et al.*, June 19, 1953; University of Hawaii No. 1703, 8 specimens, 21.0–27.2 mm., off Waikiki reef, Oahu, T. H., Gosline, *et al.*, Dec. 31, 1952.

Depth of body contained about 4 times in the standard length.

Head somewhat wider than deep, its greatest depth contained about 1.5 times in the head length. Mouth oblique, the lower jaw protruding. Front of mouth about on a level with the middle of pupil; rear of jaw about reaching to below front border of pupil. Eye bordered by a shallow groove posterodorsally, its diameter contained about 4 times in head in a 2-inch specimen. Least distance between eye and groove behind upper lip contained a little over 2 times in the eye diameter. Anterior nostril placed just above the groove behind upper lip, the posterior above the level of the top of pupil. Interorbital gently concave, not in a deep trench between the eyeballs, its width contained about 4 times in the eye diameter. Thirteen moderate, pectinate gill rakers on the lower limb of the outer arch in one specimen. Tongue rounded but usually with a central notch at tip.

Body completely scaled, those scales above the pectoral base rather irregularly placed. A few scattered rows of papillae crossing certain of the body scales. Head scaled forward to the groove behind each eye. No scales on cheek or operculum. Thirty to 33 scales in a longitudinal series, 9 or 10 in a transverse series; about 13 predorsal scales.

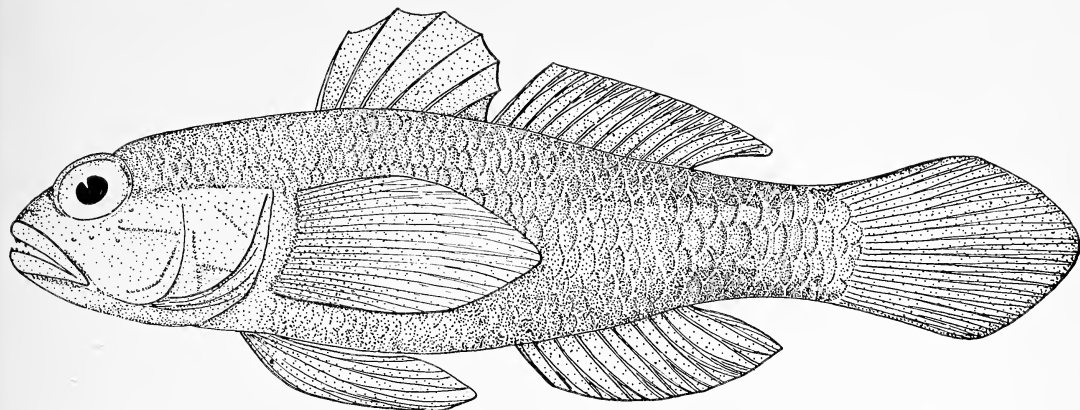
Some of the spines in the first dorsal filamentous. Second dorsal with a spine and 10 or 11 soft rays. Anal with a spine and 8 or 9 soft rays. Pectoral with about 19 rays.

TABLE 1
CERTAIN COUNTS IN THREE HAWAIIAN SPECIES OF *Quisquilius*

SPECIES	LATERAL LINE SCALES*								TRANSVERSE SCALE ROWS†					TOTAL 2ND DORSAL RAYS				TOTAL ANAL RAYS		
	26	27	28	29	30	31	32	33	7	8	9	10	11	10	11	12	13	9	10	11
<i>Q. eugenius</i>		1	1	3							2	2	1			4	1	1	3	1
<i>Q. aureoviridis</i>																				
Holotype								1				1				1			1	
Paratypes				1	1	1		1			3	2			2	3			3	2
<i>Q. limbatosquamis</i>																				
Holotype		1							1						1				1	
Paratypes	2	4							3	3					6				5	1

* Counted from the upper angle of the gill opening to the crease at the end of the hypural fan.

† Counted from the beginning of the anal upward and forward to the dorsal base.

FIG. 1. *Quisquilius aureoviridis*, holotype.

Color in life yellowish green to yellowish brown with faint slightly darker vertical bars. In alcohol a broad, lighter longitudinal bar becomes apparent along the middle of the body posteriorly. Fins light or dusky. Small specimens show traces of dark vertical bars on the head.

Quisquilius aureoviridis differs from *Q. eugenius* most notably in interorbital structure. In the latter species the eyes are raised, leaving a deep, narrow trench between them, the bottom of which is hardly visible; in *Q. aureoviridis* the eyes are little raised above the level of the relatively broad interorbital. In *Q. eugenius* the scales on the cheek and opercle are prominent in adults; in *Q. aureoviridis* they are absent. Finally, the two species may at once be separated in life by coloration, for *Q. eugenius* is a brownish black with vertical stripes.

Koumans (1953: 131) has synonymized four other species with *Q. eugenius*. Of these, three at least—*Q. cinctus*, *Q. naraharae*, and *Q. profundus*—do not seem to belong there. They appear, on the contrary, to be somewhat nearer *Q. aureoviridis* at least in the lack of squamation on the cheek and (usually) on the operculum. All of them differ from *Q. aureoviridis*, however, in having the body dark with light bands and in the punctate soft dorsal and anal fins.

Quisquilius malayanus and *Q. macrophthalm-*

mus appear to be relatively large scaled forms, as is the species described below.

Aureoviridis = (L.) yellow green.

Quisquilius limbatosquamis sp. nov.

Fig. 2, Table 1

HOLOTYPE: USNM 175012, 20.0 mm. in standard length, taken in a rotenone station about 2 mi. west of Haleiwa, Oahu, Territory of Hawaii by Gosline, *et al.*, July 23, 1955.

PARATYPES: University of Hawaii No. 1704, 8 specimens, 15.6–18.5 mm., off Waikiki reef, Oahu, T. H., Gosline, *et al.*, Dec. 31, 1952.

Depth of body contained 4.5 times in the standard length.

Greatest width of head considerably greater than greatest depth of head, the latter contained about 1.9 times in the head length. Mouth oblique, the lower jaw protruding. Front of mouth about on level with center of pupil. Rear of jaw below front of pupil. Eye not surrounded by a recessed groove above or posteriorly, its diameter contained about 3.7 times in the head length. Smallest distance between eye and groove behind upper lip contained about 2.5 times in the eye diameter. Anterior nostril about $\frac{1}{3}$ as far from the groove behind upper lip as from the posterior nostril. Posterior nostril slightly above top of pupil. Interorbital narrow, not in a deep recess, its width contained perhaps 5 times in

the eye diameter. No pores on head. Rows of papillae on head less markedly developed than in *Q. aureoviridis*. Ten gill rakers on the outside row of the lower limb of the first arch. Pseudobranch composed of 4 lobes. Tongue as seen from below rounded but with a slight indentation in middle.

Body completely scaled except apparently on the middorsal ridge that runs about one eye diameter forward from the first dorsal fin. Head scaled forward to an imaginary line drawn across between the rear of the orbits. Cheek and opercle scaleless. Twenty-six or 27 scales in a longitudinal series; 7 or 8 transverse rows; predorsal scale row incomplete. Scales ctenoid, except perhaps for those on breast.

None of the dorsal spines filamentous. Membrane between the two dorsals not quite connecting them. Second dorsal with a spine and 9 or 10 rays. Anal with a spine and 8 rays. Pectoral 19 or 20.

Color light with a light, dark-bordered vertical band crossing the nape and enclosing the pectoral base. Behind this are 6 vague dark vertical bands, one of these at caudal base, the others darkest on the middorsal and mid-ventral lines. Each scale on the body completely and prominently outlined by a series of large melanophores. Dorsal fins, particularly the first, with dark smudges at the base of the rays. Soft dorsal rays speckled. Head with traces of 3 broad vertical bands running down cheek and operculum.

This species was taken along with *Quisquilius aureoviridis*. It resembles that species rather than *Q. eugenius* in that the orbits are not partially enclosed in a deep trench and in the absence of scales on the cheek and head. However, *Q. limbatosquamis* differs from both the other Hawaiian species of the genus in the somewhat flatter head, in having a triangular naked area on the top of the head between and behind the eyes, in having a naked ridge extending forward from the first dorsal, in the larger scales and fewer dorsal rays. In color *Q. limbatosquamis* differs from the other two in having each of the scales distinctly outlined

by a series of melanophores.

Of other described species *Q. limbatosquamis* seems to differ from *Q. malayanus* in color and from *Q. macrophtthalmus* in the far higher pectoral count.

Limbatosquamis = (L.) edged scale.

Family GOBIIDAE, Genus HAZEUS

The relationships of the fish described below are most obscure, at least to the present author. It has been placed in the genus *Hazeus* because nothing better could be found. As one source of confusion this author has never seen the type species of *Hazeus*, *H. otakii* Jordan and Snyder (1902: 51, fig. 3). As another, the genus has frequently been considered a synonym of *Gnatholepis*, e.g., by Jordan and Evermann (1905: 487) and by Koumans (1931: 86; 1953: 168), but until it can be determined what fish *G. anjerensis*, the type species of *Gnatholepis*, represents there can be no final decision on the matter.

Hazeus unisquamis sp. nov.

Fig. 3

HOLOTYPE: USNM 175009, 18.2 mm. in standard length, taken by means of rotenone in a cut in the reef about 200 yds. west of Diamond Head, Oahu, Territory of Hawaii, by Gosline and class, May 16, 1950.

Depth of body contained 4 times in the standard length. Depth of caudal peduncle contained about 2.5 times in its length.

Head considerably wider than deep, the greatest depth of head contained about 1.4 times in the head length. Cleft of mouth broad and very slightly oblique, the lower jaw somewhat projecting. Front of mouth about on a level with lower border of pupil; maxillary reaching to below middle of eye. Upper lip narrow, its greatest width somewhat less than that of lower lip. Eye directed superolaterally, its diameter contained about 2.2 times in the head length. Smallest distance between eye and groove behind upper lip contained about 4 times in the eye diameter. Both

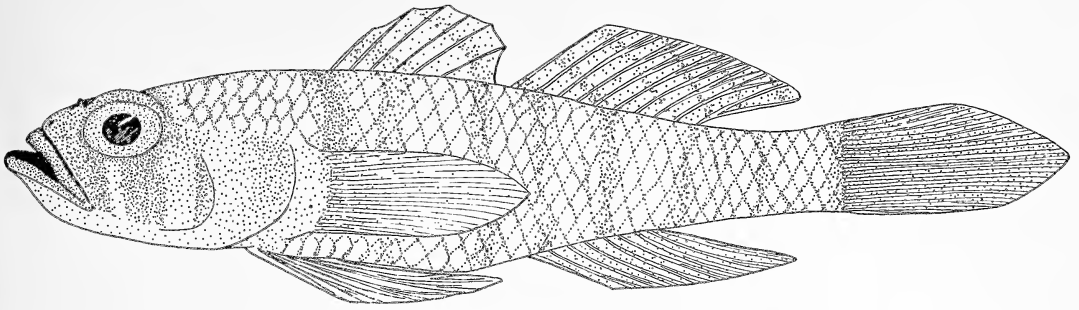


FIG. 2. *Quisquilius limbatoquamis*, holotype.

nostrils bordered by a low, raised collar, the anterior slightly nearer the posterior than the groove behind upper lip. Interorbital very narrow, hidden in a groove between the raised orbital borders. No pores on the head. Superior borders of orbit raised in a series of low flaps, these bordered behind by a groove; behind the interorbital region this groove is also bordered on the side away from the eye by a series of raised, scalelike flaps. No papillae on top of head, snout, or around eye, but two rows following the lower portion of the preopercular border and extending forward below the ramus of the lower jaw; another weakly developed vertical row on anterior portion of operculum. Gill cover free from the isthmus, the gill openings extending far forward about to below front of pupil. Ten widely spaced, pectinate gill rakers on the lower limb of the outer arch. Pseudobranch consisting of 5 lobes. Tongue with a broad, shallow median indentation as seen from below. Teeth in a narrow band in both jaws, some of the teeth on the inner border of the band somewhat enlarged; none of the outer teeth in either jaw especially enlarged.

Top of head scaled forward to the eye. Operculum almost completely covered by about 12 large, ctenoid scales. A single, large, embedded scale on the upper portion of each cheek. Twenty-six scales in a longitudinal series from above the upper end of the gill cover to the base of the caudal; 6 scales in a transverse series. Breast in front of pelvics without scales.

All of the fins with short, heavy rays maintained more or less erect. First spine in both dorsal fins more slender than the succeeding rays and with a soft tip. Dorsal VI-I,7. Anal I,7. Pectoral without silky rays above, with 18 rays in all; the upper 11 rays branched, the lower 7 simple, swollen and extending somewhat beyond the interradiial membranes. Pelvics united, with a thin, smooth-edged frenum anteriorly.

In alcohol the only prominent marks are narrow black borders to the two dorsal fins and a blackish bar across the caudal peduncle just in front of the caudal base; chromatophores are scattered more or less evenly over the rest of the body and head, giving a plain gray ground color.

So far as I can see from the species descriptions available to me *Hazeus unisquamis* may be differentiated from related forms by having only a single scale on the cheek, dark borders to the two dorsal fins, and only 7 soft rays in the dorsal and anal.

Unisquamis = (L.) one scale, in reference to the single cheek scale.

Family CALLIONYMIDAE

POGONYMUS gen. nov.

TYPE SPECIES: *Pogonimus pogognathus* sp. nov.

Head and body depressed forward of the anal origin, compressed posteriorly. Head flat above, the eyes completely separated by a slightly concave interorbital area. No supra-orbital tentacle. Preopercular process with an

upturned tip and with one additional dorsally directed spine ahead of tip; without an antrorse spine on its outer surface. Gill opening a small hole beneath the dorsal portion of the well-developed opercular flap. Lower jaw included, without a reverted lip but with a fringe of about 12 to 16 forwardly projecting papillae the tips of which extend beyond the upper jaw when the mouth is closed. Teeth elongate, in one or a few rows in both jaws, those above pointing backward, those below projecting up and back. A single lateral line running along sides, without notable side branches except for one at the rear, which forms a saddle across the caudal peduncle. Two dorsal fins, the first very low, of 2, 3, or 4 spines none of which reach the second dorsal origin when the first dorsal is depressed. Rays of second dorsal unbranched except for the last. All of the anal rays branched at tip, except for the last, which is divided to the base. Pelvic fins without separated rays and not attached to the middle of the pectoral fins by a membrane.

Judging from the keys to callionymid genera given by Schultz and Woods (1948: 419-420) and others, *Pogonimus* is most closely related to *Eleutherochir*. It differs from that genus and most other callionymids in the presence of a fringe of papillae on the lower jaw and in having the anal, but not the soft dorsal, rays divided at the tips.

Pogon = (Gr.) beard; onyma = (Gr.) name.

Pogonimus pogognathus sp. nov.

Fig. 4

HOLOTYPE: USNM 175010, a nearly ripe female 25 mm. in standard length, taken in 3 to 10 ft. of water in a small cove just west of Hanalei Bay, Kauai, Territory of Hawaii, by Gosline and Ohai, June 19, 1952.

PARATYPES: USNM 175011, 5 specimens, 15-21 mm.; University of Hawaii No. 1626, 34 specimens, 11-22 mm., all with the same data as the holotype.

Head broad and flat, its greatest depth con-

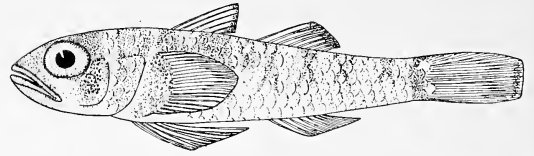


FIG. 3. *Hazeus unisquamis*, holotype.

tained about 1.6 times in its greatest width, which in turn is contained about 1.2 times in the head length to the end of the opercular flap. Eyes large, contained about 4 times in the head length, not projecting above the dorsal surface of the head, separated by a bony interorbital that is about equal to a pupil diameter in width and that contains two median pores. Snout broad and blunt, its length about $\frac{2}{3}$ an eye diameter. Gape nearly twice as broad as deep, the maxillary reaching about to the anterior border of the eye when the mouth is closed. Gill covers attached to one another below by a free fold across the isthmus.

Lateral line dropping down to the mid-sides about at the pectoral tip, giving rise to about 15 pores along its length, some of these slightly above the lateral line and others slightly below; terminating posteriorly about halfway out along the caudal rays.

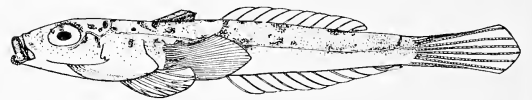


FIG. 4. *Pogonimus pogognathus*, paratype.

First dorsal originating about $\frac{1}{3}$ of the way back along the standard length, its rays low and rather tightly bound to the midline of the back by the membrane behind the last ray. Longest dorsal spine considerably shorter than the distance between dorsal fins. Soft dorsal with 9 or 10 rays, lying somewhat ahead of anal, its last ray not nearly reaching caudal base when depressed. Anal with 9 or 10 rays, the tip of the last about reaching caudal base.

Caudal fin slightly shorter than the head length, with 6 principal rays, all of which are somewhat branched at tip, the outermost least so; 10 caudal rays in all, the outermost short, splintlike, and unsegmented. Pelvic fins with a spine and 5 branched rays, the fourth of which is the longest. Pectoral with about 19 rays, the longest of which reach about to above the anal origin.

A 15 mm. (standard length) specimen has black spots at the base of each soft dorsal and anal ray and another at the base of tail. Between 15 and 20 mm. these markings fade, so that the specimens are a plain yellowish brown except for some incipient markings on the back and on the first dorsal. At a length of 25 mm. the first dorsal is almost completely black, and there are prominent dark bars and spots symmetrically arranged on either side of the middorsal line on the body and head.

The three specimens sexed, 22 to 25 mm. in standard length, proved to be nearly ripe females. If adult males are represented among the types, they show no striking external differences.

The species has been taken only once. This was from a poison station run in a small, semi-protected cove in which a vertical, algae-covered ledge dropped vertically to a uniform sand bottom 3 to 10 feet below. *Pogonymbus pogognathus* was the most abundant species taken. Whether the individuals were living on the ledge or in the sand below (as seems more probable judging from the fringed lip) was not verified at the time. Just how this habitat differed from that of innumerable other poison stations run from ledges dropping off to a sand bottom remains unknown to the author.

Pogon = (Gr.) bearded; gnathos = (Gr.) jaw.

Suborder SCHINDLERIOIDEI

The two known species of *Schindleria* (see Fig. 5) were first described as members of the genus *Hemiramphus* in the 1930's. They have been bounced about from order to order ever since. The members of the genus are neotenic

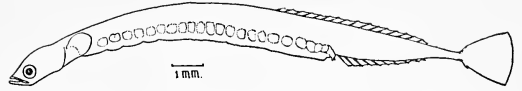


FIG. 5. *Schindleria praematurus*, female with eggs. (After Bruun.)

fishes, apparently without close relatives, which have lost the adult characteristics that would presumably indicate their relationships. The present erection of a new suborder of perciform fishes for *Schindleria* is not made on the basis of any decisive new material; it merely seems to be the best available solution to a difficult problem. Knowledge of *Schindleria* may be marshaled under four heads: neoteny, sexual differentiation, soft anatomy, and "osteology." These will be dealt with only in so far as they bear on the systematic position of the genus.

Neoteny: That a 20 mm. *Schindleria* may be sexually mature is often indicated by the conspicuous presence of large eggs in the females. That the rest of the fish is in a larval stage of development is shown by the presence of the atrium directly behind, i.e., on the same horizontal plane with, the ventricle (Schindler, 1932: pl. 4c); by what is apparently a functional pronephros (Schindler, 1932: 25); by the well-developed opercular gill (Schindler, 1932: 12); the tremendous, protruding eyes; the rounded pectoral fin attached to a lobate, fleshy base; the transparent body; and by the degree and nature of the "ossification" of the skeleton (see below).

Neoteny in fishes is rare, and nowhere is it carried to the extreme found in *Schindleria*. It is also apparently sporadic, occurring as it does in some of the Clupeiformes (e.g., Salangidae), in at least one member of the Beloniformes (*Cololabis adocetus*), and perhaps in the gobioid Perciformes. Consequently, its neotenic nature is of no great aid in the systematic placement of *Schindleria*. One is merely inclined to ask the irrelevant question why neoteny does not occur more often among fishes of the open ocean.

Sexual Differentiation: Aside from the primary sex organs there is in the males (but not the females) of *Schindleria*, especially in *S. praematurus*, a long urogenital papilla (Schindler, 1932: 6, 8; Bruun, 1940: 7, fig. 2). In addition, the anus of both species lies farther back along the body in females than in males (Schindler, 1932: 6, 8; Bruun, 1940: 5).

Soft Anatomy: In 1932 Schindler described the soft parts of *Schindleria praematurus* with special reference to the heart, swim-bladder, gills, and the digestive and urogenital systems. None of the features described, nor the sexual differentiation, provides the present author with any clue as to the taxonomic relationships of the genus.

"Osteology": There is some difficulty in determining what should be included under "osteology." Schindler (1932: 6) states: "An ossification or deposit of lime in the vertebrae is not present." However, the vertebrae take up alizarin stain. In the account of the osteology that follows all those portions that stain with alizarin will be considered "ossifications."

As the final comment in his paper on *Schindleria*, Giltay (1934: 10) has said: "Des matériaux plus nombreux nous permettront de mieux définir ses affinités, surtout quand on aura mieux pu étudier le squelette qui est déjà relativement bien développé." There are several difficulties with this proposition. First, additional material has been gathered and it has not helped much. Second, the degree of ossification in the additional specimens is about the same as in those taken earlier, and there seems little hope of finding an adult-type ossification in *Schindleria*. Third, the "ossification" that is present occurs to approximately the same extent and in about the same areas as in a larval anchovy of the same size. To what extent this larval-type ossification in *Schindleria* is comparable to the bony structure of other adult fishes is an open question. (In this author's opinion, the "ossifications" that do occur in *Schindleria* are not of an adult fish type at all but are merely calcifications of normally larval structures. Indeed,

it seems that the adult *Schindleria* has retained larval features which have to some extent "ossified" precociously as compared to the ontogenetic development of the same features in normal fishes. If this is true, the calcifications in *Schindleria* bear little comparison with normal adult fishes and are only incompletely comparable with any larval stage.)

Judging from the absorption of alizarin stain, the jaws, vertebral centra, and fin rays are the best ossified portions of *Schindleria*. The upper jaw consists of a toothed premaxillary and a toothless maxillary of about equal length (Fig. 6a). The premaxillary has an upwardly projecting flange a little more than halfway out. The premaxillary pedicel is broad and low, articulating medially with a large cartilaginous (?) median pad and laterally with the maxillary. The latter bone has an abrupt, sharp-angled bend (Fig. 6b) that hooks around the premaxillary pedicel; the bone then projects medially inside the pedicel.

The lower jaw consists, so far as can be determined, of a single ossification (Fig. 6e), though an obscure "suture" between dentary and articular may have been missed.

The suspensorium runs very obliquely forward in order to pass below the very large eye (Fig. 6c) between the skull and the lower jaw. The only portion of the suspensorium that takes stain is a long splint made up of the quadrate below and the hyomandibular above (Fig. 6e). From the rear of the hyomandibular projects an elongated, leaf-shaped operculum.

The hyoid apparatus (Fig. 6e) consists of a vaguely ossified glossohyal in front, an elongate ceratohyal, and an epihyal. The last bone loops around posteriorly to join the upper portion of the hyomandibular. There are 5 short branchiostegals; 2 on the ceratohyal and 3 on the epihyal. There are 4 gill arches (Schindler, 1932: 11); the lower pharyngeals are separate.

The forward portion of the cranium does not take up stain. To the rear above there are three small, partial ossifications which are here

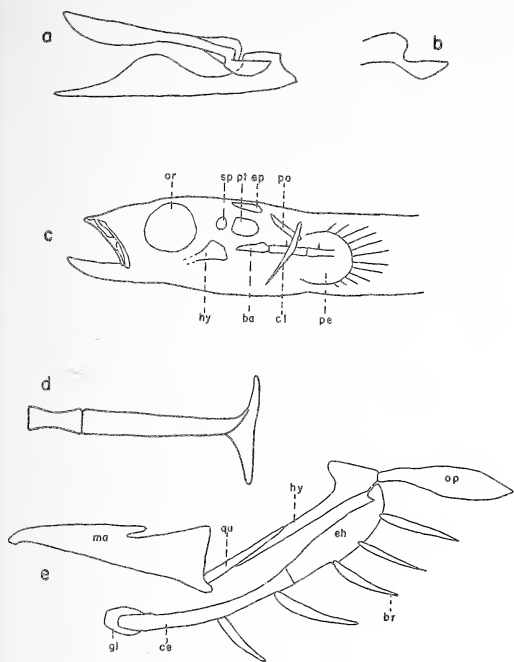


FIG. 6. *Schindleria*. a, Left premaxillary and maxillary from the inside, the posterior end of the maxillary somewhat raised. b, Median end of left maxillary from above. c, Head and fore part of body to show certain "ossifications." d, Caudal skeleton and posterior portion of "vertebral column." e, Mandible, suspensorium, opercle, and hyoid apparatus. ba, "Basioccipital"; br, branchiostegal ray; ce, ceratohyal; cl, cleithrum; eh, epihyal; ep, epiotic; gl, "glossohyal"; hy, hyomandibula; ma, mandible; op, opercle; or, orbit; pe, pectoral lobe; po, "posttemporal"; pt, pterotic; qu, quadrate; and sp, sphenotic.

provisionally identified as epiotic, sphenotic, and pterotic. Running in under the skull is a projection of the vertebral column which may represent the basioccipital (Fig. 6c); a possible alternate interpretation of this "bone" is suggested below.

The pectoral girdle consists of two simple struts (Fig. 6c) representing the cleithrum and probably the posttemporal. There is nothing in the fleshy lobe between the cleithrum and the pectoral rays that absorbs alizarin stain.

The vertebral centra stain clearly but the neural and haemal arches seem to be represented only by short spines that ride on the

centra. The number of differentiated vertebrae vary from 33 to 39 in the genus (Schindler, 1932: 6, 8). At the rear of the vertebral column is a rodlike structure with an upturned tip that runs for the length of about 3 normal vertebrae. To its posterolateral face is attached a plate (Fig. 6d). Both of these features take stain well.

Since it is this terminal portion of the axial skeleton that forms the feature of *Schindleria* unique among all known fishes, some discussion of it seems in order. The terminal plate would appear to take the place of the hypural fan, differing from the usual caudal skeleton in the complete lack of separate ossifications. The rodlike portion of the "vertebral column" ahead of it is difficult to interpret satisfactorily. When the vertebral column first ossifies in an anchovy, the caudal portion of the column forms early as a number of small elements which eventually fuse to a considerable extent to form the adult caudal skeleton. One presumes that the tail rod of *Schindleria* evolved in a different ontogenetic fashion. The most satisfactory explanation for it that the author can find is that it represents the posterior portion of the notochord which has been replaced by cartilage and/or bone without dividing into discrete vertebral segments.

In this connection it is necessary to revert to the skull bone that was provisionally called the basioccipital in earlier paragraphs. The alternative explanation is that it is the forward end of this same notochord which has taken up stain in the same way suggested for the posterior rod.

In the caudal fin there are 13 rays, 11 of which are branched. The interneurals and interhaemals of the dorsal and anal fins respectively bear a one-to-one relationship with the vertebrae (see Bruun, 1940, fig. 2). There are from 15 to 20 unbranched dorsal rays, and from 11 to 17 unbranched rays in the anal; the pectoral contains 15 to 17 rays (Schindler, 1932: 7, 8).

Relationships: As mentioned, *Schindleria* was first described as a neotenic *Hemiramphus*.

Giltay (1934) demonstrated the incorrectness of this allocation. *Inter alia*, *Schindleria* differs from all of the Beloniformes in the low number of branchiostegal rays, the absence of fused pharyngeals, and the one-to-one relationship between dorsal or anal fin rays and vertebrae.

A rather better case could be made for placing *Schindleria* in the Syngnathiformes or Gasterosteiformes. However, the Syngnathiformes are characterized by having the first 3 to 6 vertebrae immovably united. The lack of a tubular snout, of external bony plates, and of a soft dorsal fin with closely spaced rays argues against placing *Schindleria* in either of these orders.

Turning from negative to positive indications of relationships, there appears to be only one character in *Schindleria* which provides any clues. This is, as already noted by Giltay (1934), the one-to-one relationship between the dorsal or anal fin rays and the vertebrae. It appears that this characteristic is limited to the Perciformes, being found there in the trachinoid, ammodytoid, blennioid, and many of the gobioid fishes. However, the basal perciform stock has, like other fishes, two or three soft dorsal and anal rays (with their interneurons and interhaemals) per vertebra. Just why certain perciform groups should have a one-to-one relationship between these features remains unknown. That it is a polyphyletic development is shown by the gobioid fishes, where this relationship seems to have developed within the group itself. At least, *Ptereleotris* has the usual two or three interneurons per vertebrae whereas most of the other gobioids have only one (Gosline, 1955: 166). If the one-to-one relationship has occurred several times within the perciform fishes, could it not also occur within other orders? The best available answer to this question seems to be that it apparently has not done so.

To sum up regarding the ordinal position of *Schindleria*, the genus seems to rest most easily (or rather least uneasily) among the

Perciformes. There is nothing to really invalidate such a position and there is the one-to-one fin ray to vertebra relationship to recommend it. Where *Schindleria* belongs among the Perciformes is obscure. The best that can be done is to place *Schindleria* in the neighborhood of the blennioid fishes.

The reason for raising *Schindleria* to subordinal rank (rather than placing it in the Blennioidei as Giltay, 1934, has done) lies in the rodlike terminal section of the spinal column. There seems to be nothing like it elsewhere in fishes. The author has looked through the literature on both adult and larval fishes without finding anything similar. He has discussed this precaudal rod with E. A. Ahlstrom, A. F. Bruun, and C. L. Hubbs, and wishes to thank them for their help on this matter; nevertheless, nothing resembling this rod has come to light. In the great majority of modern fishes the notochord is replaced by vertebrae. However, when this occurs the vertebral replacement runs all the way back to the caudal skeleton. The uniqueness of *Schindleria* lies in the fact that vertebral development stops short some distance before the caudal skeleton.

There is one other feature of *Schindleria* that this author has never encountered elsewhere in fishes or in the literature (although this may simply indicate a gap in the author's knowledge, especially in regard to larval fishes). In *Schindleria* the hyoid apparatus (Fig. 6) articulates with the upper head of the hyomandibular. In all the fishes the author knows, the hyoid apparatus articulates by means of the interhyal at the lower extremity of the hyomandibular.

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A New Species of Polychaetous Annelid (Family Capitellidae) from Southern California¹

DONALD J. REISH²

DURING THE COURSE of studying the quantitative distribution of polychaetous annelids in Newport Bay, California, a new species belonging to the capitellid genus *Scyphoproctus* Gravier 1904 was encountered. This is the first report of the genus in the eastern Pacific Ocean.

Only two species of this genus have been reported previously. *Scyphoproctus djiboutiensis* was described from the Red Sea by Gravier (1904, 1906), and subsequently was reported from India by Fauvel (1930, 1953). Okuda (1940) described *S. gravieri* from Okinawa.

The author wishes to express his thanks to Dr. Russell Cangialosi for his assistance with the drawings.

Scyphoproctus oculatus n. sp.

A total of 28 specimens was collected from the bottom of Newport Bay, California, with a size one Hayward orange-peel bucket. These stations were all located near the Pacific Coast Highway (Alternate 101) Bridge which passes over Newport Bay.

The holotype measures 20 mm. in length and 1.0 mm. in width. Other complete specimens ranged from 8 to 20 mm. in length. The prostomium (Fig. 1) is broadly rounded in front and bears one pair of elliptical-shaped eyes on either side. The peristomium lacks setae. The following 12 segments are setigerous with only simple capillary setae (Fig. 2)

in both the notopodium and neuropodium.

The abdominal region of the holotype consists of 85 setigerous segments. Hooded hooks (Fig. 3) are present in both the notopodium and the neuropodium of each segment, except at the posterior end (see below). The hooks bear one large tooth, three smaller teeth, and are covered in part by a hood (Fig. 3). Just anterior to the anal funnel (Fig. 4) at the posterior end of the animal, the hooded hooks in the notopodium are replaced by simple acicular spines (Fig. 5). The first appearance of these spines ranges from the sixth to the second segment from the anal funnel. The acicular spines of the two notopodia of a segment shift towards the median line with each succeeding segment so that the spines of either side at the segment just anterior to the anal funnel nearly touch one another. This approaches the condition of a single dorsal line of acicular spines at this segment in *S. djiboutiensis* (Gravier, 1904, 1906).

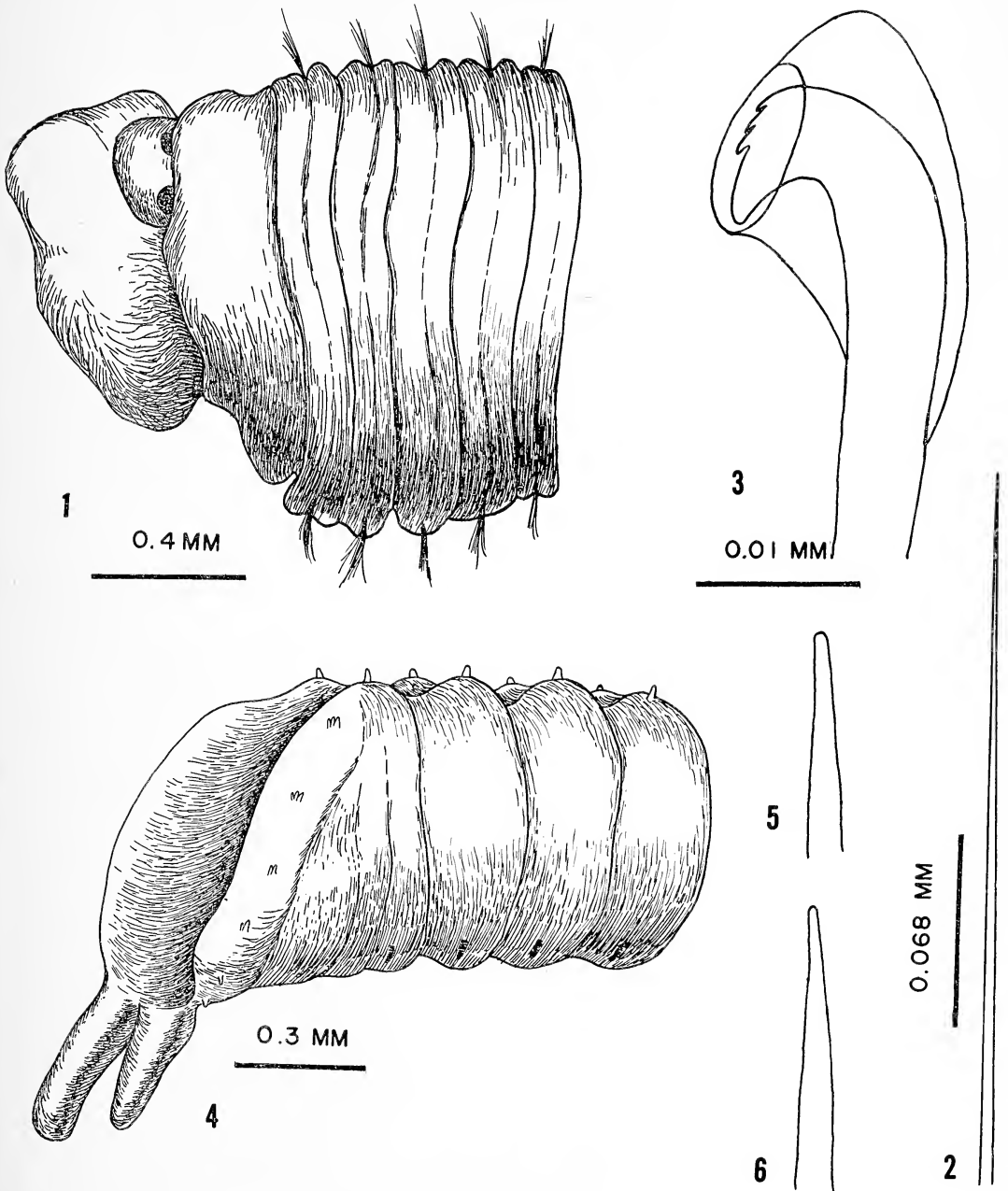
The anal funnel (Fig. 4) is composed of six groups of acicular spines (Fig. 6) on each side. The number of spines varies dorsoventrally, right and left, and from specimen to specimen. Typically there are 3, 3, 2, 2, 1, 1 (dorsal to ventral) acicular spines on each side. However, the following variations were observed: for the left side 4, 4, 4, 2, 2, 2, and 4, 3, 2, 2, 1, 1; for the right side 4, 4, 2, 2, 2, 2, and 4, 4, 2, 2, 1, 1.

DISCUSSION

Scyphoproctus oculatus differs from the other two species in the genus by the possession of a pair of eyes on the prostomium and by only six groups of acicular spines on each side of the anal funnel. The prostomium of *S. djibou-*

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FIGS. 1-6. *Scyphoproctus oculatus* n. sp. 1, Anterior end in lateral view; left to right, everted proboscis, prostomium with both eyes shown, peristomium, setigerous segments 1 to 5 bearing capillary setae. 2, Capillary seta from segment 7. 3, Hooded hook from segment 15. 4, Posterior end in lateral view; left to right, anal funnel bearing two anal cirri and six groups of acicular spines and the posterior setigerous segments with acicular spines in the notopodium and hooded hooks in the neuropodium. 5, Acicular spine from a posterior notopodium; magnification as 2. 6, Acicular spine from anal funnel; magnification as 2.

tiensis lacks eyes, and the anterior end is unknown in *S. gravieri*. Both *S. djiboutiensis* and *S. gravieri* are characterized by having 11 groups of acicular spines on either side of the anal funnel. The number of spines is 4, 4, 3, 3, 3, 2, 2, 2, 1, 1, 1 in the former, and 13 (or 12), 7, 5, 5 (or 4), 4, 3, 2 (or 3), 2, 2, 2, 1 in the latter species.

Type Material

The holotype, seven paratypes, and additional specimens have been deposited in the polychaete collections of the Allan Hancock Foundation, University of Southern California.

Type Locality

Bottom of Newport Bay near the Pacific Coast Highway (Alternate 101) Bridge. The substrate consisted of sand and shell fragments at these stations.

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Evapotranspiration in Hong Kong: A Second Report¹

C. S. RAMAGE²

THE FIRST REPORT on evapotranspiration in Hong Kong (Ramage, 1953)³ describes installation of an evapotranspirometer battery, twenty months' measurement of potential evapotranspiration (P.E.) from grass surfaces, and comparisons of P.E. from grass and some common vegetables.

Comparison of measured P.E. with that computed from Thornthwaite's (1948) formula reveals that the formula when applied in Hong Kong gives values consistently low in winter and high in summer.

This leads to two possible conclusions:

- 1) The site of the evapotranspirometers is not representative of the area.
- 2) Thornthwaite's formula is not valid for Hong Kong.

The present paper will summarise the first five years' P.E. measurements at Hong Kong (October 1951 through September 1956), present arguments on the two possibilities mentioned above, discuss Penman's (1948) transpiration formula, and, finally, describe

the derivation of a simple P.E. formula for Hong Kong.

FIVE YEARS' POTENTIAL EVAPOTRANSPIRATION MEASUREMENTS

Table I shows monthly totals of P.E. measured for three grass-covered soil tanks at the King's Park Radiosonde Station (22°19'N., 114°10'E., 213 feet above mean sea level) together with relevant meteorological data. Each tank has an internal area of four square meters. To save material, the central tank has a wall in common with each of the others. The site was unchanged throughout the period and there were no variations in methods of watering or of measuring rainfall and overflow. Except when one or two tanks were used briefly for growing vegetables, the results are means derived from all three tanks in the battery. Readings varied insignificantly and randomly between tanks, indicating a satisfactory local exposure and unlikelihood of leaks. In wet weather the overflow tanks occasionally flooded. Resulting errors have been eliminated from the final values.

POTENTIAL EVAPOTRANSPIRATION OF VEGETABLES

Validity of P.E. relative to grass for tomatoes, Chinese cabbage, and lettuce determined during the 1952 winter (table 1 of first report) was tested in the winter of 1953-54. The results appear in Table 2. It can be seen that ratios of vegetable P.E. to grass P.E. varied little from one winter to the next. The method of comparison thus appears to give results of real value to irrigation planners.

¹ Contribution No. 7 of Hawaii Institute of Geophysics. Scientific Report No. 1 of Contract No. AF 19 (604)-1942. The research in this document has been sponsored in part by the Air Force Cambridge Research Center, Air Research and Development Command, under Contract No. AF 19 (604)-1942. Presented at the Ninth Pacific Science Congress, Bangkok, November, 1957. Manuscript received September 19, 1957.

² Meteorology Division, Hawaii Institute of Geophysics, University of Hawaii.

³ This report also appeared on pages 112-124 of Johns Hopkins University Laboratory of Climatology, Publications in Climatology Vol. VII, No. 1, edited by J. R. Mather. (Contracts AF19 (604)-193, AF 19 (604)-289.)

TABLE 1
MONTHLY POTENTIAL EVAPOTRANSPIRATION AND METEOROLOGICAL OBSERVATIONS MADE AT KING'S PARK
(22°19'N., 114°10'E., 213 FT. ABOVE M.S.L.) AND AT ROYAL OBSERVATORY (22°18'N., 114°10'E.,
109 FT. ABOVE M.S.L.) FOR THE FIVE-YEAR PERIOD, OCTOBER 1951-SEPTEMBER 1956,
AND ALSO FOR OCTOBER 1956-DECEMBER 1956

	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
Potential evapotranspiration (King's Park) mm.	1951										144	100	91
	1952	74	79	80	88	120	95	113	104	81	139	100	76
	1953	72	49	73	72	99	130	133	100	119	122	93	81
	1954	72	77	88	80	140	102	148	147	161	133	136	83
	1955	79	81	106	107	110	116	118	101	125	147	121	87
	1956	64	84	95	131	142	157	157	124	140	141	116	78
	5-YEAR MEAN	72	74	88	96	122	120	134	115	125	137	110	84
Rainfall (King's Park) mm.	1951										104	75	15
	1952	26	32	40	183	184	560	189	376	838	17	9	24
	1953	27	64	135	95	354	407	138	374	564	48	41	76
	1954	53	30	58	160	89	207	147	294	171	20	133	0
	1955	2	0	61	162	446	322	546	580	115	11	49	18
	1956	67	80	7	79	299	367	170	455	165	37	34	7
	5-Year Mean	35	41	60	136	274	373	238	416	371	40	61	27
Mean temperature (King's Park) °F.	1951										77	70	64
	1952	62	61	65	72	80	82	83	81	80	77	73	61
	1953	61	61	65	66	76	82	83	83	80	79	71	64
	1954	63	61	61	71	80	82	83	83	81	76	70	61
	1955	57	64	69	72	79	81	82	82	83	77	68	66
	1956	58	61	66	75	79	83	84	82	83	77	68	62

REPRESENTATIVENESS OF THE
KING'S PARK SITE

An oil-drum evapotranspirometer (see Garnier, 1954) was installed at Kai Tak Airport (22°20'N., 114°12'E., 12 feet above mean sea level) and readings began in September, 1954. The tank was turfed with and surrounded by grass clipped to 1-2 inches and was watered

from above. The site being in an extensive flat area near sea level differs considerably from King's Park where the evapotranspirometer is atop a small isolated hill.

Figure 1 shows results of the first year's simultaneous readings. For this period it is safe to assume that the oil drum did not develop leaks. At Kai Tak, in moisture deficient

TABLE 1, *continued*
 MONTHLY POTENTIAL EVAPOTRANSPIRATION AND METEOROLOGICAL OBSERVATIONS MADE AT KING'S PARK
 (22°19'N., 114°10'E., 213 FT. ABOVE M.S.L.) AND AT ROYAL OBSERVATORY (22°18'N., 114°10'E.,
 109 FT. ABOVE M.S.L.) FOR THE FIVE-YEAR PERIOD, OCTOBER 1951–SEPTEMBER 1956,
 AND ALSO FOR OCTOBER 1956–DECEMBER 1956

	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEPT.	OCT.	NOV.	DEC.
	5-Year Mean	60	62	65	71	79	82	83	82	81	77	70	63
Mean dew point temperature (Royal Observatory) °F.	1951										68	61	50
	1952	52	55	61	68	75	77	77	77	75	68	62	47
	1953	51	56	60	60	71	77	77	78	74	73	61	55
	1954	57	54	53	67	74	77	77	77	73	65	59	48
	1955	41	53	62	64	72	75	77	76	76	64	53	53
	1956	46	55	59	67	73	76	77	76	72	65	52	51
	5-Year Mean	49	55	59	65	73	76	77	77	74	68	59	51
Sunshine duration (Royal Observatory) hours	1951										197	135	189
	1952	168	78	84	114	196	152	192	177	165	240	264	138
	1953	130	59	75	61	125	194	275	241	114	211	141	153
	1954	160	116	109	69	221	159	254	206	218	256	213	150
	1955	210	147	121	174	169	137	160	208	253	289	181	229
	1956	165	66	102	175	137	214	263	229	229	242	172	164
	5-Year Mean	167	93	98	119	170	171	229	212	196	239	187	172
Mean wind speed (Royal Observatory) knots	1951										9.5	10.9	9.9
	1952	9.6	11.7	13.2	10.8	8.9	8.1	8.1	7.0	9.0	9.8	7.5	8.4
	1953	10.2	11.5	10.9	11.3	9.5	8.8	6.4	5.7	10.3	9.5	8.3	9.4
	1954	9.3	9.4	9.1	11.0	6.7	7.7	5.9	7.3	10.5	8.8	10.6	9.3
	1955	9.4	11.6	11.1	9.3	8.0	9.1	6.8	4.7	6.5	11.2	11.6	10.8
	1956	9.3	12.1	12.5	10.4	9.5	8.2	6.6	9.6	9.1	9.9	9.4	7.8
	5-Year Mean	9.6	11.3	11.4	10.6	8.5	8.4	6.8	6.9	9.1	9.8	9.8	9.6

months, grass surrounding the tanks could not be watered, while some flooding possibly occurred in moisture-surplus months. Since King's Park is not subject to these mensural

drawbacks they may account for some of the differences between the two curves. It seems reasonable then to conclude that the King's Park site is probably a representative one.

TABLE 2
COMPARISON OF POTENTIAL EVAPOTRANSPIRATION
FROM VEGETABLES AND GRASS

CROP	TOMATOES	CHINESE CABBAGE	LETTUCE
Planting date.....	28 Oct. 1953	28 Oct. 1953	2 Jan. 1954
Days to reach maturity.....	128 (last fruit)	61	79
Total crop weight (lbs.).....	85 (poor crop)	34½	
(1) Total P.E. (mm.)	838	282	271
Average daily P.E. (mm.)....	6.5	4.6	3.4
(2) Total P.E. of grass in same period (mm.)..	354	182	193
Average daily P.E. of grass in same period. (1)	2.8	3.0	2.4
Ratio ————— (2)	2.4	1.5	1.4
Mean temperature during period (°F.) (1)	65	68	62
Ratio ————— for 1952 (2) winter.....	2.3	1.6	1.7

COMPARISON OF MEASURED POTENTIAL EVAPO-
TRANSPIRATION WITH VALUES DERIVED FROM
THORNTHWAITE'S AND PENMAN'S FORMULAE

Thornthwaite's Formula

The conclusions of the first report are amply confirmed by the longer period of record. Figure 2 shows monthly means of P.E. derived from the five years' measurements. Again calculated values are too low in the dry winter and too high in the wet summer. Since investigators in Australia (Leeper, 1950), Nigeria (Garnier, 1954), and Trinidad (Smith, 1954) report similar shortcomings in the formula one must conclude that it should not be assumed to be valid for any monsoon or tropical maritime region.

Penman's Formula

Penman (1948, 1950), using energy con-

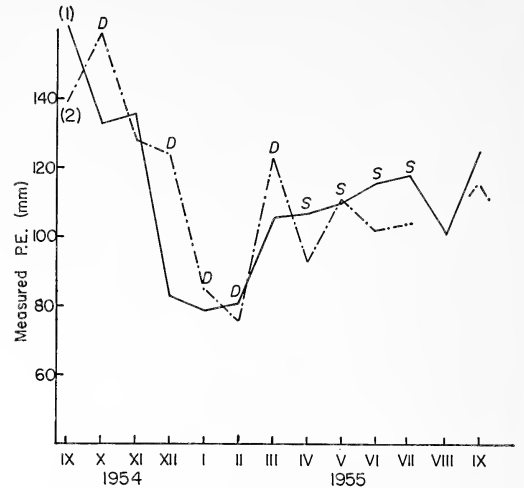


FIG. 1. Monthly potential evapotranspiration measured at King's Park (1), and at Kai Tak Airport (2). September 1954 through September 1955. "D" signifies that P.E. exceeded rainfall by at least 75 per cent and the letter "S" that rainfall was in excess by at least 35 per cent.

ceptions, derives the following formula for estimating potential transpiration from vegetated areas. (It checks well with observations made in America and Europe.)

$$E_T = E_o \times f = f (\Delta H + 0.27E_a) / (\Delta + 0.27) \text{ mm/day.}$$

Where E_T = potential transpiration

E_o = the hypothetical evaporation that would take place from an extended sheet of open water exposed to the weather conditions found over the site.

f , an empirically determined seasonal factor converting E_o to E_T , has the following values:

- Nov. through Feb. 0.6
- Mar., Apr., Sept., Oct. 0.7
- May through Aug. 0.8

Δ = slope of vapor-pressure curve for water at mean air temperature T_a (mm mercury/°F)

$$H = R_A (1 - r) (0.18 + 0.55n/N) - \sigma T_a^4 (0.56 - 0.092 \sqrt{e_d}) / (0.10 + 0.90n/N)$$

0.27 = the constant of the standard hygrometer equation (mm/°F)

$$E_a = 0.35 (e_a - e_d) (1 + u_2 \times 10^{-2}) \text{ mm/day}$$

R_A = theoretically calculable amount of radiation that would reach the earth in the

absence of an atmosphere, converted to an evaporation equivalent by putting $59 \text{ cal/cm}^2 = 1 \text{ mm. evaporation.}$

r = reflection coefficient, to be taken as 0.05. For standard evaporation tanks with light walls and clean water it may be very much greater.

n/N = actual/possible hours of sunshine. In the first term in H it is a factor limiting incoming short-wave radiation; in the second it is a transform of a cloudiness factor limiting outward long-wave radiation.

σT_a^4 = theoretical black-body radiation at mean air temperature T_a ; this too is in evaporation units like R_A .

e_d = saturation vapor pressure at dewpoint (mm Hg).

e_a = saturation vapor pressure at mean air temperature; hence $(e_a - e_d)$ is the mean saturation deficit.

u_2 = average wind speed in miles/day at 2 m. above the ground.

Since the formula incorporates both humidity and wind parameters it appeared likely to give more reasonable results than Thornthwaite's formula when applied in Hong Kong. The data listed in Table 1 have been used to calculate mean monthly P.E. according to Penman's formula and the values are plotted in Figure 2. They approach the observed values more closely than those determined by Thornthwaite's formula but err in the same sense, overestimating summer and underestimating winter P.E.

POTENTIAL EVAPOTRANSPIRATION
FORMULA FOR HONG KONG

Deriving the Formula

In Penman's formula, the expression $E_a = 0.35 (e_a - e_d) (1 + u_2 \times 10^{-2})$ mm/day incorporates humidity and wind parameters.

Figure 3 shows a plot of both E_a and mean daily observed P.E. at Hong Kong derived from the monthly means for five years. From October through January and from February

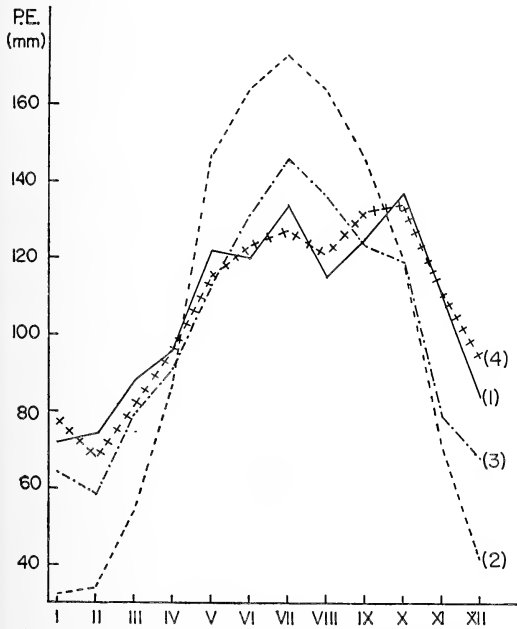


FIG. 2. Monthly means of potential evapotranspiration measured at King's Park (1), and calculated according to Thornthwaite's formula (2), Penman's formula (3), and the new formula (4). Based on five years' data.

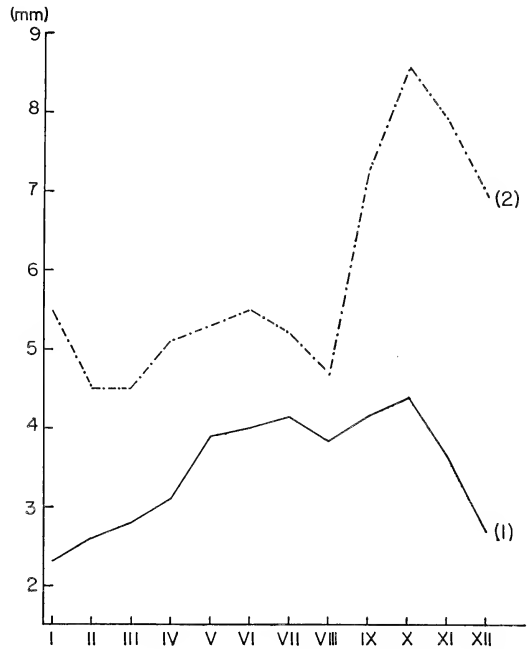


FIG. 3. Mean daily potential evapotranspiration measured at King's Park (1), and E_a (2). Based on five years' data.

TABLE 3
MEASURED AND CALCULATED MONTHLY POTENTIAL EVAPOTRANSPIRATION AT HONG KONG
FOR 1953 AND OCTOBER THROUGH DECEMBER 1956 (MM.)

	1953												1956		
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Oct.	Nov.	Dec.
Measured.....	72	49	73	72	99	130	133	100	119	122	93	81	141	116	78
Thornthwaite formula.....	35	33	53	59	122	165	175	168	138	135	73	45	115	58	38
Difference.....	+37	+16	+20	+13	-23	-35	-42	-68	-19	-13	+20	+36	+26	+58	+40
Penman formula	64	46	65	76	106	140	160	144	114	104	69	59	125	85	57
Difference.....	+8	+3	+8	-4	-7	-10	-27	-44	+5	+18	+24	+22	+16	+31	+21
New formula...	81	57	78	81	106	126	127	121	129	124	105	84	142	111	81
Difference.....	-9	-8	-5	-9	-7	+4	+6	-21	-10	-2	-12	-3	-1	+5	-3

through August the curves are similar although between these periods they undergo sharp relative displacements. Nevertheless, E_a seems to bear some intraseasonal relationship to measured P.E. This may explain why Penman's formula approximates Hong Kong observations more closely than does Thornthwaite's formula which does not explicitly embody humidity and wind parameters.

Thornthwaite attaches great importance to temperature in the evapotranspiration process. This was allowed for by combining e_a with E_a in the form $\sqrt{E_a} + \sqrt{e_a}$. When this expression is plotted against mean daily measured P.E. (Fig. 4), a good fit is provided by a straight

line whose equation is

$$P.E. = \sqrt{E_a} + \sqrt{e_a} - 3.5 \text{ mm/day}$$

Values calculated from this equation and plotted in Figure 2 are in reasonable agreement with mean monthly measured P.E.

Testing the Formula

1953 was the most abnormal year of the five-year period. Table 3 and Figure 5 depict

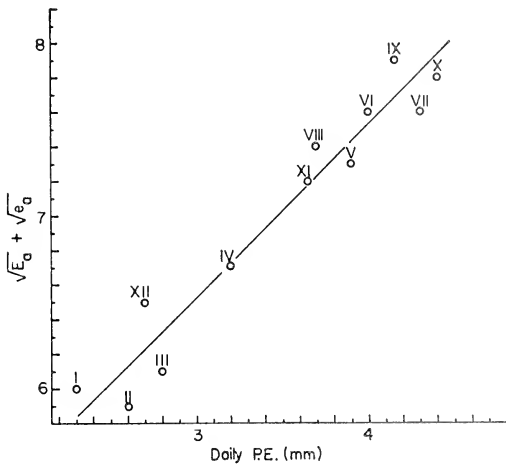


FIG. 4. Mean daily potential evapotranspiration measured at King's Park plotted against $\sqrt{E_a} + \sqrt{e_a}$. Based on five years' data.

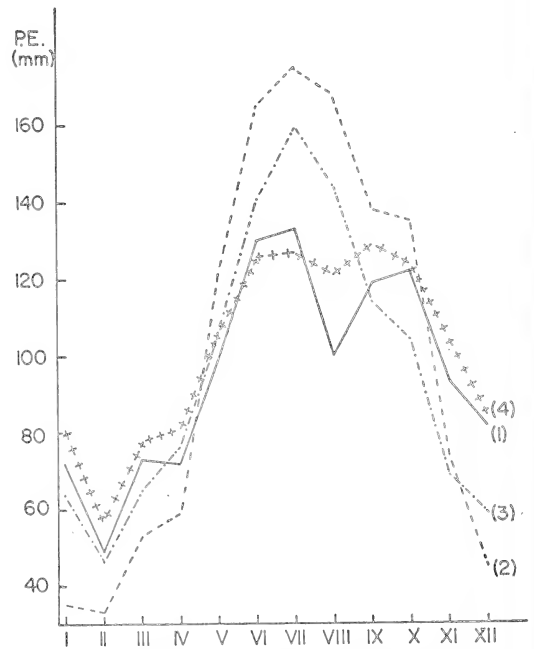


FIG. 5. Monthly potential evapotranspiration for 1953 measured at King's Park (1), and calculated according to Thornthwaite's formula (2), Penman's formula (3), and the new formula (4).

measured P.E. and P.E. calculated by the Thornthwaite, Penman, and new formulae. In addition, Table 3 compares the formulae for the three months following the five-year period. Again the new formula best approximates Hong Kong measurements.

CONCLUSIONS

Evapotranspiration formulae based on mid-latitude data should not be uncritically used in estimating P.E. for monsoonal or tropical maritime regions.

In such regions, humidity and wind may be as important parameters as temperature, and simple formulae similar to that derived for Hong Kong might fairly be used to calculate potential evapotranspiration.

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The Flora of Namonuito and the Hall Islands

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APPROXIMATELY 160 miles northwest of Truk, in the Caroline Islands, lies Namonuito Atoll, straddling the 150th W. meridian. Lying successively to the east are Fayu, Nomwin, and Murilo atolls, comprising the Hall Islands. Together these strips of land amount to no more than a few square miles, but they are scattered over three and a half degrees of latitude, approximately eight and a half degrees north of the equator. Namonuito consists of some seven major islets and several minor ones. Beginning at the southwest, these are: Ulul (or Olol), Namonuito, Magerik (Magurchuk), Magur (Magerlap), Ono, Onari, Weltot, and Pisarach. Sixty miles east is Fayu, an uninhabited island which is visited from time to time because of the abundant fish and turtles. Thirty miles farther east is Nomwin Atoll, with its two inhabited islets, Nomwin and Fananu, and other smaller islets. East again of Nomwin is Murilo Atoll, of which Ruo and Murilo islets are inhabited. These major islets are strips of coralline land, rising to a height of 5 feet or rarely somewhat more, usually with a central depression.

The general aspect of any one of these islets is much like any other; a reef, a strip of beach, and the coconut-palm skyline. Granted the sparse flora and the omnipresent coralline soils, they have rather considerable variation. The three atolls here considered differed not only among themselves but also as a group differ from other atoll groups, such as the Marshall and the Gilbert islands. There are important differences in the floristic make-up and, consequently, in the ecological balance of the species present. Yet in a broader sense there is a remarkable sameness about the forested atolls of the Pacific, and many of the

species herein recorded might reasonably be expected to occur on any of the Micronesian, or even Polynesian, atolls. This applies not only to indigenous species but to weeds and crop plants.

Namonuito, Nomwin, and Murilo were visited by the author in June and July of 1957 while collecting *Pandanus* specimens for Dr. Harold St. John's National Science Foundation Project, which was begun at the University of Hawaii in 1955.

These atolls have a fairly constant temperature usually ranging from 75° to 90° F.; breezes are nearly always present; rainfall, though scattered, supports a thriving forest flora in the less disturbed islets. Extreme dryness, such as may be encountered in the northern Marshall Islands, is not a feature of this area, though droughts may occur. The heat is most extreme on sandy spits with little or no plant cover, situations which are unfavorable to many species but which may be colonized by *Ipomoea pes-caprae*, *Scaevola frutescens*, *Fimbristylis atollensis*, and *Lepturus repens*.

Several of the islets have swampy central depressions, and on Pisarach there is a true swamp at the southern end with characteristic swamp species including *Acrostichum aureum*, *Cyclosorus goggilodus*, and *Bruguiera conjugata*. On certain islets, ordinarily uninhabited, a rather well-developed *Pisonia* forest flourishes, usually in company or codominant with *Eugenia*. The trees are large-boled and may rise to 70 or 80 feet. The undisturbed forests have little or no ground cover beneath the trees. These presumably native forests are now much cut-over and cleared, or burned for clearings. In these clearings a wide array of species, both native and weedy, occurs; near villages various crop plants are cultivated, namely, coconut palms, taros, bananas, papayas, and tobacco. Other large trees fre-

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quently found are *Calophyllum Inophyllum*, *Ficus tinctoria*, *Barringtonia asiatica*, and *Ochrosia oppositifolia*, which are noticeable along the beaches behind the front ranks of *Scaevola* and *Messerschmidia*. *Ochrosia* tends to form pure stands here and there, and in such places its seedlings are very numerous. Besides these tree species, and a few others, most of the vegetation is of shrubs, rising to 15 or 25 feet on occasion, and of vines, herbs, and crop plants. Needless to say, the flora is not a rich one. There are 94 species recorded here, of which about 52 can be reasonably construed as indigenous; of the remaining 42 species, 22 are clearly introduced food or ornamental plants; the remaining 20 species are presumably accidental introductions and weeds.

Nevertheless there is some diversity in the vegetation; islets differ from one another, and each islet consists of two or more zones. The indigenous ecological zones probably consisted of the following:

(1) The strand forest, the outermost line of vegetation on the beaches, consisting of *Scaevola*, *Messerschmidia*, *Morinda*, and *Guetarda* as the usual dominants, with *Ochrosia*, *Terminalia*, *Pandanus*, *Cordia*, *Allophylus*, and *Hernandia* occurring locally as individuals or sometimes in small stands. Less frequent members of the strand association are *Suriana* and *Sophora*. Several creeping or scandent vines are present, chiefly *Ipomoea pes-caprae*, *I. gracilis*, *Vigna*, *Canavalia*, *Triumfetta*, and the parasitic *Cassytha*. *Wedelia* is a scandent or rarely erect shrub of both exposed and shady areas. The grass *Lepturus* and the sedge *Fimbristylis* are both very common, but tend to occur most abundantly in a savannah-like subassociation of windswept narrow extremities, often in company with stunted, scattered shrubs, especially *Pandanus*.

(2) *Pisonia* forest. Before the coming of the Micronesian inhabitants, it seems possible that many, if not all, of the islets may have had dense pure stands of *Pisonia grandis*, the viscid fruits of which are spread by birds. Some remnants of these stands remain on

Megererik, Magur, and according to another observer, on Fayu. As noted by the author, the *Pisonia* forest on Magur was not a pure stand, but contained many large trees of *Eugenia javanica*. This is perhaps the result of deliberate cultivation or at any rate a long-term result of such cultivation. *Eugenia* is not known from the Marshall Islands and seems not to be present on any of the Caroline Islands atolls in the vicinity of Ponape (such as Mokiell, Pingelap, Ngatik, Nukuoro, and Kapingamarangi).

(3) Intermediate forest. This comprises an area variable in extent, sometimes lacking, sometimes replacing the *Pisonia* forest. It is actually not a homogeneous association but consists of varying proportions of the smaller trees, either in stands or mixed, including *Ochrosia* (usually in pure stands), *Pipturus*, *Allophylus*, *Pandanus*, *Barringtonia* (which may also be in the open strand), *Calophyllum* (more usually along the strand), and occasionally *Hibiscus tiliaceus*.

(4) Coconut and breadfruit forests. These dominate most of the central areas of the islets and are the result (at least originally) of deliberate planting. The seeded breadfruit varieties replenish the forest quickly and naturally, and there are on some islets almost pure stands of breadfruit trees. Often they will be accompanied by *Ficus*, *Eugenia*, and *Crataeva*. The coconut groves may be open, with a sparse ground cover, or choked with shrubs. On Pesarach many coconuts grow in a sub-swampy area.

(5) Swamps, both artificial and natural, occur in several islets. The artificial swamps are pits planted with *Cyrtosperma* or *Colocasia*. On Pesarach Islet the naturally swampy southern end is partially utilized for taro cultivation. A few trees of *Bruguiera conjugata* occur here, characterized by white calyces rather than the usual glossy red calyces, and herein described as forma *alba*. Other swamp species include the ferns *Acrostichum aureum* and *Cyclosorus goggilodus*, and the small sedge *Eleocharis geniculata*.

The intertidal zone, whether of calm, sandy-bottom lagoons or of coral pavement or boulders, is a very important ecological feature of an atoll, but except for the ubiquitous marine angiosperm *Thalassia*, which was noted at Nomwin Atoll, the vegetation is of algae and is not cataloged here.

Collections were made on Ulul (June 22, 1957), Magur (June 29), Ono (June 30), and Pisarach (July 2) islets of Namonuito Atoll; on Nomwin (July 3) and Fananu (July 4) islets of Nomwin Atoll; and on Ruo Islet (July 5) of Murilo Atoll. The specimens have been deposited in the herbarium of the Bernice P. Bishop Museum, Honolulu, Hawaii.

Economy

The island economy is completely agricultural. The coconut furnishes, in the form of copra exports, the principal or only source of income, as well as a wide array of uses for food, shelter, and cordage. Wherever possible, coconut palms have been planted and the original forests replaced. In Namonuito Atoll, on Magererik and Magur islets, there are some stands of *Pisonia* forest in relatively undisturbed condition, however. These are usually intermixed with breadfruit and *Eugenia* trees. Breadfruits are one of the staple foods; the tubers of *Cyrtosperma*, and to a lesser degree, of *Colocasia*, are the other staples. Breadfruits are preserved for future use in shallow depressions in the earth which are lined with banana leaves and covered with stones. In this manner they are kept several months as a reserve to be used in the months during which the breadfruit trees bear no fruit. Breadfruit seeds furnish a minor but well-liked source of food. *Alocasia*, the third "taro," is not actively cultivated, but grows spontaneously and is used on occasion for food, especially during droughts or famines. *Tacca* is a similar reserve food. Papayas, bananas, pumpkins, sweet potatoes, and pandanus fill out the vegetable diet. Chickens, pigs, and seafood are the main sources of meat. Much of the income derived from the sale of

copra is spent for imported foods, such as rice, flour, sugar, coffee, and tinned meats, as well as for clothing, hardware, and tobacco. Most islets also have some plants of *Nicotiana* to furnish tobacco between visits of the copra steamer.

Brief Description of the Islets

The islet of Ulul, or as it is sometimes spelled, Olol, is dominated by coconut palms. Other trees include breadfruits, *Pandanus*, *Ficus*, *Eugenia*, *Hernandia*, *Barringtonia*, *Hibiscus*, *Allophylus*, *Premna*, *Calophyllum*, and *Casuarina*. Abundant shrubs are *Scaevola*, *Messerschmidia*, *Callicarpa*, *Pipturus*, and *Clerodendrum*. *Glochidion* and *Wedelia* are also rather frequent. The low herbaceous species include *Oplismenus*, *Thuarea*, *Fimbristylis*, *Microsorium*, *Nephrolepis*, *Portulaca*, *Ipomoea*, and *Triumfetta*; climbing and creeping vines include the very abundant *Piper fragile?* and *Piper ponapense*, *Vigna*, *Canavalia*, and *Cassytha*. Introduced weeds include *Eleusine*, *Chrysopogon*, *Cenchrus*, all grasses, and *Euphorbia hirta*, *E. thymifolia*, and *Vernonia*. In the village, *Plumeria*, *Nerium*, *Crinum*, *Hibiscus rosa-sinensis*, *Mirabilis*, and *Zephyranthes* are cultivated as ornamentals. Characteristic of Ulul and the greater part of Namonuito Atoll is the great abundance of *Piper* vines in the forest, forming a ground cover and climbing high up tree trunks. *Glochidion*, however, is infrequent here, and is not nearly so important a component of the under-story as it is on Nomwin Islet.

On Magur Islet, there is a good stand of forest, consisting of *Pisonia*, *Eugenia*, and breadfruits. The second story of this forest, developed especially at the forest fringes, consists of *Morinda*, *Allophylus*, *Crataeva*, *Ficus*, papayas, and seedlings of the upper-story trees. The ground cover is chiefly *Piper fragile?*, *Nephrolepis*, *Microsorium*, *Wedelia*, and *Vigna*. *Asplenium nidus* is an abundant epiphyte and is also sometimes terrestrial. The soil developed here is a light black organic mulch mixed with white coral sand and coral

fragments. In depth this soil may reach six inches, a fairly good soil for an atoll.

Ono Islet consists chiefly of coconut groves and the usual strand species. *Pisonia* is absent, and so, apparently, is *Glochidion*.

Pisarach Islet has both the largest village (over 100 people) and the most varied vegetation. Although no *Pisonia* forest was seen, the abundant large breadfruit trees, mixed with *Eugenia*, *Ficus*, *Ochrosia*, *Crataeva*, and coconut palms make up a tall shady forest with a sparse under-story over much of the islet. The southern end of the islet is a natural swamp. Irrigation channels crisscross part of it, and *Cyrtosperma*, *Colocasia*, and bananas are planted. Most of the swamp is, however, a tangled mass of small trees, clambering vines, and clumps of marsh fern, all rooted in mud or standing pools. The seaward margin of the area is sandy, and behind this is a line of coral fragments, which quickly merges into the inner area of black, sandy, then mucky soil. Coconuts grow here to some extent. Trees of the swamp are *Hibiscus tiliaceus*, *Barringtonia*, *Premna*, *Pandanus*, *Eugenia*, and *Bruguiera*. In the cultivated portions, besides the taros, there are *Eleocharis*, *Cyclosorus*, *Cyperus*, *Jussiaea*, *Vigna*, *Clerodendrum*, and *Digitaria*. Forming thickets or clumps, often over large areas, is *Acrostichum*, and *Vigna* and *Clerodendrum* scramble over the other species. In the muddy but not water-covered areas coconut palms, breadfruits, *Ficus*, *Eugenia*, and *Crataeva* are found, with *Nephtrolepis*, *Microsorium*, *Piper*, *Thuarea*, and *Digitaria* as ground cover.

Nomwin Atoll is notable for the abundance of *Glochidion*, which is the dominant shrub in the forest under-story. It accounts for at least fifty per cent of the ground cover on Nomwin Islet. The eastern extremity of Nomwin Islet, however, is a wind-swept savannah dominated by dwarf stunted pandanus and the rosette-forming *Fimbristylis atollensis*. The usual strand shrubs occur only as severely stunted individuals. The weedy *Eragrostis amabilis* is abundant here also, complete flowering speci-

mens of which may measure only one inch in length. The soil is a rough mass of coral fragments slightly intermixed with fine sand, and no organic layer except fallen pandanus leaves.

Murilo Atoll is very similar to Nomwin, being dryish, with no swamps, the soil light, thin, and sandy. The islet profile shows a considerable central dip, the seaward rim being built up of coral boulders forming a "cliff" some eight feet in height, sloping steeply to a narrow sandy beach fronted by a reef of coral pavement. The forest is chiefly coconut palms, breadfruits, *Eugenia*, *Pandanus*, *Crataeva*, and the strand trees. The forest under-story is mainly *Wedelia*, both species of *Piper*, *Calli-carpa*, *Vigna*, *Morinda*, and *Ipomoea gracilis*. *Glochidion* is conspicuously absent. The lagoon shore is dry, wind-swept, and open; it is notable for the presence of *Suriana*, *Sophora*, and *Euphorbia Chamissonis*, all in great abundance, as well as the usual strand species.

As can be seen from the brief summaries above, the floristic composition and the ecological patterns of the various islets differ to a surprising extent. The abundance of *Piper* on many islets, and the abundance of *Glochidion*, on Nomwin especially, though also to a lesser extent on Ulul, is in marked distinction from atolls in the Marshall Islands, or from Moki-el, Pingelap, Ngatik, Nukuoro, or Kapingamarangi. Curiously, the reef islets of Truk, like Nomwin, abound in *Glochidion*; but on most of Namonuito and Murilo it is apparently absent. On the high islands of Truk is a large shrub, abundant on low hillsides, which is probably *Glochidion ramiflorum* Forst. Whether the atoll *Glochidion* is conspecific is a matter of doubt, and until a monographic treatment appears, there seems little value in appending one of the dubious names to these plants. As Croizat (1943) shows, the delimitation of species in the genus is still highly problematic. Another plant quite common on both the high and low islands of Truk, but which apparently does not occur at all in Namonuito or the Hall Islands, is *Polyscias grandifolia*.

Vernacular Names

The people of the Namonuito and Hall islands are culturally and linguistically close to the Trukese. The plant names recorded here are frequently identical with, or at least similar to, the Trukese names; but variations in pronunciation, especially in certain characteristic consonant changes, will be frequently noted. The spelling used here is only an approach to the actual pronunciation, but should be understandable if the following rules are followed: the vowels are pronounced as in Spanish, except that à is the short sound, as in the English "fat"; ö, with the umlaut, is equivalent to the German sound of ö or oe; the r is rolled; j, ch, and sh are more or less equivalent and interchangeable sounds, depending on locale and other factors; k and g are similarly often interchangeable; and the consonants l, n, and r, are very flexible, and interchange or supersede each other from area to area. A few differences in the spoken language between Namonuito, Nomwin, and Murilo occur, mostly in pronunciation, and even between different islets of Namonuito Atoll (which may be out of sight of each other, over the horizon). For example, the edible pandanus variety called "kenlau" in Ulul is "kinlau," "killau," "kirau," or "genlau" in other islets; and on Truk it may be called "killau," "sillau," or even "sinnau." It must be cautioned that the names given are very local. For further information on the Trukese language, consult Samuel H. Elbert's

Trukese-English Dictionary published by the U. S. Naval Military Government.

Check-list

The catalog of the flora is brief and includes no descriptions or full synonymies. However, a key is supplied to aid in the identification of species. Most of the plants are well known and widely distributed, but a few present problems of nomenclature or identification which are indicated.

The families are arranged according to Engler and Prantl merely for convenience. The original source of the species description or combination is given for each plant.

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KEY TO THE SPECIES

Though most of these plants are familiar to botanists, I have included this key for the use of anyone who may visit these islands. The key is of course highly artificial, and should not be used in other areas; it is not technical, and certain oversimplifications and omissions of more fundamental characters will be overlooked, I hope, in the interest of simplicity.

Group I. Ferns

Flowerless plants bearing spores usually as a brown powder in sporangia grouped in sori as round dots, long lines, or solid masses, on the backs of the fronds or pinnae

Fronds simple, up to several feet long, forming a large rosette; sori in long oblique lines..... **Asplenium**

Fronds lobed or divided

- Spores not grouped in sori, but covering the entire back of the fertile frond. **Acrostichum**
- Spores grouped in sori, not covering the back of the frond
 - Fronds deeply parted, the segments entire. **Microsorium**
 - Fronds pinnate, the segments dentately or crenately lobed or parted
 - Segments crenately lobed; sori reniform; forest fern with fronds up to 4 ft. long. **Nephrolepis**
 - Segments dentately parted; sori round; swamp fern with fronds usually less than 2 ft. long. **Cyclosorus**

Group II. Flowering Plants

- A. Trees or shrubs with woody stems (See also B and C)
 - Leaves minute, toothlike, borne at the joints of the needlelike, green, jointed stems which function as leaves; fruit a small woody cone. **Casuarina**
 - Not as above
 - Leaves 8–12 ft. long, pinnate; trunk unbranched. **Cocos**
 - Leaves not as above; trunk usually branched
 - Leaves 2–7 ft. long, spiny along the edges and along the midrib on the underside; fruit a head of green to orange woody drupes. **Pandanus**
 - Leaves and fruit not as above
 - Leaves lobed, parted, or divided into leaflets
 - Leaves lobed or parted, or subentire occasionally, but never divided into leaflets; sap milky
 - Leaves palmately-pinnately divided; trunk often unbranched; fruit pearshaped, fleshy, orange. **Carica**
 - Leaves pinnately lobed or parted, or occasionally subentire; fruit globose or elongate, green, of many carpels. **Artocarpus**
 - Leaves divided into leaflets
 - Leaves ternate, i. e., divided into 3 leaflets
 - Fruit red, globose, $\frac{1}{4}$ – $\frac{1}{2}$ in. diameter; flowers minute, greenish, borne in spikes. **Allophylus**
 - Fruit brownish or greenish, flecked with white, 4–10 in. long; flowers large, with white or creamy stalked petals. **Crataeva**
 - Leaves divided into more than 3 leaflets
 - Flowers yellow and red; leaflets smooth, green. **Caesalpinia**
 - Flowers yellow; leaflets with white hairs. **Sophora**
 - Leaves simple, not at all divided or lobed, never compound
 - Sap milky or yellowish, viscid
 - Sap yellowish; secondary leaf-veins curving-parallel; fruit spherical, woody, 1 in. diameter. **Calophyllum**
 - Sap milky-white; leaf-veins reticulate
 - Flowers less than $\frac{1}{8}$ in. long, hidden inside a globose, fruitlike organ
 - Leaves unequal at base; veins raised below; leaves up to 12 in. long. **Ficus tinctoria**
 - Leaves subequal at base; veins not conspicuously raised below; leaves 2–4 in. long. **Ficus ramentacea?**
 - Flowers larger than $\frac{1}{8}$ in. long, borne externally, with evident petals, $\frac{1}{4}$ – $1\frac{1}{2}$ in. long

- Flowers white; petals linear, less than $\frac{1}{2}$ in. long; fruits twinned. **Ochrosia**
- Flowers red, yellow, or white, with broad petals
 Leaves narrowly elliptic or lanceolate, dull green, 4-6 in. long; flowers red, pink, or white, solid color. **Nerium**
- Leaves glossy, broader, elliptic to obovate, up to 1 ft. long; flowers red and yellow, yellow and white, or varicolored. **Plumeria**
- Sap clear, watery
- Stems and twigs thorny; small tree. **Citrus**
- Stems and twigs thornless
- Leaves cordate, more or less heart shaped
- Scandent shrub; leaves opposite; flowers yellow, in heads. . . . **Wedelia**
- Erect shrubs or trees; leaves alternate or spiral
- Flowers tubular, red or yellow; stamens joined in a column
 Flowers red; village shrub. **Hibiscus rosa-sinensis**
 Flowers yellow with a maroon eye. **H. tiliaceus**
- Flowers and stamens not as above
- Leaves with silvery hairs below; fruit a whitish fleshy berry. **Pipturus**
 Leaves smooth, hairless; fruit a black nut set in a green cup.
 **Hernandia**
- Leaves not cordate or heart shaped
- Leaves narrow, elliptic to lanceolate, with tapering pointed tips
- Scandent shrubs; leaves opposite; flowers tubular, white, with pink exerted stamens. **Clerodendrum**
- Erect shrubs or trees; flowers not as above
- Leaves opposite
- Trees; leaves smooth, hairless; flowers white to cream. . . **Eugenia**
 Shrubs; leaves with silver-green hairs below; flowers lavender or bluish. **Callicarpa**
- Leaves alternate or spiral
- Leaves varicolored red, green, and yellow. **Codiaeum**
- Leaves green, not varicolored
- Shrubs, leaves paper thin
- Flowers yellow, not enclosed by bracts; sparsely branching weak shrub. **Jussiaea**
 Flowers white, enclosed by conspicuous pink or magenta bracts; branching shrub. **Bougainvillea**
- Trees; leaves thick to leathery. **Bruguiera**
- Leaves broad, ovate or obovate, or if narrow the tip blunt to obtuse-angled
- Leaves fleshy, lanceolate-obovate, 1-2 in. long; flowers yellow; twiggy shrub. **Suriana**
- Not with the above combination of characters
- Leaves markedly obovate
- Flowers borne in spikes
- Fruit red, ovoid, keeled, slightly flattened, 1-seeded, ca. 1 in. long. **Terminalia**
 Fruit greenish-yellow, flat, with 2 horns, 2-seeded, $\frac{1}{2}$ - $\frac{3}{4}$ in. long
 **Soulamea**

- Flowers borne singly or in panicles
 - Flowers borne in panicles
 - Leaves with white hairs; flowers borne in a scorpioid cyme **Messerschmidia**
 - Leaves smooth green; flowers not borne in a scorpioid cyme
 - Flowers less than ½ in. long, bilabiate, bluish, borne in flat-topped corymbose panicles; stamens 4 **Premna**
 - Flowers more than ½ in. long, white, regular, borne in loose panicles; stamens numerous **Eugenia**
 - Flowers borne singly
 - Leaves opposite; flowers tubular, white, 4-petaled . **Guettarda**
 - Leaves alternate or spiral
 - Flowers tubular at base but split along the upper side, white; fruit a small white berry; leaves slightly fleshy **Scaevola**
 - Flowers with separate white petals, numerous pink stamens, 3 in. across; fruit a large woody box; leaves thin with a reddish midrib **Barringtonia**
 - Leaves round, ovate to elliptic, but not markedly obovate
 - Leaves round, concave, saucer-like **Nothopanax**
 - Leaves not as above
 - Flowers tubular, red or orange **Cordia**
 - Flowers never red or orange
 - Flowers borne in umbels; fruits narrow, sticky; large forest trees **Pisonia**
 - Flowers borne otherwise; fruits not as above; shrubs
 - Fuits compound, white, fleshy, 1–2 in. long **Morinda**
 - Fruits flattened, greenish, dry, ¼–½ in. wide, with red wedge-shaped seeds **Glochidion**

B. Herbs, sometimes very large, or vines (See also A and C)

- Marine plants growing in salt water, with thin flat elongate leaves **Thalassia**
- Not marine plants
 - Leafless vines with greenish or orange stems, parasitic **Cassytha**
 - Not leafless vines
 - Large herbs with auriculate leaves, growing from tubers
 - Leaves with rounded auricles
 - Leaves pale green or glaucous; plants seldom over 2 ft. tall in cultivation **Colocasia**
 - Leaves glossy green; plants up to 10 ft. or more **Alocasia**
 - Leaves with sharp-pointed auricles **Cyrtosperma**
 - Leaves not auriculate; roots not tuberous (except *Tacca*)
 - Leaves palmately then pinnately divided; flowers bearing numerous long threadlike filaments **Tacca**
 - Leaves and flowers not as above
 - Vines with climbing or creeping stems
 - Leaves ternate, of 3 leaflets

- Flowers pink; pods flattened *Canavalia*
 Flowers yellow; pods cylindrical *Vigna*
 Leaves not ternate
 Leaves pinnately compound *Derris*
 Leaves simple or lobed, not compound
 Leaves lobed
 Leaves trilobate, hairy; fruit prickly; flowers yellow *Triumfetta*
 Leaves bilobate, smooth; fruit smooth; flowers pink
 *Ipomoea pes-caprae*
 Leaves not lobed
 Leaves cordate
 Leaves reddish or purplish *Ipomoea batatas*
 Leaves green
 Flowers tubular, over 1 in. long
 Flowers pink or purple *Ipomoea gracilis*
 Flowers yellow *Cucurbita Pepo*
 Flowers minute, less than $\frac{1}{8}$ in. long, without petals, borne in
 spikes
 Spikes 1 in. long, $\frac{1}{4}$ in. wide *Piper fragile?*
 Spikes 2-5 in. long, $\frac{1}{8}$ in. wide *Piper ponapense*
 Leaves not cordate, glaucous below *Piper ponapense*
 Not vines; erect or low herbs
 Large treelike herbs with entire leaves 3-6 ft. long; fruits in clusters, pendent,
 yellow, fleshy *Musa*
 Not treelike
 Flowers 3-petaled, white; leaves oblong-lanceolate, in 2 ranks; roots with
 ginger odor *Hedychium*
 Not as above
 Leaves elongate, forming rosettes, up to 3 ft. long
 Flowers pink; plants usually less than a foot high *Zephyranthes*
 Flowers white; plants 2-5 ft. tall *Crinum*
 Leaves not elongate, not in rosettes
 Sap milky
 Flowers small, white
 Leaves purplish; stems herbaceous
 Leaves minute, less than $\frac{1}{2}$ in. long, hairless; plants prostrate . .
 *Euphorbia thymifolia*
 Leaves larger, hairy; plants erect *E. hirta*
 Leaves green; stems sometimes woody at base *E. Chamissonis*
 Flowers red and yellow *Asclepias*
 Sap not milky
 Flowers tubular, pink or purplish
 Flowers borne in heads; small herbs *Vernonia*
 Flowers not in heads; shrubs or large herbs
 Leaves hairy *Nicotiana*
 Leaves hairless *Mirabilis*

- Flowers yellow or white
 - Flowers borne in heads *Synedrella*
 - Flowers not borne in heads
 - Leaves minute, less than ¼ in. long; plants prostrate, often on rocks *Pilea*
 - Leaves larger; plants erect
 - Leaves fleshy, salty to taste, ½-1 in. long
 - Stems reddish; leaves obovate *Portulaca* sp.
 - Stems green; leaves elliptic *Portulaca samoensis*
 - Leaves thin, tasteless
 - Stems reddish; leaves toothed *Fleurya*
 - Stems green; leaves entire
 - Flowers not tubular
 - Flowers down-pointing, borne in terminal spikes *Achyranthes*
 - Flowers lateral, axillary *Phyllanthus*
 - Flowers tubular, 4-petaled *Hedyotis*

- C. Grasses and sedges; flowers small, greenish or brownish; leaves narrow, elongate (See also A and B)
- Stems triangular; inflorescence subtended by leaflike bracts *Cyperus*
 - Stems round; inflorescence not bracteate
 - Rosette plants with solid stems
 - Inflorescence branching, borne on leafless scapes *Fimbristylis*
 - Inflorescence a single subglobose head *Eleocharis*
 - Not rosette plants, or if so, stems hollow
 - Fruit a spiny burr, borne in a spike *Cenchrus*
 - Fruit not spiny
 - Inflorescence a narrow cylindrical spike breaking at joints when old; plants sometimes rosette-forming *Lepturus*
 - Inflorescence not jointed and disarticulating
 - Spikes digitate, 2 or more borne palmately
 - Spikelets with several florets *Eleusine*
 - Spikelets with 1 floret
 - Spikes 3 or more, digitate; fruit cartilaginous-indurate, not rigid. *Digitaria*
 - Spikes 2, conjugate; fruit indurate, rigid *Paspalum*
 - Spikes not digitate
 - Giant grass with long silky panicles 1 ft. or more long; culms woody, often striped with purple *Saccharum*
 - Not as above
 - Spikelets on one side of the rachis
 - Spikes several, distant *Oplismenus*
 - Spikes 1 or 2, close, hidden *Thuarea*
 - Spikelets on both sides of rachis
 - Spikelets in a diffuse panicle; panicle compound, greenish, the spikelets minute *Eragrostis*
 - Spikelets in a stiff panicle which is simple, reddish *Chrysopogon*

TAXONOMIC CHECK-LIST

PTEROPSIDA

Class *FILICINAE*

POLYPODIACEAE

Acrostichum aureum L., Sp. Pl. 1069, 1753.

NAMONUITO: Pisarach Islet, south end, abundant in swamps, July 2, 1957, Stone 2137. N.v. "apeu."

Asplenium nidus L., Sp. Pl. 1079, 1753.

NAMONUITO: Magur Islet, epiphytic, June 29, 1957, Stone 2121. Observed on most islets.

Cyclosorus goggilodus (Schkuhr) Link, Hort. berol. 2: 128, 1833.

NAMONUITO: Pisarach Islet, south end, in swamps and taro patches, July 2, 1957, Stone 2142.

Microsorium scolopendria (Burm. f.) Copeland, Calif. Univ., Pubs., Bot. 16:112, 1929.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia* forest, terrestrial or with climbing rhizomes, June 29, 1957, Stone 2101. NOMWIN: Nomwin Islet, in forest west of village, common, July 3, 1957, Stone 2162. Observed on all islets. A highly variable fern, extremely narrow-segmented forms of which, without much taxonomic basis, have been distinguished as var. *longisecta* H. Ito ex Hosokawa. Since ecological conditions seem to account for dwarf, nonpinnate forms, for the varying thickness of the fronds in various conditions of exposure and moisture, and for absolute size, it seems probable that this variety also is so determined. Glassman (1952:49) places this variety in synonymy with the species. N.v. "tiji."

Nephrolepis biserrata (Sw.) Schott, Gen. Fil. t. 3, 1834.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia* forest, frequent, June 29, 1957, Stone 2094. Observed on all islets. N.v. "amerei."

Class *ANGIOSPERMAE*Subclass *MONOCOTYLEDONAE*

PANDANACEAE

Pandanus sp.

Thirty-eight specimens were collected in the three atolls, all of them of section *Pandanus* and representing a wide array of fruiting and flowering material. Heretofore usually construed as *P. tectorius* Sol. or *P. odoratissimus* L.f., the identity of these specimens must await the completion of current research. However, two readily recognizable edible varieties may be listed here: one, which has been named *P. cylindricus* Kanehira, bears a large, elongate, cylindrical syncarp up to 45 cm. long, composed of flat-topped, smooth-sided, 15-carpellate phalanges. These are nearly always completely sterile, the seeds aborting, and as a result, little if any hard endocarp develops, and the phalanges, after weathering, may be pulled apart with one hand. The other varieties have a tough and almost unbreakable endocarp. This one is commonly called "kinlau," "killau," or "kinnau."

Another edible variety is "fàch-era," which has a large elliptic syncarp, and phalanges with 10-15 carpels; the middle area of each phalange is expanded, and the sides are creased and lined with corky scars. This variety is called "ajbwirik" in the Marshall Islands, where it is abundant. It has been found also in the Ponape district.

The general term for *Pandanus* is "fàch." A variety used only for its leaves, with a shrub habit and conspicuous reddish bark, is called "fàch-en-luta," and is said to be from Rota, in the Marianas. It is apparently sterile. "Fàch" is also the term for an individual phalange of the fruit; "umun" means syncarp or head; "chön" means leaf. "Fàch-en-wan," applied to all the "wild" forms, apparently means "forest pandan." Several of the wild forms are used, on occasion, for food, but "kinlau" and "fàch-era" are the really prized edible fruits.

Besides the coconut palm, the pandanus is perhaps the most useful plant, its leaves providing thatch for roofing and walls, and plaiting materials for mats, handbags, handi-

crafts, and, in ancient times, sails; the root fibers are useful for temporary cordage; and the fruits of certain varieties are a valuable food.

HYDROCHARITACEAE

Thalassia hemprichii (Ehrenb.) Aschers., in Engler and Prantl, Nat. Pflanzenfam. 2(1): 254, 1889.

NOMWIN: Nomwin, lagoon waters, observed.

GRAMINEAE

Chrysopogon aciculatus (Retz.) Trin., Fund. Agrost., 188, 1820.

NAMONUITO: Ulul Islet, observed in village. N.v. "fadil."

Cenchrus echinatus L., Sp. Pl. 1050, 1753.

NAMONUITO: Ulul Islet, observed. A weed on many islets.

Digitaria pruriens (Fisch. ex Trin.) Buse, Miq. Pl. Jungh. 379, 1854.

NAMONUITO: Magur Islet, in burned-over clearing, frequent, often diseased, June 29, 1957, Stone 2123. Observed on several islets.

Eragrostis amabilis (L.) Wight and Arnott ex Hook. and Arnott, Bot. Beechey Voy. 251, 1841.

NAMONUITO: Magur Islet, in village, June 29, 1957, Stone 2106. Observed on all islets. N.v. "namanaman."

Eleusine indica (L.) Gaertner, Fruct. et Seminif. Pl. 1: 8, 1788.

NAMONUITO: Ulul Islet, observed. Magur Islet, in village, June 29, 1957, Stone 2107. A common weed. N.v. "bukúr."

Lepturus repens (Forst.f.) R.Br., Prodr. 207, 1810.

NOMWIN: Nomwin Islet, along strand and in woods, July 5, 1957, Stone 2164. Observed on most islets. The shade forms are larger, more lax, not so markedly rosette forming, and seem to be var. *subulata* Fosberg; the plants found in exposed sandy beach areas tend to be smaller and to form rosettes, as in var. *septentrionalis* Fosberg. These seem to be merely ecologically induced extremes, however.

Oplismenus compositus (L.) Beauv., Ess. Agrost. 54, 1812.

NAMONUITO: Ulul Islet, observed.

NOMWIN: Nomwin Islet, observed. A common ground cover in forests.

Paspalum conjugatum Berg., Act. Helvet. Phys. Math. 7:129, pl. 8, 1762.

NAMONUITO: Ulul Islet, observed in clearings.

Thuarea involuta (Forst.f.) R. and S., Syst. 2: 872, 1817.

NAMONUITO: Ulul Islet, observed. Common on most islets, especially in shaded or partly shaded strand locations.

Saccharum officinarum L., Sp. Pl. 54, 1753.

MURILO: Ruo Islet, observed, cultivated in village. Sugar cane.

CYPERACEAE

Cyperus ferax L.C. Rich., Act. Soc. Hist. Nat. Paris, 1: 106, 1792.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2138.

Eleocharis geniculata (L.) R. and S., System. Veg. 2: 150, 1817.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2139.

Finbristylis atollensis St. John, Pacific Sci. 6: 145-150, fig. 2, 1952.

NAMONUITO: Pisarach Islet, along strand, July 2, 1957, Stone 2152.

MURILO: Ruo Islet, lagoon shore, July 5, 1957, Stone 2180. Observed on all islets. An abundant rosette former, common in exposed coastal situations, frequently in association with *Eragrostis amabilis*. The flowering scapes are highly variable in length, amount of branching, and number of spikes produced.

PALMAE

Cocos nucifera L., Sp. Pl. 1188, 1753.

On all islets. N.v. "nu."

ARACEAE

Alocasia macrorrhiza (L.) Schott ex Schott and Endlicher, Melet. Bot. 1: 18, 1832.

Observed on all islets. N.v. "oht."

Colocasia esculenta (L.) Schott, ex Schott and Endlicher, Melet. Bot. 1: 18, 1832.

NAMONUITO: Pisarach Islet, observed in taro swamps. Cultivated, less common than the following species. The plants on Pisarach were pink petioled, the petioles set with a few basal prickles.

Cyrtosperma chamissonis (Schott) Merrill, Philippine Jour. Sci. Bot. 9: 65, 1914.

Observed on all islets.

AMARYLLIDACEAE

Zephyranthes rosea (Spreng.) Lindl., Bot. Reg. t. 821, 1824.

NAMONUITO: Ulul Islet, cultivated in village. A small pink-flowered ornamental. N.v. "kaje."

Crinum asiaticum L., Sp. Pl. 292, 1753.

Observed on most islets. N.v. "kiup."

TACCACEAE

Tacca leontopetaloides (L.) Ktze., Rev. Gen. Pl. 704, 1891.

Observed on all islets. N.v. "mukmuk."

MUSACEAE

Musa paradisiaca L., Sp. Pl. 1043, 1753.

Observed on all islets. Both plantains and eating bananas are planted, often in or near taro patches, and around villages, on all the inhabited islets. N.v. "ul."

ZINGIBERACEAE

Hedychium coronarium Koenig ap. Retzius, Obs. Bot. 3: 73, 1783.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2145. Flowers white. N.v. "zinzer" (English corruption).

Subclass DICOTYLEDONAE

CASUARINACEAE

Casuarina equisetifolia L., Amoen. Acad. 4: 153, 1759.

NAMONUITO: Ulul Islet, observed. Introduced.

PIPERACEAE

Piper fragile? Bentham.

NAMONUITO: Ulul Islet, climbing and terrestrial, abundant, June 22, 1957, Stone 2079. Observed on all islets. N. v. "adogobwe." The determination is doubtful.

Piper ponapense C.DC., Engler's Bot. Jahrb. 56: 502, 1921.

NAMONUITO: Ulul Islet, climbing on breadfruit tree, June 22, 1957, Stone 2078.

NOMWIN: Nomwin Islet, observed.

MURILO: Ruo Islet, observed.

MORACEAE

Artocarpus incisus (Thunb.) L.f., Suppl. Pl. 411, 1781.

Abundant on most islets. N.v. "mai."

Ficus tinctoria Forst.f., Prodr. 76, 1786.

NAMONUITO: Magur Islet, large tree in breadfruit-*Pisonia-Eugenia* forest, seedlings frequent, June 29, 1957, Stone 2103. Observed on most islets. N.v. "mok."

Ficus sp. (aff. *ramentacea* Roxb.?)

NAMONUITO: Pisarach Islet, tree with basally auriculate leaves, sterile, July 2, 1957, Stone 2051.

URTICACEAE

Fleurya ruderalis (Forst.f.) Gaud., Freyc. Voy. Bot. 497, 1826.

NAMONUITO: Magur Islet, weed in village, June 29, 1957, Stone 2127.

Pipturus argenteus (Forst.f.) Wedd., DC. Prodr. 16: 235, 1869.

NAMONUITO: Magur Islet, in shrub woodland near lagoon shore, June 29, 1957, Stone 2125.

Pilea microphylla Liebm., Vidensk. Selsk. Skr. 5(2): 302, 1851.

NAMONUITO: Ulul Islet, terrestrial or on coral boulders or cement walls, observed.

AMARANTHACEAE

Achyranthes aspera L., Sp. Pl. 204, 1753.

NAMONUITO: Ulul Islet, weed in village, June 22, 1957, Stone 2081.

NYCTAGINACEAE

Bougainvillea spectabilis Willd., Sp. Pl. 2: 348, 1799.

MURILO: Ruo Islet, cultivated in village. Native of Madagascar.

Mirabilis jalapa L., Sp. Pl. 177, 1753.

NAMONUITO: Magur Islet, observed in village. Native of Mexico.

Pisonia grandis R. Br., Prodr. 422, 1810.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia-Artocarpus* forest, June 29, 1957, Stone 2098. N.v. "mahk."

PORTULACACEAE

Portulaca oleracea L., Sp. Pl. 445, 1753.

NAMONUITO: Pisarach Islet, in sand near shore, July 2, 1957, Stone 2149.

Portulaca samoensis v. Poelln., Fedde Rep. Sp. Nov. 33: 163, 1933.

NAMONUITO: Pisarach Islet, in sand near shore, July 2, 1957, Stone 2150.

LAURACEAE

Cassytha filiformis L., Sp. Pl. 35, 1753.

Observed on all islets, in savannahs and outer strand forest, climbing parasitically on various species.

HERNANDIACEAE

Hernandia sonora L., Sp. Pl. 981, 1753.

NAMONUITO: Ulul Islet, observed. Present on most islets. N.v. "ojal."

CAPPARIDACEAE

Crataeva speciosa Volkens, Engler's Bot. Jahrb. 31: 463, 1902.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia* forest, small tree with ternate leaves, June 29, 1957, Stone 2095.

MURILO: Ruo Islet, observed. A small tree with ternate leaves, white clawed petals, and pendent, long ovoid, brownish-green and white-flecked fruits which are edible when cooked. Native to Caroline Islands, occasionally cultivated. N.v. "afúch."

LEGUMINOSAE

Caesalpinia pulcherrima (L.) Sw., Obs. Bot. 166, 1791.

MURILO: Ruo Islet, cultivated in village. Native of Tropical America.

Canavalia maritima (Aublet) Thouars, Desv. Jour. Bot. 1: 80, 1813.

NAMONUITO: Magur Islet, observed. Pisarach Islet, lagoon shores, climbing on *Scaevola*, flowers pink, July 2, 1957, Stone 2147. Observed on most islets.

Derris elliptica (Roxb.) Benth, Linn. Soc. Bot., Jour., Suppl. 4: 111, 1860.

NAMONUITO: Ulul Islet, observed in clearings and open woods. N.v. "up."

Sophora tomentosa L., Sp. Pl. 373, 1753.

MURILO: Ruo Islet, lagoon shores, July 5, 1957, Stone 2176.

Vigna marina (Burm.) Merrill, Interp. Herb. Amboinense, 285, 1917.

NOMWIN: Fananu Islet, creeping in woods, July 4, 1957, Stone 2170. N.v. "olu" (Namonuito), "ulu" (Nomwin).

RUTACEAE

Citrus aurantifolia (Christm.) Swingle, Wash. Acad. Sci., Jour. 3: 465, 1913.

NAMONUITO: Pisarach Islet, observed. The lime, cultivated on most islets.

SIMARUBACEAE

Soulamea amara Lamarck, Encycl. Meth. 1: 449, 1785.

NAMONUITO: Ulul Islet, along shore, June 22, 1957, Stone 2075. Pisarach Islet, observed.

Suriana maritima L., Sp. Pl. 284, 1753.

MURILO: Ruo Islet, along lagoon shore, July 5, 1957, Stone 2175.

EUPHORBIACEAE

Codiaeum variegatum (L.) Bl. var. *pictum* (Lodd.) Muell.-Arg., DC. Prodr. 15: 1119, 1866.

NAMONUITO: Ulul Islet, observed in village. A widely cultivated ornamental hedge plant. *Euphorbia Chamissonis* (Klotzsch and Garcke)

Boissier, DC. Prodr. 15(2): 14, 1862.

NAMONUITO: Ulul Islet, on sandy open beach, in full sun, June 22, 1957, Stone 2080. Observed on several islets.

Euphorbia hirta L., Sp. Pl. 454, 1753.

NAMONUITO: Ulul Islet, observed. Present on most islets.

Euphorbia thymifolia L., Sp. Pl. 454, 1753.

NAMONUITO: Ulul Islet, observed.

Phyllanthus niruri L., Sp. Pl. 981, 1753.

NAMONUITO: Magur Islet, in village, June 29, 1957, Stone 2105. N.v. "sigamör." The above three species are common weeds.

Glochidion sp. (aff. *ramiflorum* Forst.).

NOMWIN: Nomwin Islet, abundant low shrubs in forest, seeds red, July 3, 1957, Stone 2163.

NAMONUITO: Ulul Islet, observed, rare. (Collected also on Truk, Stone 2047 and 2055). N.v. "efar." Until a monographic treatment of *Glochidion* appears, it seems best to leave this unnamed.

SAPINDACEAE

Allophylus timorensis (DC.) Blume, Rumphia 3:130, 1847.

NAMONUITO: Magur Islet, in coastal woods, common, June 29, 1957, Stone 2102. Observed on most islets. A ternate-leaved shrub or small tree with spikes of small greenish flowers which produce small globose red berries. N.v. "ngö."

TILIACEAE

Triumfetta procumbens Forst. f., Prodr. 35, 1786.

Observed on all islets. A common prostrate creeper of sandy shores among grasses and low shrubs. Leaves usually somewhat 3-lobed, thick, rough; flowers yellow; fruits prickly. N.v. "ara."

MALVACEAE

Hibiscus rosa-sinensis L., Sp. Pl. 694, 1753.

NAMONUITO: Ulul Islet, observed, ornamental shrub in village.

Hibiscus tiliaceus L., Sp. Pl. 694, 1753.

NAMONUITO: Pisarach Islet, abundant in

swamp, observed. Observed on several islets, along sandy shores.

GUTTIFERAE

Calophyllum Inophyllum L., Sp. Pl. 513, 1753.

NAMONUITO: Magur Islet, large tree on shore, June 29, 1957, Stone 2116. Observed on all islets. N.v. "ráguch."

CARICACEAE

Carica Papaya L., Sp. Pl. 1036, 1753.

Observed on all islets. N.v. "bwebwao" (Magur), "kipwae" (Ono).

BARRINGTONIACEAE

Barringtonia asiatica (L.) Kurz, Asiatic Soc. Bengal, Jour. 45: 70, 1876.

NAMONUITO: Magur Islet, in coastal woods, June 29, 1957, Stone 2117. Observed on most islets. The fruits are used to poison fish. N.v. "kul."

RHIZOPHORACEAE

Bruguiera conjugata (L.) Merrill, Philippine Jour. Sci., Bot. 9: 118, 1914.

This is forma *alba* n. f. In calyci albi differet. Like the species but with white rather than red calyces.

NAMONUITO: Pisarach Islet, in swamp, July 2, 1957, Stone 2144 (type). N.v. "ong."

COMBRETACEAE

Terminalia samoensis Rech., Fedde, Rpt. Sp. Nov. 4: 229, 1907.

NAMONUITO: Magur Islet, shrub in coastal woods, flowers white, drupes red, June 29, 1957, Stone 2113. Observed on most islets. N.v. "kön."

MYRTACEAE

Eugenia javanica Lam., Encycl. Meth. 3: 200, 1789.

NAMONUITO: Magur Islet, in *Pisonia-Eugenia-Artocarpus* forest, June 29, 1957, Stone 2097. Observed on most islets. N.v. "fániép."

ONAGRACEAE

Jussiaea suffruticosa L., Sp. Pl. 388, 1753.

NAMONUITO: Pisarach Islet, in taro swamp, July 2, 1957, Stone 2140.

NOMWIN: Nomwin Islet, observed.

ARALIACEAE

Nothopanax scutellarium (Burm. f.) Merrill, Interp. Herb. Amboinense 409, 1917.

NAMONUITO: Ulul Islet, observed. A common hedge plant in villages.

APOCYNACEAE

Nerium oleander L., Sp. Pl. 229, 1753.

NAMONUITO: Ulul Islet, observed in village.

Ocrosia oppositifolia (Lamarck) K. Schum., Nat. Pflanzenfam. 4(2): 156, 1895.

NAMONUITO: Magur Islet, in coastal forest, abundant, June 29, 1957, Stone 2108. Observed on most islets. A common littoral tree, often tending to form pure stands, with long-ovate glossy leaves, small white linear-petalled flowers, twinned fruits, and abundant milky sap. N.v. "umwá."

Plumeria rubra L., Sp. Pl. 209, 1753.

NAMONUITO: Pisarach Islet, cultivated in village, flowers yellow and white, July 2, 1957, Stone 2146. Observed on Ruo Islet. Native of tropical America. N.v. "séur." (On Truk this word, pronounced "sour," is applied to a species of *Fagraea*; on Ponape, pronounced "sair," to *Fagraea sair* Gilg and Benedict.)

ASCLEPIADACEAE

Asclepias curassavica L., Sp. Pl. 209, 1753.

NAMONUITO: Pisarach Islet, cultivated in village, observed. Magur Islet, in clearing, observed.

CONVOLVULACEAE

Ipomoea Batatas (L.) Poir. ex Lamarck, Encycl. Meth., 6: 14, 1804.

MURILO: Ruo Islet, cultivated. The sweet potato.

Ipomoea gracilis R. Br., Prodr. 484, 1810.

NAMONUITO: Magur Islet, in clearing, June 29, 1957, Stone 2120. Observed on most islets.

Ipomoea pes-caprae (L.) Sweet, Hort. Sub. Lond. 35, 1818.

NAMONUITO: Ulul Islet, observed on sandy beaches. Common on most islets.

BORAGINACEAE

Cordia subcordata Lamarck, Tabl. Encycl. 1: 421, 1791.

NAMONUITO: Magur Islet, in coastal forest, flowers orange, June 29, 1957, Stone 2109. N.v. "anögut."

Messerschmidia argentea (L.) I.M. Johnston Arnold Arboretum Jour. 16: 164, 1935.

NAMONUITO: Magur Islet, in coastal forest, June 29, 1957, Stone 2112. Observed on all islets. N.v. "jin."

VERBENACEAE

Clerodendrum inerme (L.) Gaertner, Fruct. et Seminif. Pl. 1: 271, 1788.

NAMONUITO: Pisarach Islet, scandent shrub in swamp area, July 2, 1957, Stone 2141. N.v. "ula."

Callicarpa cana L., Mant. 2: 198, 1771.

NAMONUITO: Ulul Islet, in forest, June 22, 1957, Stone 2082.

MURILO: Ruo Islet, in forest, July 5, 1957, Stone 2177. A fish poison.

Premna obtusifolia R.Br., Prodr. Fl. N. Holl., 512, 1810.

NAMONUITO: Ulul Islet, in clearing, June 22, 1957, Stone 2077. Pisarach Islet, in swamp, July 2, 1957, Stone 2143. Observed on most islets. For a discussion of the nomenclature of this variable species, see Fosberg, 1953.

SOLANACEAE

Nicotiana tabacum L., Sp. Pl. 180, 1753.

NAMONUITO: Ulul Islet, observed. Magur Islet, June 29, 1957, Stone 2124. N.v. "tabák."

RUBIACEAE

Guettarda speciosa L., Sp. Pl. 991, 1753.

NAMONUITO: Magur Islet, in coastal forest

along beach, flowers white, June 29, 1957, Stone 2110. Observed commonly on most islets. N.v. "mosér."

Hedyotis biflora (L.) Lamarck, Tabl. Encycl. 1: 272, 1791.

NAMONUITO: Magur Islet, weed, June 29, 1957, Stone 2122.

Morinda citrifolia L., Sp. Pl. 176, 1753.

NAMONUITO: Magur Islet, in coastal forest, June 29, 1957, Stone 2099. Observed on all islets. N.v. "nen."

CUCURBITACEAE

Cucurbita Pepo L., Sp. Pl. 1010, 1753.

MURILO: Ruo Islet, observed in cultivation.

NAMONUITO: Magur Islet, cultivated, June 29, 1957, Stone 2126. N.v. "panke."

GOODENIACEAE

Scaevola frutescens (Miller) Krause, Pflanzenreich 54 (IV, 277): 125, 1912.

NAMONUITO: Magur Islet, along strand, June 29, 1957, Stone 2111. Observed commonly on all islets. N.v. "nöt" or "nüt."

COMPOSITAE

Synedrella nodiflora (L.) Gaertner, Fruct. et Seminif. Pl. 2: 456, pl. 171, fig. 7, 1791.

NAMONUITO: Ulul Islet, observed. A common tropical weed.

Vernonia cinerea (L.) Less., Linnaea 4: 291, 1829.

NAMONUITO: Ulul Islet, observed. A weed present on most islets.

Wedelia biflora (L.) DC. ex Wight, Contr. Bot. Ind. 18, 1834.

NAMONUITO: Magur Islet, in forest, June 29, 1957, Stone 2092. Observed on all islets, common. N.v. "atugat" (Magur), "adiat" (Ono).

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- WAGNER, W. H., and D. F. GREYER. 1948. Pteridophytes of Guam. *Bernice P. Bishop Mus. Occas. Paper* 19(2): 25-99.

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——— 1920b. Cerotrioza (Psyllidae, Homoptera). *Hawaii. Ent. Soc., Proc.* 4 (2): 374-375.

ROCK, JOSEPH F. 1916. The sandalwoods of Hawaii; a revision of the Hawaiian species of the genus *Santalum*. *Hawaii Bd. Commrs. Agr. and Forestry, Div. Forestry Bot., Bul.* 3: 1-43, 13 pls.

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PACIFIC SCIENCE

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



IN THIS ISSUE: Hurley—*Ecology and Adaptations of Terrestrial Amphipoda* • Banner—*Alpeid Shrimp of the Central Pacific Area* • St. John—*Botanical Novelties on Niuhau* • Miller and Pen—*Composition and Nutritive Value of Palolo* • Carlquist—*Vegetative Anatomy of Dubautia, Argyroxiphium, and Wilkesia* • Notes



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Notes on the Ecology and Environmental Adaptations of the Terrestrial Amphipoda¹

D. E. HURLEY²

OF THE FEW CRUSTACEAN groups which have achieved some degree of freedom from the marine or freshwater environment, the Amphipoda have received least attention. The terrestrial Talitridae, to which family all of the terrestrial species belong, have been treated in various systematic papers but there is little else. The only nonsystematic work, to my knowledge, is contained in no more than four papers, those of Grimmett (1926), Birch and Clark (1953), Lawrence (1953), and Clark (1955).

Reasons for this neglect are not hard to find. The distribution of the terrestrial species is limited to countries bordering the Indian and Pacific oceans and to the Pacific islands (Fig. 1). In these countries development of zoological studies along other than descriptive lines is relatively recent. It would not be unreasonable to suggest that only South Africa, Australia, and New Zealand have a terrestrial amphipod fauna of sufficient extent and variety to attract attention to their ecology and physiology. And, as Dresel and Moyle (1950) have commented, and I can confirm, the mechanical problems involved in experimental work with the Talitridae are considerable, due in particular to their very great agility and to their susceptibility to desiccation. This probably accounts for a general neglect of physiological work, even on littoral amphipods, when compared to the body of research on the closely related Isopoda.

¹ This paper is, in part, the result of studies carried out at Victoria University College, Wellington, New Zealand, during the tenure of a New Zealand University Research Fund Fellowship. Manuscript received July 8, 1957.

² New Zealand Oceanographic Institute, Department of Scientific and Industrial Research, Wellington, New Zealand.

Certainly, the difficulties in collecting terrestrial amphipods are reflected in the two or three species previously described from New Zealand, in contrast to some 40 species or more of terrestrial Isopoda. These difficulties have been overcome to some extent in recent years by modern methods of collecting, and many of the observations made in this paper have resulted from the study of Berlese Funnel material.

Considering the limited systematic work on terrestrial amphipods and the resultant lack of appreciation of their importance in the cryptozoic fauna, one might reasonably expect other research to be somewhat delayed. Nevertheless, there is an open field in Pacific countries for studies on the ecology and physiology of terrestrial amphipods, particularly in relation to soil formation. Such studies, in association with work on other cryptozoic groups, e.g., millipedes and isopods, would be of considerable value in understanding the conversion of leafmould and litter of Pacific forests into highly productive soil.

The abundance of the cryptozoic fauna is often not fully realised. In one particular instance, the animals in a bag of leafmould of less than one cubic foot capacity from Stephens Island, New Zealand, more than half filled a 2-ounce jar, the bulk of weight being made up of a relatively small amphipod, *Orchestia rubroannulata*. Similar large yields of *Talitrus sylvaticus* have been taken under hedges of African boxthorn and other plants in Taranaki, New Zealand.

The abundance of *Talitrus sylvaticus* has also been noted in Australia, where it is widespread in tropical and subtropical rainforests. "In some rain forests near Sydney we have

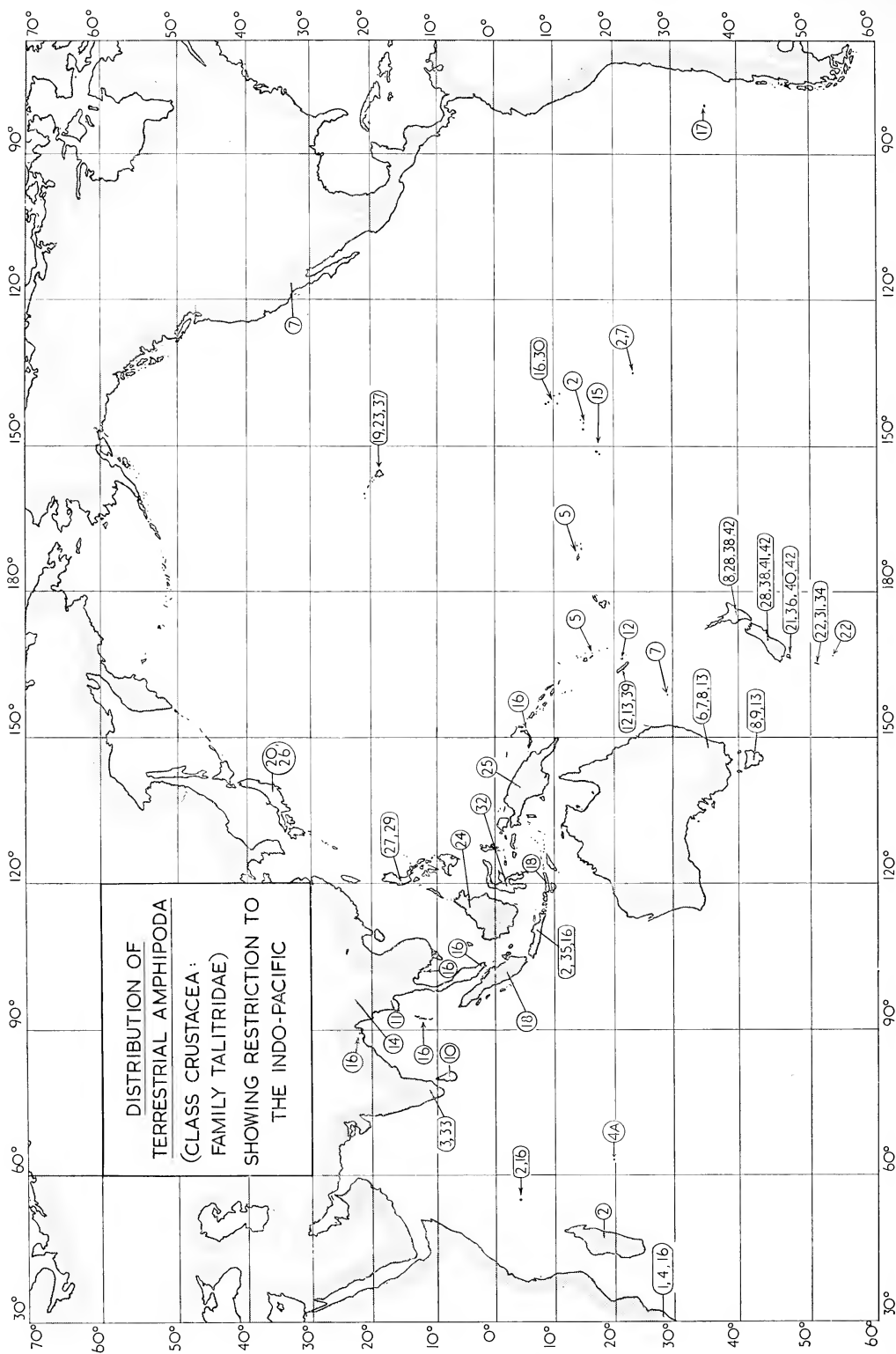


FIG. 1. Distribution of terrestrial Talitridae. A general map based mainly on the literature to show their restriction to the Indo-Pacific. Misidentifications may contribute to the wide distribution of a few species, e.g., *Orchestia anomala* (16).

The literature references are to papers giving summary and more recent distributional data. This information is not necessarily complete.

1. *Talitrus africanus* South Africa (K. H. Barnard, 1940).
2. *Talitrus alluaudi* Seychelles, Madagascar, Java, Tuamotus, Gambier Archipelago, (Stephensen, 1935). Greenhouses and botanical gardens: Belgium, France, Monaco, Switzerland, Germany, Denmark, Hungary, British Isles, Sweden (Shoemaker, 1936; Stephensen, 1935); Czechoslovakia (Cerny and Straskraba, 1957?); U.S.A. (Shoemaker, 1936); U.S.A. and Canada (Medcof, 1939).
3. *Talitrus decoratus* Nilgiris, India (Carl, 1934).
4. *Talitrus eastwoodae* South Africa (K. H. Barnard, 1940).
- 4a. *Talitrus galliveri* Annobon Island, Rodriguez Island (Ruffo, 1947).
5. *Talitrus hortulanus* Samoa, New Hebrides (Stephensen, 1943). Greenhouses: Kew Gardens.
6. *Talitrus kershawi* Australia (Stephensen, 1935).
7. *Talitrus pacificus* Australia, Marquesas, Norfolk Island (Hurley, 1955). Botanical gardens: U.S.A. (Shoemaker, 1936).
8. *Talitrus sylvaticus* Australia, New Zealand (Hurley, 1955); Tasmania (Ruffo, 1948). Botanical gardens: Scilly Isles, Ireland (Hurley, 1955).
9. *Talitrus tasmaniae* Tasmania (Ruffo, 1948).
10. *Talitrus topitotum* Ceylon (Burt, 1934).
11. *Talitrus* sp. Burma (K. H. Barnard, 1935).
12. *Talorchestia antennulata* New Caledonia, Loyalty Islands (Stephensen, 1935).
13. *Talorchestia diemensis* Australia, New Caledonia, Tasmania (Stephensen, 1935).
14. *Talorchestia kempfi* Assam (Stephensen, 1935).
15. *Talorchestia rectimana* Tahiti (Stephensen, 1935).
16. *Orchestia anomala* Seychelles, Marquesas, ?Andaman Islands, Bismarck Archipelago, Gulf of Siam, Lower Bengal, Singapore, Java, Bali, Westfiores, New Britain (Schellenberg, 1938); ?South Africa (K. H. Barnard—*Talorchestia malayensis*, 1955).
17. *Orchestia chiliensis gracilis* Juan Fernandez (Stephensen, 1935).
18. *Orchestia floresiana* Flores, Sumatra (Ruffo, 1948).
19. *Orchestia hawaiiensis* Hawaii (Stephensen, 1935; J. L. Barnard, 1955).
20. *Orchestia humicola* Japan (Stephensen, 1935).
21. *Orchestia improvisa* Snares and Stewart islands (Hurley, 1957).
22. *Orchestia insularis* Campbell and Auckland islands (Hurley, 1957).
23. *Orchestia kaalensis* Hawaii (J. L. Barnard, 1955).
24. *Orchestia kinabaluensis* North Borneo (Shoemaker, 1935).
25. *Orchestia* sp. prope *kinabaluensis* New Guinea (Ruffo, 1948).
26. *Orchestia kokuboi* Japan (Stephensen, 1935; Bulycheva, 1957).
27. *Orchestia lagunae* Philippines (Stephensen, 1935).
28. *Orchestia lesliensis* North and South islands of New Zealand, Stewart Island (Hurley, 1957).
29. *Orchestia luzonensis* Philippines (Stephensen, 1935).
30. *Orchestia marquesana* Marquesas (Stephensen, 1935a).
31. *Orchestia maynei* Auckland Islands (Hurley, 1957).
32. *Orchestia montana* South Celebes (Stephensen, 1935).
33. *Orchestia notabilis* Cochin State—India (K. H. Barnard, 1935).
34. *Orchestia parva* Auckland Islands (Hurley, 1957).
35. *Orchestia parvispinosa* Java (Stephensen, 1935).
36. *Orchestia patersoni* Snares and Stewart islands (Hurley, 1957).
37. *Orchestia pickeringi* Hawaii (J. L. Barnard, 1955).
38. *Orchestia rubroannulata* North Island and Stephens Island of New Zealand (Hurley, 1957).
39. *Orchestia sarasini* New Caledonia (Stephensen, 1935).
40. *Orchestia similaris* Snares Island (Hurley, 1957).
41. *Orchestia sinbadensis* South Island of New Zealand (Hurley, 1957).
42. *Orchestia tenuis* North and South islands of New Zealand, Stewart Island (Hurley, 1957).

recorded as many as 4000 amphipods per square meter. They are a very conspicuous part of the fauna, both because of their numbers and also because of their habit of jumping when the litter is disturbed. They eat fallen leaves, and there is little doubt that they play a major part in the disintegration of leaf litter in Australian rain forests" (Birch and Clark, 1953).

The observations which follow represent an attempt to piece together information acquired incidentally in systematic studies. They are almost entirely unsupported by experimental evidence, but are tentatively put forward to draw attention to the problems involved and to opportunities for future research.

ACKNOWLEDGMENTS

I wish to thank Professor L. R. Richardson of the Zoology Department, Victoria University College, Wellington, New Zealand, under whose supervision this work was originally carried out, for his advice and assistance; and also Dr. B. M. Bary and Mr. W. H. Dawbin, who have most generously read the manuscript and offered valuable criticism and encouragement.

DEFINITION

It is necessary to draw attention to past misuse of the term "terrestrial" in speaking of amphipods.

In each of the three talitrid genera, *Talitrus*, *Talorchestia*, and *Orchestia*, there are species of "sandhoppers," amphipods which live in the beach zone above low-tide level and often reach some distance above high-tide mark. These are quite distinct from the terrestrial Amphipoda which inhabit the forest floor of the Indo-Pacific region. In the European zone, where terrestrial species are not indigenous, there has been a tendency to speak of the littoral species as being "terrestrial"; for instance, Dahl (1946) speaks of *Talitrus saltator* as a terrestrial species, one "whose most important functions—eating, breeding, etc.

are performed on land." He remarks further that "their main distribution is passive and takes place in sea water." This conclusion points up one of the differences between the truly terrestrial species and those of which Dahl is speaking. The ecology of the terrestrial species is not sufficiently well known to assert in definition that their distribution is active, but it is clear that it does not take place in sea water. Those species of which Dahl speaks should be referred to, I propose, as "supralittoral" (cf., T. A. and Anne Stephenson, 1949). Those species which are essentially independent of sea water, that is, which may occur in leafmould at the water's edge but may equally as well occur in leafmould thousands of feet above sea level and miles away from the seashore, may then properly be referred to as "terrestrial."

The term "cryptozoic" is also used in this paper. It was first proposed by Dendy (1895) for "the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, and the bark of trees, and in other similar situations." Interestingly enough, Dendy specifically includes the amphipods, *Orchestia sylvicola*, from New Zealand, and *Talitrus sylvaticus* from Australia, in this fauna.

As an alternative, I have occasionally used the more colloquial term "leafmould species" which is both apt and accurate in describing the niche which these animals fill. It avoids confusion with the supralittoral species, but is of less universal application.

DISTRIBUTION

The most striking feature of the distribution of terrestrial Amphipoda is that they are domiciled essentially in the Indo-Pacific region, and especially in the Southern Hemisphere. Stephenson (1935) no doubt had this localisation in mind when he compiled his paper on "The Indo-Pacific Terrestrial Talitridae," but he did not elaborate any thesis beyond observing that the terrestrial species were characteristic of the Indo-Pacific Ocean,

TABLE 1
GEOGRAPHICAL DISTRIBUTION OF TERRESTRIAL AMPHIPODS
Based on arbitrary geographical regions

SPECIES	REGION																
	Africa—Madagascar	Bay of Bengal	Malay Peninsula	Japan	Philippines	Indonesia—Borneo	New Guinea—Bismarck Arch.	New Hebrides	Loyalty Isles	Australia—Tasmania—Norfolk Is.	New Zealand	Subantarctic Isles	Juan Fernandez	Tuamotu Group	Samoa	Hawaii	U.S.A.
<i>Talitrus africanus</i>	+																
<i>Talitrus alluaudi</i>	+					+											
<i>Talitrus decoratus</i>		+															
<i>Talitrus eastwoodae</i>	+																
<i>Talitrus gulliveri</i>	+																
<i>Talitrus hortulanus</i>								+									
<i>Talitrus kershawi</i>										+	+						
<i>Talitrus pacificus</i>										+	+						
<i>Talitrus sylvaticus</i>										+	+			+			
<i>Talitrus tasmaniae</i>										+	+						
<i>Talitrus topitotum</i>																	
<i>Talitrus</i> sp.		+															
<i>Talorchestia antennulata</i>									+								
<i>Talorchestia diemensis</i>									+	+							
<i>Talorchestia kempfi</i>																	
<i>Talorchestia rectimana</i>		+															
<i>Orchestia anomala</i>	+	+	+			+	+										
<i>Orchestia chilensis gracilis</i>													+				
<i>Orchestia floresiana</i>																	
<i>Orchestia hawaiiensis</i>																+	
<i>Orchestia humicola</i>				+													
<i>Orchestia improvisa</i>											+						
<i>Orchestia insularis</i>												+					
<i>Orchestia kaalensis</i>													+				
<i>Orchestia kinabaluensis</i>																+	
<i>Orchestia</i> sp. prope <i>kinabaluensis</i>																+	
<i>Orchestia kookuboi</i>				+													
<i>Orchestia lagunae</i>					+												
<i>Orchestia lesliensis</i>											+						
<i>Orchestia luzonensis</i>																	
<i>Orchestia marquesana</i>														+			
<i>Orchestia maynei</i>													+				
<i>Orchestia montana</i>																	
<i>Orchestia notabilis</i>		+															
<i>Orchestia parva</i>													+				
<i>Orchestia parvispinosa</i>					+												
<i>Orchestia patersoni</i>												+					
<i>Orchestia pickeringi</i>												+					
<i>Orchestia rubroannulata</i>												+					
<i>Orchestia sarasini</i>								+									
<i>Orchestia simularis</i>												+					
<i>Orchestia sinbadensis</i>												+					
<i>Orchestia tenuis</i>												+					

and that "some species of Talitridae with truly terrestrial habits bear the impression of their terrestrial life." Figure 1, based on available records of distribution in the Pacific area, does not claim to be complete, but does give some idea of the extent of this fauna.

The distribution of species in the Indo-Pacific generally, as at present known, reveals little pattern, due mainly to the fact that most records are of one or two species from each of many island localities.

It is likewise practically impossible to make anything of distributional patterns in Polynesia and Micronesia, but it is interesting to speculate how much of this apparently chaotic distribution, making due allowance for mis-identifications, is due to the voyages of the Polynesians. The custom of carrying ample stocks of fern root, taro, yam, gourds, and kumara on long journeys in the very humid and moist atmosphere of their canoes, makes them likely agents of distribution. When more is known of the amphipod distribution pattern, it may be interesting to attempt a reconciliation with ethnological theories of migration and botanical theories of plant distribution by natives in the Pacific.

One might predict an endemic fauna in each island or country where the terrestrial species occur, and where information is available this does seem to be the case. Chilton (1909) recorded five new species of *Orchestia* not found elsewhere from Auckland, Campbell, Snares, and Stewart Island. Stephenson (1938) described *Orchestia patersoni* (as *Talorchestia patersoni*) from Stewart Island. This has since been taken on Snares Island, Bench Island in Foveaux Strait, and Solander Island, all quite close to the original type locality, and there appear to be slight racial differences between some of these localities (Hurley, 1957). The New Zealand fauna includes six described species endemic to the mainland (Hurley, 1957) and at least two further species as yet undescribed, as well as the six species already mentioned from the outlying islands. Of these, only *Talitrus sylvaticus* is

known to occur elsewhere. If evidence can be produced to show that the Australian form of *T. sylvaticus* has not been introduced there in the last 200 years from New Zealand, then perhaps the solution to its distribution is to be looked for in the geological history of the two countries. It has been suggested that a New Zealand land mass was connected to Australia and farther north as late as Mid-Cretaceous time but probably not later, and had good connections much earlier which probably extended to take in various northern islands including New Guinea, New Britain, the Solomon Islands, and New Caledonia (Fleming, 1957).

One further possibility is that of transportation by birds, a theory of amphipod distribution for which Segerstrale, *et al.* (1954) has produced considerable geographical and experimental evidence. While there is evidence of considerable migration of bird populations between New Zealand and Australia, it must be said that the distances and the difficulties involved make this theory much less appealing in this instance than, for example, in explaining anomalous discontinuous distribution within New Zealand.

Certain affinities have been suggested in the past between the New Zealand and South African faunas. At present, the terrestrial amphipods of the two countries are considered specifically distinct, and the evidence, in my opinion, suggests parallel evolution from littoral ancestors in the two countries.

There is one surprising fact in this distributional pattern. It is the complete absence of any records from Central and South America, which is especially striking since the forest conditions there are just those which would be expected to support a large fauna of cryptozoic amphipods. Nor do any of the North American records suggest an indigenous fauna. This absence does not seem due to lack of collecting. Allee (1926a) in a comprehensive study of leafmould fauna of Barro Colorado Island, Panama Canal Zone, lists no amphipods whatsoever. Other papers I have

noted, including one on the rainforests of Mexico, similarly fail to note their presence. (Allee's paper, surprisingly, also fails to mention Collembola.) Strickland (1945) does not mention amphipods in a study of the soil and litter fauna of forest reserves and cacao estates in Trinidad, British West Indies, although his thorough sampling methods yielded Collembola and Isopoda.³ The nearest to a South American report is Chilton's description of *Orchestia chiliensis* var. *gracilis* found under stones on Juan Fernandez Island, 590 metres above the sea shore (Chilton, 1920). The shorehopper, *Orchestia chiliensis* s.str., is found on the littoral zone of Juan Fernandez—as well as in Chile and New Zealand.

It is rather less surprising that terrestrial species should be absent from the European continent and the British Isles, especially when the type of forest found there is taken into consideration. It is indicative of this absence that as recently as 1956 a reputable British authority should say: "While the Isopoda have . . . successfully invaded the land, and woodlice lead a completely terrestrial existence, no Amphipoda occur right away from water, although some, like the sandhopper, live around the water's edge. . . . Failure to evolve suitable habits may have prevented the amphipods from becoming truly terrestrial" (Hynes, 1956). (In view of my definition already given of "terrestrial" Amphipoda, it is pertinent to note his reference to occurrence near water.)

Bornebusch (1930), in an extensive survey of the Danish leafmould fauna, failed to record any amphipods whatsoever, although he listed Isopoda, Collembola, Diplopoda, and all other major groups commonly found associated with amphipods in New Zealand

leafmoulds. All other accounts of similar collections from the European continent are similarly lacking in amphipods.

The only occurrences on the European continent or in the North American region are those recorded from botanical gardens or greenhouses where they have been accidentally introduced. In every case, the species concerned have since been tracked back to an endemic Pacific origin.

Talitrus alluadi Chevreux was first recorded from the "serres chaudes du Jardin des Plantes de Paris" (Chevreux, 1896). Considered identical with this species are *Orchestia senni*, described by Menzel (1911) from the botanical garden at Basel, and *Talitroides bonnier* (the name proposed by Stebbing, 1906, for a species described by Bonnier, 1898) found in a conservatory at Ghent. This species, since found endemic in Seychelles, Madagascar, and Archipel de Gambier, Paumotu (Tautomu Islands) and Java, has also been found in greenhouses or botanical gardens in Copenhagen, Cambrai, Grenoble, several cities in Germany, Glasgow, and Norwich (Stephenson, *et al.*, 1924), and in New Jersey and Ohio, U.S.A. (Shoemaker, 1936).

Talitrus hortulanus (Calman, 1912) was described from the Royal Botanical Gardens, Kew, and has since been recorded from Samoa and the New Hebrides (Stephenson, 1943).

Talitrus sylvaticus (Haswell) was recorded as *Talitroides dorrieni* (Hunt, 1925) from Tresco Abbey Gardens in the Scilly Isles. This species, described originally from Australia, has since been found under conditions which suggest that it is endemic to New Zealand. It may also be endemic in Australia or it may have been introduced sufficiently long ago from New Zealand to have achieved a fairly wide distribution and to show minor differences in pleopod armature which possibly warrant subspecific rank (Hurley, 1955).

Talitrus pacificus Hurley, known in the Pacific from Norfolk Island and Australia (Hurley, 1955) and from the Marquesas (Stephenson, 1935, as *T. sylvaticus*) has also been

³ Since this paper was submitted, Dr. E. L. Bousfield has told me (personal communication) of a "*Talitriator* (sens. Methuen)" from 4,200 feet altitude in Jamaica, B. W. I., and says, "It seems closest to *T. eastwoodae* and may have been introduced, but its wide distribution remote from human habitation and at such altitudes suggests otherwise." I suspect this will prove an exotic species, probably from Africa, associated with plantation introductions. (D. E. H.)

recorded from the United States. Shoemaker (1936) has noted it from Louisiana, and from Balboa Park, San Diego, and Pasadena, California. "*Talitrus pacificus* (is) quite abundant around San Diego. Dr. Johnson used to find dead ones every morning at the east entrance to Ritter Hall. Apparently they had been attracted by the light over the entrance which was left on all night and killed by the insecticide there." (Dr. T. E. Bowman, personal communication.) It is hardly necessary to add that to the Australian or New Zealand visitor to Southern California, the most striking botanical feature there is the widespread cultivation of Australian trees and shrubs.

It has been recognised for many years that there is a considerable "hothouse" fauna. *Placocephalus kewensis* Mosley, a terricolous turbellarian found originally only in greenhouses, and later discovered endemic in a different part of the world, is a good example. Kraepelin (1900) lists a considerable number of introduced animals of different groups found in hothouses in Hamburg, whilst Hatch (1949) discusses Isopoda, Coleoptera, Dermaptera, Orthoptera, and Gasteropoda commonly found in greenhouses of the Pacific Northwest of the United States. Hatch cites the isopod, *Porcellio dilatatus*, as a "properly adapted species which can spread from greenhouse to greenhouse without being able to live in the surrounding situations." In speaking of a "properly adapted species," however, one is overlooking a rather essential feature of this fauna. The fact is that the species is properly adapted for forest floor conditions, but that few situations could be more to the liking of terrestrial amphipods and other cryptozoic fauna than the continuous humidity and the plentiful supply of leafmould for food and cover which most greenhouses provide. If the term "properly adapted" is to be used of anything in this context, it must be applied not to the animals but to the greenhouses.

On this point, Lawrence (1953) makes a most interesting comparison: "The great sur-

face evaporation of the leaves creates a humid mantle around the [South African rain] forest while the foliage of the canopy blankets the substratum from the direct rays of the sun so that it keeps its moisture longer. The atmosphere . . . especially upon a hot day, often recalls that of a greenhouse."

ECOLOGY AND EVOLUTION

The most significant recorded fact in the literature of the terrestrial species is the repeated theme of habitat—"in damp soil in the forests," "among damp fallen leaves," "in burrows in soft damp soil under dead leaves," "on damp earth under logs," "under decaying leaves," and so on. The terrestrial species of amphipods are essentially inhabitants of the leafmould of the forests. They have evolved a habit of life which, while enabling them to colonise a sizable area of the Indo-Pacific land masses, yet imposes very great limitations. Or, bearing in mind the direction from which they have colonised the forests, and that taken by their more advanced relatives, the terrestrial isopods, it would be more correct perhaps to say that the terrestrial amphipods have not yet emerged from the limitations imposed by their cryptozoic environment to any more rigorous habitat.

The change to a terrestrial environment is a major one. There is a complete change of surrounding medium—air is substituted for water. There is a complete change in primary mode of progression, from swimming to jumping, and there is need for modification in most of the important functions of life: breeding, breathing, and excreting. The supralittoral species make the best of both environments. They live within easy reach of the sea, burrowing in wet sand or under stones; they feed on seaweed and animal matter washed up on the shore; they achieve distribution by means of the sea. Many species are able to swim to a certain extent and can survive immersion in sea water (Dahl, 1946).

Carter (1931) considers that the majority of terrestrial animals have reached the land by way of fresh water rather than directly from the sea. "The suggestion is made that this has been partly caused by the favourable series of intermediate environments between the fresh waters and the land, and that the evolution of many of the numerous adaptations necessary for terrestrial life has been induced in these environments serially and therefore with greater ease. The much greater variability of the fresh-water environments has undoubtedly been important in producing this result. The importance of the tide in maintaining the constancy of conditions on the marine littoral is emphasised."

Yet neither amphipods nor isopods fit this general pattern. Among the constituent groups of the cryptozoic fauna Dendy (1895) includes "isolated representatives of typically aquatic groups of animals which have as yet become little modified in accordance with their new life." He comments, "Every naturalist knows how many small animals swarm beneath half-dry stones on the seashore. Such species appear to me to be taking the first step towards a terrestrial life. Gradually, they will make their way inland, still keeping beneath logs and stones for the sake of moisture and coolness, until finally they accustom themselves to a thoroughly terrestrial existence. In this section of the cryptozoic fauna we must place the shrimplike Amphipoda and Isopoda which certainly look strangely out of place on land."

Edney (1954) speaks similarly of the isopods. "There is little doubt that the route to land was across the littoral zone rather than by way of estuaries and swamps (Pearse, 1929). Evidence for this is the existence today of littoral and halophilic forms such as *Ligia* sp. and *Halophiloscia*, which are undoubtedly primitive morphologically."

These views are further supported by the fact that the genera *Talorchestia*, *Talitrus*, and *Orchestia* all embrace supralittoral as well as terrestrial species, whilst the fresh-water spe-

cies of the family Talitridae all belong to genera which are represented only in fresh water and are morphologically closer to the marine genera of Talitridae than to the supralittoral and terrestrial genera. The constancy of conditions on the marine littoral seems to have barred neither amphipods nor isopods from entering the terrestrial environment.

The forest floor was perhaps the most suitable place for a littoral animal to enter, especially considering that "animals crossing [the littoral] zone may well be subjected to extremely high temperatures" (Edney, 1954). In many lands, the forest reaches right to the water's edge or borders streams running down to the sea, and often beaches are the only barriers between sea and forest. In these places, the supralittoral zone is the beachhead for invasion by littoral species. And, in countries bordering the Pacific where the climate is relatively humid and the conditions of the forest floor are more or less uniform throughout the year, the leafmould zone is relatively moist and stable. Light intensity is considerably reduced by the nature of the zone itself, and by the strata of the forest canopy above. Humidity and temperature are relatively constant. "Forest temperatures are generally lower in summer and higher in winter than temperatures of adjacent areas. Similarly forests are cooler during the heat of the day and warmer during the night than areas external to them. Relative humidity is characteristically higher and evaporation rate lower within the forest than in adjacent, less dense terrestrial communities. Similarly, relative humidity is higher and evaporation rate lower within forests during the night than in daytime" (Allee, Emerson, Park, Park, Schmidt, 1949, references omitted). These tendencies towards a stable and more equable climate are intensified in the leafmould zone which, of its nature, has an insulating effect from the surrounding atmosphere. "The cryptozoa are not only sheltered by the growth of the forest and shrub which mitigates the extremes of light and temperature, but they are further covered

by the damp layer of humus which cuts off all light and movements of air, further reducing the comparatively small fluctuations of temperature and humidity that prevail throughout the forest" (Lawrence, 1953).

The microclimate may change a little but presumably the animals living therein can meet these changes by retreating a little farther and deeper into the leafmould and even into the soil beneath. The annual rhythm of adaptation to climate is then vertical and not horizontal as in the case of, say, the larger vertebrates. For smaller animals, this is an inestimable advantage. In unfavourable conditions their route of escape is not barred by large intractable areas of a biotype in which they cannot survive. In short, they can adjust themselves to seasonal changes without leaving their very specialised niche. When conditions do change abnormally, they may still survive in islands in the forest floor formed, for example, by deep pockets of leafmould, and by fallen and rotting logs which protect the ground beneath. This is well illustrated where forests have been felled or burned off. Under the remnant logs, there is usually a damp area with a relict cryptozoic fauna, absent in the immediately surrounding pasture or scrub. Examination will usually reveal isopods, millipedes, pseudoscorpions, opiliones, centipedes, endemic worms (found very rarely in New Zealand pastures, the pasture species being exotic ones), and, if the area is large and moist enough, amphipods. That land isopods tend to collect in such protected places has been recorded by Allee (1926) who has further shown that isopods will often conserve moisture still longer by aggregating together. This is of positive survival value since aggregated isopods lose moisture more slowly than isolated ones.

In areas of remnant native bush, often the only places where endemic terrestrial isopods are present in any numbers are the ecological islands provided by decaying trees and logs lying on the ground, an effect noted by Dendy (1895) for the cryptozoic fauna generally. "It

is far easier to find cryptozoic animals in partially-cleared localities, where they are collected together under the remaining fallen logs, than in virgin forest, where there is so much cover that the animals are widely scattered, and the search becomes very laborious."

On the east coast of the North Island, New Zealand, where there are many such remnants, it is common to find the conglobating and relatively thick-skinned isopod, *Cubaris danae*, in the space between the log and the compact soil below, where there is a little but not a great deal more moisture than in the surrounding unprotected ground. The comparatively thin-skeletoned and nonconglobating *Styloniscus otakensis* is only found in the much moister, rotting wood of the log, associated with ants, peripatus, termites, millipedes, and other invertebrates with similar environmental preferences.

In Australian conditions, Birch and Clark (1953) have noted that amphipods occur in wet years "in the leaf litter of stands of timber in drier habitats such as *Casuarina*, *Eucalyptus*, and *Angophora* forests. But in most years the leaf litter in these forests is too dry for *Talitrus* to survive." However, the fact that repopulation occurs in wet years suggests a survival population in the "drier habitats" or in close proximity.

The fact that no great change in feeding is necessary would facilitate entry to the terrestrial environment. The decaying seaweed diet of supralittoral amphipods is not markedly different from the decaying leaf diet of the terrestrial ones. Birch and Clark (1953) include the amphipod *Talitrus sylvaticus* amongst the litter feeders or "decomposers," commenting that it feeds on leaves only after they have been on the ground for some months.

Terrestrial amphipods, like supralittoral ones, will turn cannibalistic and carnivorous in laboratory conditions when other food is not available, but in normal conditions they seem to be ectophagous rather than predatory. Lawrence (1953) remarks that "the intestine of *Talitrus (Talitroides) eastwoodae*

living in South African indigenous forests contains only the small fibrous particles of plants and other woody detritus."

Grimmett (1926) attempted to correlate the distribution of male talitrids with the nature of the forests in which they occurred and was led to this statement. "The males of [*Parorchestia sylvicola*] are known to be rather rare. All the specimens collected were therefore determined for sex, the large flattened front legs of the male being, on the suggestion of Dr. Chilton, used as a guide. It was found that in a total of 383 specimens from the beech-forest locality, 43, or 11.2 per cent were males, while in a total of 333 from the tawa forest no males were discovered, though each specimen was carefully examined with a dissecting lens. Moreover, the males in the former were fairly evenly distributed throughout all the samples. It would thus appear that males are extremely rare, or are not produced in the lower-altitude forest during this portion of the year. Temperature, dependent on altitude, is suggested as the environmental factor most likely to be involved."

Unfortunately, there is a simpler explanation which makes his conclusions of little value. Almost certainly he was dealing with two species, one an *Orchestia* with a large well-developed second gnathopod in the male, and the other a species of *Talitrus* with the feebly developed, femalelike second gnathopod in the male which is characteristic of that genus (cf. Fig. 3). It is worth noting that Forster (1954) finds no evidence of altitudinal speciation or correlation between distribution and type of forest cover in the opiliones, and I believe this finding applies equally well to the amphipods.

However, males are often absent from samples—Grimmett's figures suggest a normal proportion of one male in ten—but whether this is due to ecological factors is doubtful. When collecting by hand, there is possibly more chance of favouring one sex, due to such things as size and agility differences between sexes, or the possibility of

sexual preferences for different depths in the leafmould. The season of the year, the biology of the species concerned, and location of the sample may affect the percentage of males. There is also no evidence that Grimmett's figures are the norm for all species.

SPECIATION

In spite of our relatively poor knowledge of the cryptozoic amphipods, the number of species already known is surprisingly high and past experience suggests that future work will reveal many more. From the New Zealand region alone, some 14 species are known, and the fauna is by no means intensively studied.

There are two lines of development towards the terrestrial environment, represented by *Talitrus* and *Orchestia* (and perhaps a third by *Talorchestia*). The supralittoral species of these genera form a basically compact group, varying generically only in combinations of gnathopod shape and other comparatively minor morphological variations—minor, that is, compared to generic distinctions in other families. There is, in fact, a tendency for *Talorchestia* and *Orchestia* to intergrade. However, the morphology of the terrestrial species of *Orchestia* and *Talitrus* suggests that they have arisen independently from supralittoral species.

It is also of interest that, whereas littoral species tend to be somewhat cosmopolitan, as may be seen by comparing the faunal lists for New Zealand and South Africa, the terrestrial species are noticeably localised.

It is not difficult to suggest reasons for the proliferation of species. The island nature of the Indo-Pacific provides textbook conditions for speciation due to reproductive isolation. The terrestrial fauna of the subantarctic islands, as recorded by Chilton (1909), suggests speciation through geographical isolation. With some exceptions, the terrestrial species of Polynesia and Melanesia also suggest geographical isolation.

Within New Zealand, Forster (1954) and Dell (1955) have suggested a possible cor-

relation of geographical speciation in leafmould animals with major events in past geological history, including glaciation. According to Forster (1954), the opilionid fauna of Stewart Island "suggests a series of invasions and reinvasions from the mainland following periods of isolation of sufficient time length to permit physiological isolation to be achieved." Further, "the distribution of the fauna of the West Coast of the South Island is strongly suggestive of bio-glacial control, paralleling as it does that of the *Paryphanta* snails for which Willett (1950) postulated a similar origin."

The formation of ecological islands, to which leafmould is particularly susceptible by the presence of such faunal barriers as rivers, mountain ranges, and valleys, also provides a marked stimulus to speciation. This has been noted for other leafmould animals. Speaking of the land molluscs of Fiordland, Dell (1955) comments ". . . such isolated pockets would form ideal localities in which speciation could proceed. The comparatively high number of forms of such a genus as *Ptychodon* could well be due to such a situation, coupled with subsequent invasions."

The mechanism of speciation is perhaps less obvious but I would suggest that the most probable is speciation by neotony—the retention of juvenile or embryonic characters in the adult.

In most species of *Orchestia*, including all of the supralittoral ones, the second gnathopod is large and subchelate in the male, and small and feebly chelate in the female. In *Talitrus* the male second gnathopod is small and feebly chelate, superficially indistinguishable from that of the female. Since the greatly developed male gnathopod in *Orchestia* is known to be used for grasping and even "carrying" the female *in coitu*, there is a strong likelihood that the large size of the male gnathopod is unnecessary in *Talitrus* because of changed sexual habits.

The terrestrial species of *Orchestia*, unlike the supralittoral ones, show gradations in size

and type of male gnathopod from the typical *Orchestia* form to a form not far removed from the typical *Talitrus* gnathopod. These "intermediate" species show striking resemblances to the various stages in the development of the male second gnathopod in supralittoral species of Talitridae. A typical series is shown in Figures 2 and 3, where various adult male second gnathopods of "intermediate" forms are contrasted with growth stages of *Talorchestia bottae* (figured by Chilton, 1921, as *T. martensii*). The suspicion that these "intermediate" forms are no more than subadult is, I believe, unwarranted. All other evidence from morphology and distribution points to the animals being genuinely mature.

The other striking morphological feature of the terrestrial species is the trend to reduction of pleopods from the normal supralittoral and marine condition, with three pairs of fully-developed biramous pleopods, to the extreme in *O. patersoni*, a terrestrial species with three pairs of vestigial triangular stumps. The possibility that this trend is also an effect of species formation by neotony has been considered, but limited examination of supralittoral juveniles showed fully formed pleopods at an extremely early stage in development. While it is possible that pleopod formation passes through a bud stage similar to the vestigial stump, it would have to occur at a very early stage and would probably be revealed only by study of the late embryo. Nevertheless, the diagrammatic representation of pleopod structure in Figure 3 indicates that reduction of pleopods and reduction in size of male gnathopods occur more or less in phase and are not inconsistent with the process of neotony.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS

Work on the systematics of the terrestrial amphipods has revealed some interesting tendencies in adaptation. There are no morphological changes of any significance in the mouth parts, but in view of the similarity of

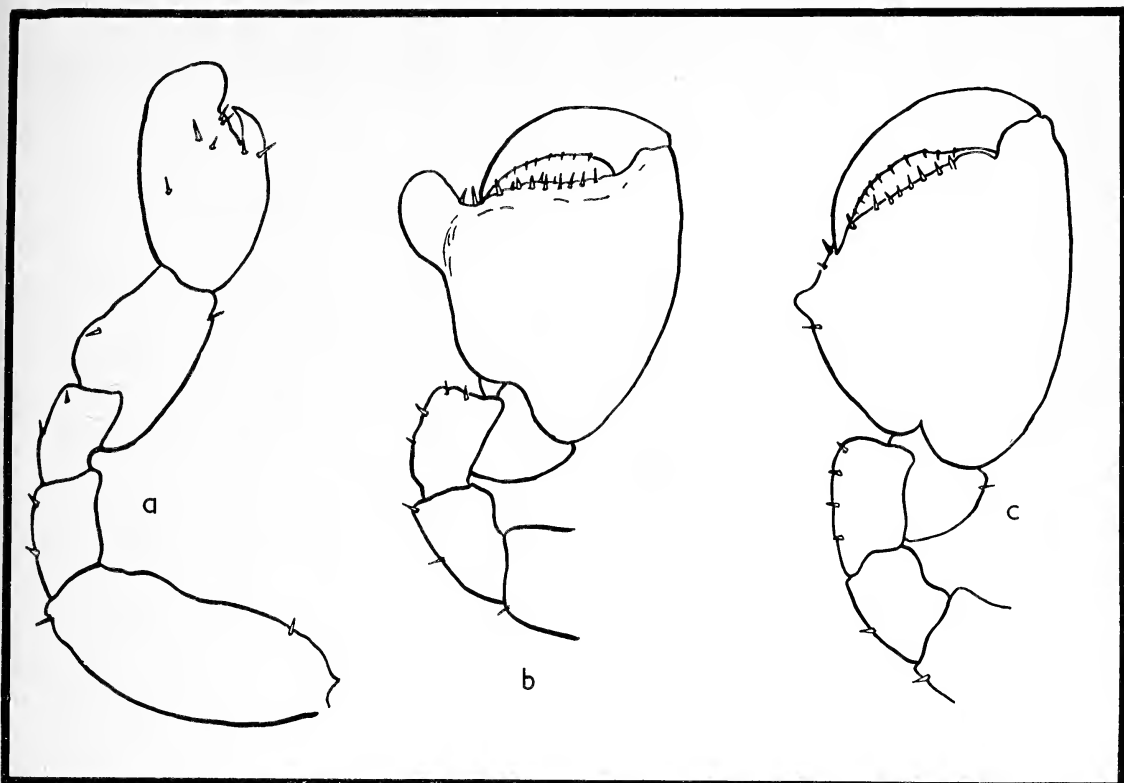


FIG. 2. *Talorchestia bottae*. Three successive stages in development of second gnathopod of male. (After Chilton, 1921.)

diet to that of the supralittoral species, this is not unexpected.

The gnathopod structure, however, does show certain modifications. Chilton, in an unpublished journal, writes of the "peculiar transparent portions of the merus, carpus, and propod" of the gnathopods of *Orchestia sylvicola* and asks, "What can be the function of these strange looking structures? In them, the integument appears semitransparent and usually more or less striated, and the joint bulges out at these places, but no muscles are to be seen in the enlargements."

Since these processes are absent from the male gnathopods in some species, it is unlikely that they are primarily connected with food or feeding habits; rather, reduction in size of the large second gnathopods from the condition found in marine and supralittoral

species, and simultaneous development of processes in terrestrial species indicate changes in sexual habits as a primary cause. The most prominent features of the "pellucid lobes" are their lack of musculature, their transparency (partly due to the absence of muscle tissue), and their scabrous surface. They are situated on the lower margin of the limb which would scrape along the ground and be most exposed to external stimuli. These features all suggest to me a tactile sensory function. McIntyre, in an unpublished work, has described the value of the peculiarly twisted female second gnathopod, which is well supplied with these pellucid processes, in combing the broodplates.

In fact, it does seem likely that there has been a change in sexual habits. Williamson (1951) studied the mating and breeding of

some supralittoral or "semiterrestrial" amphipods, and found that in *Talitrus saltator* the female is held by the male with the aid of the stout antennae and the pereopods, whereas "holding" in marine and supralittoral species is normally done with the aid of a greatly developed second gnathopod. *Talitrus saltator* is, however, the only species of *Talitrus* which shows this marked development of strong antennae. The other, more truly terrestrial, species of *Orchestia* and *Talitrus* have slender antennae. Since most of them also lack the large male "grasping hand" of the supralittoral species, it is likely that some further change in sexual habits has taken place. (A few terrestrial species retain the large "grasping hand.")

In the Gammaridae, the eggs are laid almost immediately after copulation, the time of laying in some species being determined by the time of copulation, in others by the time of moulting. In *T. saltator*, and probably in other talitrids, the time of laying is determined by the time of moulting. Laying takes place 4 days after moulting, but copulation may take place any time from 1 to 4 days before laying.

Williamson suggests that the eggs of the supralittoral Talitridae are fertilised in the brood pouch, and rules out both internal insemination and internal fertilisation. The spermatozoa, which are already present when laying takes place, are then most probably activated either by a secretion of the unfertilised egg or by a secretion which the female releases during laying. Spermatozoa of *T. saltator* can live at least 4 days in the brood pouch of the female, probably because of their inactivity and perhaps also because of their relatively large size (about 400 microns in length).

More tangible developments correlated with the terrestrial environment are evident. In aquatic species of Talitridae, the male normally carries the female around for some days before moulting, and copulation occurs immediately after moulting. "The carrying po-

sition adopted by . . . *Gammarus* . . . is obviously not suited to terrestrial conditions, . . . but it is probable that the aquatic ancestors of the Talitridae employed this form of carrying, and it is still found in the more aquatic members of the family (*Hyale* spp.)" (Williamson, 1951).

In the supralittoral species, there is no carrying before moulting. "Associated with the terrestrial habitat, therefore, we see not only modifications in the method of carrying, but also a great reduction in its duration" (Williamson, 1951).

From these facts, Williamson concludes that the delayed egg laying, associated with the longevity of the sperm, has an adaptive significance. Where the moult governs the time of laying, the delay increases the chances of mating by increasing the time, between moulting and laying, in which mating can take place; furthermore, the male does not have to carry the female. On the other hand, mating in aquatic forms "can take place over a period of several days before the moult, and the probability of mating would be very little increased if egg laying were delayed for a few hours, or even days, after the moult" (Williamson, 1951).

Correlated with the terrestrial environment, there is also a reduction in the number of eggs produced. In most species of terrestrial amphipods, I have found the number of eggs in the brood pouch ranges from 1 to 10, e.g., in *Talitrus sylvaticus* the average is between 3 and 4. Yet in marine genera of the same family, the number carried by an ovigerous female of similar size may be many times this. An *Allorchestes novizealandiae* female taken at random carried 161 eggs, the greater carrying capacity of the animal being in part due to the much smaller size of the eggs.

Sexton (1924) has shown a decrease in number of eggs produced by species of *Gammarus* from marine to pelagic species. *Gammarus locusta*, a marine species, has as many as 143 eggs in a brood. The brackish-water *G. chevreuxi* has 30-40 per brood; the fresh-

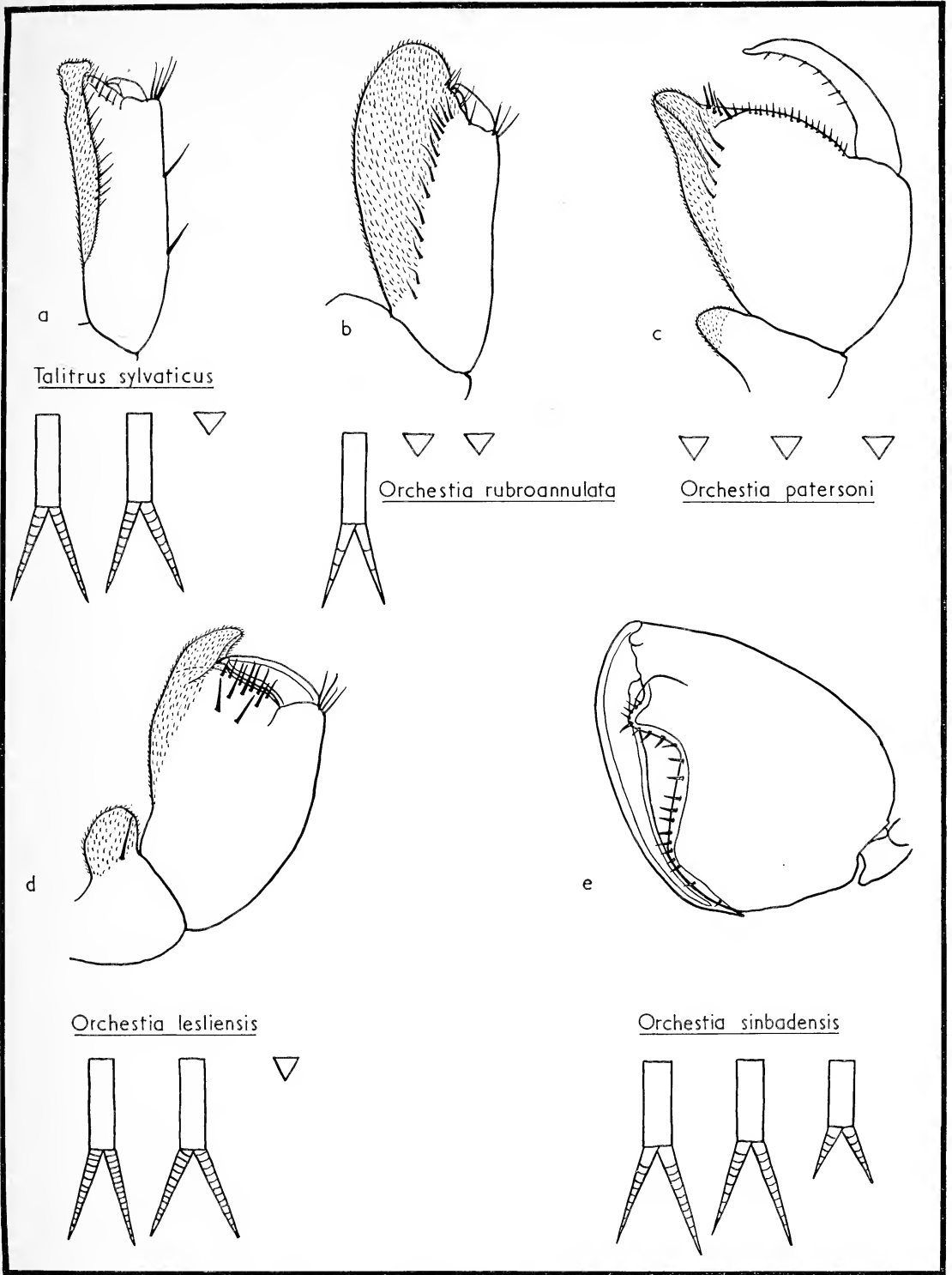


FIG. 3. Adult male second gnathopods of five species of terrestrial amphipods showing similarities to developmental stages of other species (cf. Fig. 2). Diagrammatic representations of the pleopods are given for each species. (The number of segments per ramus indicated corresponds to the number suggested by setation; in some species, actual segmentation appears superficial or incomplete.)

water *G. pulex*, 12–18; and a littoral species of *Gammarus*, 8–12. Lawrence (1953) gives a figure of 6–14 eggs for the terrestrial *Talitrus* (*Talitroides*) *eastwoodae*, "the average thus being almost identical with that of the littoral species quoted by Sexton." Lawrence further states that, as far as is known, there is only one annual brood in *T. eastwoodae*, whereas *G. chevreuxi* breeds all the year round. Sexton (1928) writes of one female *G. chevreuxi* which was known to have 29 broods in a lifetime—12 to 18 months is noted as the average breeding lifetime of a female *G. chevreuxi*—and Hynes (1955) says that *G. pulex* will breed five times in a year.

So, as in other groups of invertebrates which have adapted themselves to terrestrial or fresh-water life, the eggs tend to be larger and fewer, an example of the general tendency for the more advanced species of a group to be more sparing in the production of the young. It is reasonable to expect that, as in other advanced groups, the eggs and young will have a longer developmental period, but when launched from the protection of the parental brood pouch the young will be more mature than those of the marine species. It is significant that *Talitrus saltator* takes considerably longer to mature than the 2 to 2½ months required by the somewhat more hydrophilous *Orchestia gammarella* (Verwey, 1929, quoted by Williamson, 1951).

Thus, changes in sexual habits and breeding of the supralittoral species are directly advantageous in entering the terrestrial environment. The suggested trend in delaying of egg laying until after moulting is most significant, and one would expect the truly terrestrial species of *Talitrus* to have developed this trend even further, being limited ultimately only by the viability of the sperm.

MOISTURE REQUIREMENTS

Moisture requirements appear to have been met by the relatively stable nature of the environment. The nature of the leafmould zone itself does away with much of the necessity

for special adaptations. I have found that terrestrial amphipods in cultures uncontrolled for humidity vary specifically in resistance to changes of moisture, as would be expected from similar work on isopods (Edney, 1951) but that all species are extremely susceptible to desiccation. Apart from these variations in resistance, no specific adaptations to moisture requirements have been observed. Edney's work on isopods (1951, 1954) suggests that adaptations to this environmental factor are to be found in behavioural and physiological rather than morphological factors. He believes that terrestrial isopods have not developed the waxes characteristic of insect cuticles "which have contributed largely to their success as terrestrial animals."

However, there is evidence that such water-conserving adaptations as impermeable cuticles are not the only way of meeting the hazards of at least a limited degree of terrestrial life. "The ability to evaporate water rapidly, and thus to cool the body, may be of survival value when woodlice are exposed to high temperatures for short periods, particularly in littoral forms which may well have been intermediate in the evolution of terri-colous from maricolous isopods" (Edney, 1951*a*). This is supported by various measurements of transpiration rates in cryptozoic invertebrates quoted in Edney (1954), suggesting that "high transpiration rates are generally associated with cryptozoic arthropods."

Casual observations support the likelihood that the permeability of the exoskeleton of terrestrial amphipods is much greater even than that in isopods, and by inference, that transpiration rates may also be higher. Terrestrial amphipods, when placed in 70–95 per cent alcohol, immediately react vigorously, but in little more than 10 seconds show no further signs of life. Isopods, under the same conditions, have been observed to react for as long as 10 minutes before final quiescence. I have also noted a similar differential rate in susceptibility to desiccation. Lawrence (1953) likewise notes that *Talitrus eastwoodae*

may survive as long as 9 days in fresh tap-water, but "on the other hand it is much more susceptible to dry air in which it succumbs very quickly," a statement which incidentally raises questions regarding control of osmotic pressure within the body.

These points further emphasise a very important aspect of the ecology of the cryptozoic fauna, that "the forest community, by its very nature, solves the problem of water conservation for a host of plants and animals, making unnecessary for them the specific adaptations to economy of water that may be essential in other terrestrial environments" (Allee, Emerson, *et al.*, 1949).

EXCRETION

The excretory problems facing animals of marine origin which colonise the land are well known. Foremost amongst these is the retention of water, which requires the development of mechanisms for the resorption of water from excreta, and adaptation of the excretory end product. In most groups, this is expressed by a change in the major nitrogenous end product from the ammonia of marine groups to the urea or uric acid of terrestrial groups, with accompanying complexity of excretory organs.

Dresel and Moyle (1950) describe studies on nitrogenous excretion in amphipods and isopods, including a supralittoral species of *Orchestia*. They conclude that more than 50 per cent of the total soluble nonprotein nitrogen of the excreta is in the form of ammonia. "The level of nitrogen excretion is appreciably lower in the terrestrial species than in any of the others, indicating that, in this group, adaptation to terrestrial conditions has been attended by a general suppression of nitrogen metabolism rather than a transformation to other, less toxic products." Some excretion of uric acid, 5–10 per cent of the total soluble nonprotein nitrogen, took place in the terrestrial isopods. Associated with this excretion, "some retention of this insoluble compound usually occurs, and

it was found that among the terrestrial species the amount so stored parallels the degree of morphological and physiological adaptation to terrestrial conditions. . . . It seems more plausible, however, to attribute this increased uric acid retention in the more xerophilous species to a reduced rate of excretion rather than to a fundamental difference in metabolism."

Thus, they conclude that "adaptation to terrestrial conditions [in the Isopoda and Amphipoda] has been attended by a general suppression of nitrogen metabolism rather than by a transformation of ammonia to other, less toxic products."

Apart from this work of Dresel and Moyle, nothing is known of excretory processes or mechanisms in the terrestrial amphipods.

OXYGEN CONSUMPTION

The rate of oxygen consumption in *Talitrus sylvaticus* has been investigated by Clark (1955). Apart from a decrease in rate of respiration relative to increase of body weight, which is normal for Crustacea, he found that oxygen consumption was relatively higher in winter than in summer, the winter consumption corresponding to that at a temperature 2.5°C. higher in summer. "Of the factors influencing the rate of oxygen consumption . . . first order interactions occurred between temperature and body weight, temperature and season, and season and body weight. There was also a significant second order interaction between temperature, body weight and season. . . . Adaptation . . . to oxygen uptake by *Talitrus sylvaticus* to seasonal differences in temperature was not sufficient to enable it to maintain the same rate of output of energy in winter as in summer" (Clark, 1955).

The occurrence of a seasonal adaptation of rate of oxygen uptake has been found only infrequently in invertebrates, and the necessary physiological mechanism is unknown.

RESPIRATION AND PLEOPOD STRUCTURE

It is interesting to compare the relationship

of the pleopods to respiration in the Isopoda and the terrestrial Amphipoda.

In the Isopoda, the pleopods show a series of modifications for respiratory purposes. In marine species, the pleopods are used both in swimming and for respiration. In the terrestrial species, as in the amphipods, they are no longer of use in locomotion. In the primitive state, both exopodite and endopodite in all pleopods are respiratory. In the Ligiidae, the exopodite is the primary respiratory organ and the endopodite is a secondary one. In the more primitive terrestrial species, such as in the Oniscidae, the endopodites are transformed into branchial lamellae and take over most of the respiratory function. In *Porcellio* and other genera, the exopodites have completely lost their respiratory function and act as lamellae protecting the endopodites from desiccation. However, in the most advanced terrestrial species, the endopodites again regress and are replaced by pseudotracheae ("white bodies" or "tracheal glands") on the inner side of the exopodites. It is these pseudotracheae which enable the desert-dwelling species to survive. The pseudotracheae have evolved in three independent lines comparable to and surpassing the development of a terrestrial mode of life in the amphipod genera, *Orchestia*, *Talorchestia*, and *Talitrus*.

In marine species of amphipods, the pleopods have three functions (Watkins, 1939, 1940). They are used for swimming, they draw a constant current of water over the gills, and the same current, filtered by the gnathopods, serves as a food vehicle.

With the development of extensive pleon muscles and the change to a supralittoral jumping habit, pleopods are no longer used in feeding. Food is obtained actively and the gnathopods are used to grasp and convey it to the mouth. However, all supralittoral species possess fully developed pleopods, suggesting that they are still used in respiration. Since supralittoral species have not lost the power to swim and occasionally need to swim

if they are to survive, their pleopods may fulfil two of these functions.

Among terrestrial species there is a trend towards reduction or complete loss of pleopods except for vestigial triangular stumps, but there are exceptions to this. New Zealand species from leafmould collected 2,000 to 3,000 feet above sea level have fully developed pleopods, e.g., *Orchestia sinbadensis* Hurley (1957).

A completely terrestrial habitat removes any need of pleopods for swimming. According to Lawrence (1953), *Talitrus eastwoodae* "never swims when placed in water and is evidently unable to raise itself above the bottom of a glass jar, moving round in it precisely the same way as if walking on dry land." The absence of pleopods in *O. patersoni* (Stephensen, 1938) implies that sufficient oxygen is available to the respiratory surfaces without need for a constant current of air created by the pleopods. As might be expected, there is in most species a considerable development of respiratory surfaces correlated with this loss. "The gills of the anterior pair of pereopods are rather large, in the female especially so in pereopod 2" (Stephensen, 1935). *Talitrus sylvaticus* is a good example of this marked development; it has the gills of the fourth pereopod, as well as those of the second, much enlarged and elongated (Hurley, 1955). Possibly, the retention of pleopods in some terrestrial species depends on a burrowing habit, in which case the available air in the burrow might stagnate more rapidly were not the pleopods used to increase the circulation. A correlation has also been suggested between burrowing and reduction of eyes, or even loss of pigment, as in *Orchestia marquesana* (Stephensen, 1935), but evidence of this is very limited.

OTHER MODIFICATIONS

In the Isopoda, at the same time as the developments in the pleopods described above, other tendencies have appeared. The antennae have become reduced, probably with an as-

sociated loss of sensory perception; the body in many species has become capable of rolling into a ball, or "conglobating," thus giving the animal greater protection from desiccation and, presumably, from its natural enemies; and locomotory powers have been reduced by weakening of the pereopods (Van Name, 1936:282,328). In the terrestrial Amphipoda, the antennae are much simpler than in most marine and littoral species; they are more slender; they lack calceoli and other similar sensory structures; but there does seem to be a development of fine setae of a tactile nature. Terrestrial species are extremely mobile. There is no morphological adaptation to protect the gills—if anything they are more exposed by reason of their greater length; nor is there any sign of structural adaptation like the "conglobating" power of isopods. However, with increase in gill size, as in *Talitrus sylvaticus*, it would not have been unreasonable to have expected some physiological or morphological modification analogous to the development of pseudotracheae in the terrestrial isopods. It is probably because of the lack of just such modifications that the terrestrial amphipods, seemingly well suited for the leafmould environment, have not occupied other, more stringent niches.

What has been said of the terrestrial isopods, also may be said of the amphipods: "Any success which the group enjoys on land is due, not so much to the development of characters conferring independence of the environment, but to behavioural mechanisms which keep them for the most part in moist, cool places. . . . The general picture which emerges is of a group of animals comparatively ill equipped for life on land. All the devices which permit such existence are in some degree makeshift. . . . And yet, despite these disadvantages, the animals are by no means uncommon, and there is little doubt that the success which they do enjoy is the result not so much of morphological or physiological adaptations as of behavioural mechanisms which restrict them to the cryptozoic

niche where the rigours of true terrestrial existence, as well as its opportunities, are avoided" (Edney, 1954).

SUMMARY

The term "supralittoral" is applied to Amphipoda of the seashore zone; "terrestrial" is restricted to those species which are entirely independent of sea water. Almost all of these are leafmould species which are characteristic of, and restricted to, the Indo-Pacific islands and land masses. The terrestrial amphipods have colonised the land directly from the littoral zone. The forest floor provides the relatively stable conditions which assist colonisation and provide considerable protection in unfavourable times. Drastic changes in feeding habits have not been necessary.

Adaptations which have taken place or seem most likely to have occurred are these:

1. Feebly chelate gnathopods in *Talitrus* and reduced male second gnathopods in *Orchestia* species are correlated with changes in sexual habits, the development of large second gnathopods in the male to hold the female during copulation having been lost. In *Talitrus saltator* stout antennae are used for this purpose, but in most terrestrial amphipods the antennae are long and slender, and there must have been a further, as yet undescribed, change in sexual habits. Scabrous pellucid areas on the male gnathopods, characteristic of terrestrial amphipods, are probably of tactile sensory nature and possibly correlated with feeding habits.

2. There is a tendency for the male second gnathopod in mature animals of some species to resemble the immature males in other, less terrestrial, species. It is suggested that species formation in terrestrial amphipods is correlated with neotony.

3. There is evidence that males are comparatively few in some terrestrial populations, although this may be true only of certain species and times of the year.

4. Fewer but larger eggs are produced by

terrestrial than by aquatic species of the same family, and there is a longer growth and breeding period. Carrying of the female by the male for long periods is obviated and may be entirely lacking, and the time after egg laying during which fertilisation is possible has been lengthened, thereby increasing the chances of mating. This would greatly facilitate entry into the terrestrial environment, especially since it appears first in supralittoral species.

5. There is a tendency for pleopods to be reduced to vestigial stumps, although species found high above sea level may have fully developed pleopods. Their absence in some species suggests that sufficient air is available to the respiratory surfaces without need of a pleopod-created current of air over the gills. In some species there is a marked development in size of gills.

6. The terrestrial species show strong evidence of endemism. This is probably due partly to the nature of their environment and partly to lack of available transport as compared with marine and littoral species, although the advent of man has complicated distribution patterns to some degree. In at least two genera, *Talitrus* and *Orchestia*, terrestrial species have arisen independently from littoral species.

7. Moisture requirements are met by the leafmould environment and behavioural patterns of the animals.

8. There is some evidence that excretory problems have been solved, not by a change in end products of excretion, but by a general slowing down and suppression of nitrogen metabolism.

9. The leafmould environment provides conditions most favourable to colonisation by a marine or littoral group of animals and requires a minimum of physiological or morphological adaptations.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part IV. Various Small Collections from the Central Pacific Area, including Supplementary Notes on Alpheids from Hawaii¹

ALBERT H. BANNER²

IN THE COLLECTIONS made available to me are a number of small collections, in some cases only single specimens, made from various islands ranging from the Tuamotus to the Carolines, none being extensive enough to warrant separate papers. Some of these have been loaned by the United States National Museum, some by the Bernice P. Bishop Museum, and some by the individual collectors, e. g., the collection by R. W. Hiatt from the islands of Yap. Also, in the continuing collections made in Hawaii since the completion of my 1953 paper, three additional species have been found and two notable variations in the usual form or color of known species have been observed. Finally, a new name has been applied to a species previously described from Hawaii.

Because the specimens came from such widely separated localities and because so few species came from each collection, the collection data are listed under each species rather than in a preliminary comprehensive collection list, as has been done in previous articles.

As in previous papers in this series, instead of repeating the full synonymy for species which have been discussed in previous papers, I have made reference to the earlier papers in the series which have presented the synonymy.

The collections were made for numerous sponsors, some of whom have been forgotten

in the many years since the collections were made. This study has been done largely under a grant to the author from the National Science Foundation (NSF G-1754).

Type specimens of the new species described in this paper will be deposited in the institution from which they were borrowed; those types in my personal collection will be deposited either in the Bernice P. Bishop Museum or in the U. S. National Museum (USNM).

ARETE Stimpson

Arete dorsalis Stimpson

Arete dorsalis Stimpson, Acad. Nat. Sci. Phila., Proc. 12: 32, 1860.

LOCALITIES: 1 specimen, Station 1847, Raroia Atoll, Tuamotu Archipelago, "from green-black sea urchin from middle zone of outer reef flats Ngarumaoa Island. . ."; collected by J. E. P. Morrison, July 5, 1952. Four specimens from Station 1857, collection data as above.

DISCUSSION: These specimens will be discussed in a future paper dealing with this genus and the genus *Athanas* Leach.

Arete indicus Coutière

Arete dorsalis var. *indicus* Coutière, Soc. Philomath. Paris, Bul. IX, 5(2): 85, figs. 25-30, 1903.

Arete indicus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2: 863, figs. 134-135, 1905.

¹ Contribution No. 111, Hawaii Marine Laboratory.

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TABLE 1
COLLECTION DATA FOR SPECIMENS STUDIED

LOCATION AND COLLECTOR'S NUMBER	ISLAND	ARCHIPELAGO	COLLECTOR	LOANING AGENCY
Tomil Harbor, Nos. Y-111, 122, 214, 215, 252.....	Yap	Caroline	R. W. Hiatt	R. W. Hiatt
No. 2063.....	Oneroa	Caroline	Morrison, Doty, Herre	USNM
Kwajalein Atoll.....	Kwadak	Marshall	P. E. Cloud, Jr.	USNM
Likiep Atoll, No. 827.....	Nado	Marshall	S. V. MacNeil	USNM
No. 1742.....	Canton	Phoenix	E. H. Bryan	Bishop Museum
	Jarvis	Line Islands	Toomey, Ahia, Graf	Bishop Museum
	Washington	Line Islands	C. H. Edmondson	Bishop Museum
	Palmyra	Line Islands	C. H. Edmondson	Bishop Museum
No. 3707.....	Midway	Hawaiian	C. H. Edmondson	Bishop Museum
Nos. 1497, 1498.....	Wake		C. H. Edmondson	Bishop Museum
	Wake		C. H. Edmondson	Bishop Museum
Pearl and Hermes Reef.....		Hawaiian	U. S. Navy Ship "Dranga"	Bishop Museum
	Midway	Hawaiian	Y. D. P. Speicer	Bishop Museum
Kaneohe Bay.....	Oahu	Hawaiian	A. H. Banner	
Ahoolaka, Kaneohe Bay.....	Oahu	Hawaiian	A. H. Banner	
Wailupe pond.....	Oahu	Hawaiian	Donald C. G. McKay	Donald C. G. McKay
Raroia Atoll, No. 1847.....	Ngarumaoa	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2015.....	Otikaheru	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2187.....	Kakipuku	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2252.....	Ngarumaoa	Tuomotu	Maxwell Doty	USNM
Raroia Atoll, No. 1963.....	Hamahomo	Tuomotu	J. P. E. Morrison	USNM

LOCALITY: 1 specimen, Station 2187, Kakipuku Island, Raroia Atoll, Tuamotu Archipelago, from boring sea urchin; collected by J. E. P. Morrison, August 26, 1952.

DISCUSSION: This specimen, although it lacks all of its appendages, has been put in this species because it compares so well with specimens plainly of this species from the same habitat (holes made by the sea urchin *Echinometra*) collected from Aitutake, Cook Islands. This species will be discussed in a later paper.

SALMONEUS Holthius

Salmonus tricristata sp. nov.

Fig. 1a-e

LOCALITY: 1 specimen, Station Y-122, Tomil Harbor, Yap Island, Caroline Archipelago, an ovigerous female 12 mm. long lacking large chela, having one each of 2nd, 3rd, and 5th legs, and both 4th legs; collected by R. W. Hiatt, 1946.

DESCRIPTION: Rostrum with tip reaching to end of second antennular article, anteriorly narrow but broad at base. Orbital teeth about one-third length of rostrum, tips acute. Both orbital hoods and rostrum bearing dorsal keels, that of the rostrum extending posteriorly from tip to more than two-thirds the length of the carapace, those of the orbital hoods extending almost to the tip of the hood and somewhat shorter than rostral carina.

Antennular articles short and broad. Stylocerite reaching to end of second antennular article. Scaphocerite broad and rounded, lateral spine equal in length to rounded anterior portion.

Large chela lacking. Merus of small chela about 4.5 times as long as broad, broadest in middle; carpus equal in length and breadth to merus, but widest distally; palm a little less than half as long as carpus; fingers equal in length to palm.

First carpal article of second legs slightly longer than the sum of the four distal articles.

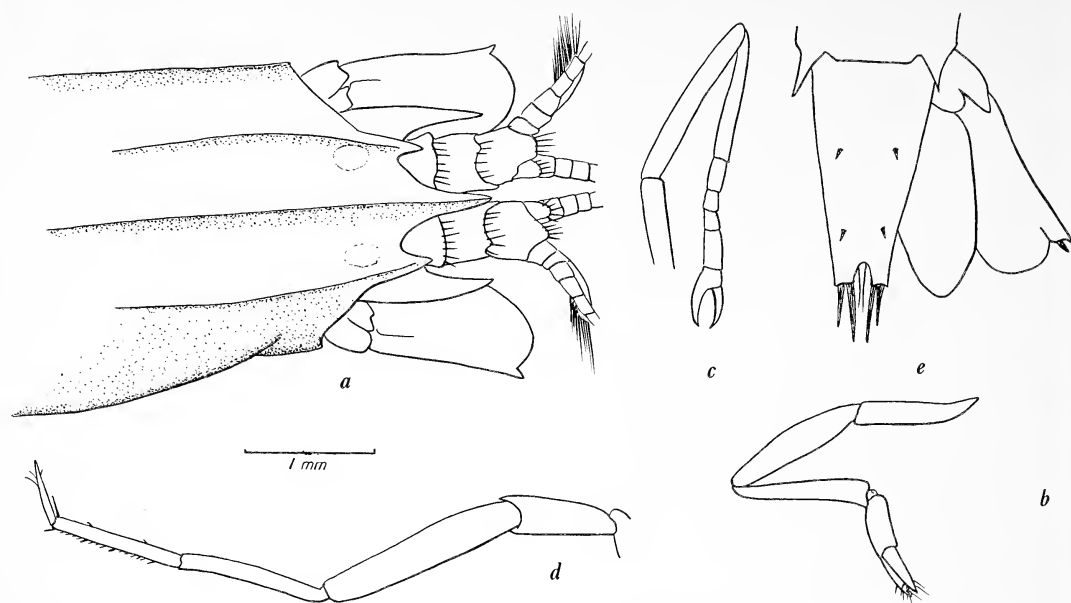


FIG. 1. *Salmoneus tricristata* sp. nov. *a*, Anterior region, dorsal aspect; *b*, small chela; *c*, second leg; *d*, third leg; *e*, telson and uropod. All drawn to same scale.

Third legs with ischium half as long as merus, a little more than twice as long as broad; merus 5 times as long as broad, unarmed; carpus about two-thirds as long and less than half as broad as merus; propodus slightly shorter and thinner than carpus, armed with 4 feeble spines on superior margin and two similar spines on inferior, armed on distal inferior margin with a longer and heavier movable spine; dactylus half as long as propodus, slender, tapering and with a slight curve.

Telson with anterior margin 2.5 breadth of posterior margin and length 4.5 times the posterior breadth; sides with uniform taper; terminal cleft one-ninth length of telson. Tip of telson armed with two pairs of spines, the inner as long as the tip is broad and the outer two-thirds the length of the inner. Cleft bearing two setae. Spines of dorsal surface of telson rather weak.

DISCUSSION: The original name of this genus, *Jousseamea*, has been changed by Holthius (1955:88) to *Salmoneus*, as the original name was preoccupied.

With Coutière's entirely inadequate description of his three species it is difficult, if not impossible, to be certain of any species. His original description of *Jousseamea latirostris* (1896:382) was:

"Les épines supra-oculaires sont très peu marquées et le rostre très large. L'une des pattes antérieures manque." In 1897 (p. 234) he added that the large chela was like that of *J. serratidigitus* Coutière, and in 1899 (p. 71, fig. 21) he supplied a dorsal view of the anterior carapace.

As a consequence, until the three species described by Coutière are redescribed adequately, every new species must be regarded as tentative. This species appears to be unique in the possession of the three crests on the anterior half of the carapace. *S. cristata* (Coutière) may have a somewhat similar medial crest, but the two lateral crests represent the continuation of the lateral margins of the rostrum and do not arise from the corneal teeth as do the ones on this species. Other species have the rostral crest, like *S. bilarula* (de Man), but in them it does not extend as

far posteriorly as it does on this species; *S. brevirostris* (Edmondson) has also the crests from the corneal teeth, but again, these do not extend far posteriorly and are not parallel.

If the development of the crests is consistent within a species, and if the interpretation of Coutière's sketches and brief descriptions are correct, this can be regarded as a separate species.

SYNALPHEUS Bate

Synalpheus coutierei Banner

Synalpheus biunguiculatus Coutière (*nec* Stimpson), Soc. Ent. de France, Bul. (11): 232, figs. 1-4, 1898.

Synalpheus coutierei Banner, Pacific Sci. 7(1): 36, 1953.

LOCALITY: 1 specimen, Bernice P. Bishop Museum No. 1742, Canton Island, Phoenix Archipelago; collected by E. H. Bryan, 1924.

DISCUSSION: While this specimen is definitely *S. coutierei*, it differs slightly in the rostrum and antennular peduncle from the illustration of Coutière. In his figures the orbital hoods are thinner than those in this specimen (which even exceeds the breadth as shown for *S. pachymeris*, *loc. cit.*, fig. 9) and the rostrum is definitely shorter than the orbital teeth and relatively thinner. In the antennular peduncle the articles are thinner and longer, but not markedly so, while the relative proportions of the parts of the antennular peduncle remain about the same. Considering the variation in the genus and the variation already reported for *S. coutierei*, this is probably not important.

Synalpheus carinatus (de Man)

Alpheus carinatus de Man, Arch. f. Naturgesch., 53: 508, pl. 22, fig. 2, 1887.

LOCALITY: 4 specimens, Kwadak, Kwajalein Atoll, Marshall Islands, from specimens of *Comanthus bennetti* (Müller) as determined by A. H. Clark, U. S. National Museum; collected by P. E. Cloud, Jr.

Synalpheus charon obscurus Banner

For synonymy, see Banner, Pacific Sci. 10(3): 329, 1956.

LOCALITIES: 1 specimen, Bishop Museum No. 3707, from Midway Island, Hawaiian Archipelago; 1 specimen, Bishop Museum No. 1497, from Wake Island (19°18' N., 166°35' E.), in coral; both collected by C. H. Edmondson, Tanager Expedition, 1923.

DISCUSSION: These specimens plainly belong to the new subspecies; the specimen from Midway, an ovigerous female, is 20 mm. long, the largest specimen yet seen.

Synalpheus paraneomeris Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 331, 1956.

LOCALITIES: 2 specimens at Station 287, USNM 194726, from Likiep Atoll, Nado Island, Marshall Islands; collected by S. V. MacNeil. Two specimens from Jarvis Island, Line Islands; collected by Toomey, Ahia, and Graf, Itaska Expedition, 1935. One specimen from Wake Island; collected by C. H. Edmondson, Tanager Expedition, 1923.

DISCUSSION: The large chela of the male specimen from Wake Island has a ratio of the chela length to the finger length of 2.6, the longest finger yet encountered (see Banner, *loc. cit.*). The specimen otherwise agrees with the variable characteristics of this species.

Synalpheus tutbilli sp. nov.

Fig. 2a-j

TYPE SPECIMEN: An ovigerous female 12.6 mm. long, Station Y-215, Tomil Harbor, Yap Island, Caroline Archipelago; collected by R. W. Hiatt, 1946. An allotype, 10.5 mm. long, and 7 paratypes from same station.

DESCRIPTION: Rostrum short, reaching less than one-third the length of the visible portion of first antennular article; sides straight, with uniform taper, orbital teeth short, slightly shorter than rostrum, tips rounded, both medial and lateral margins slightly concave.

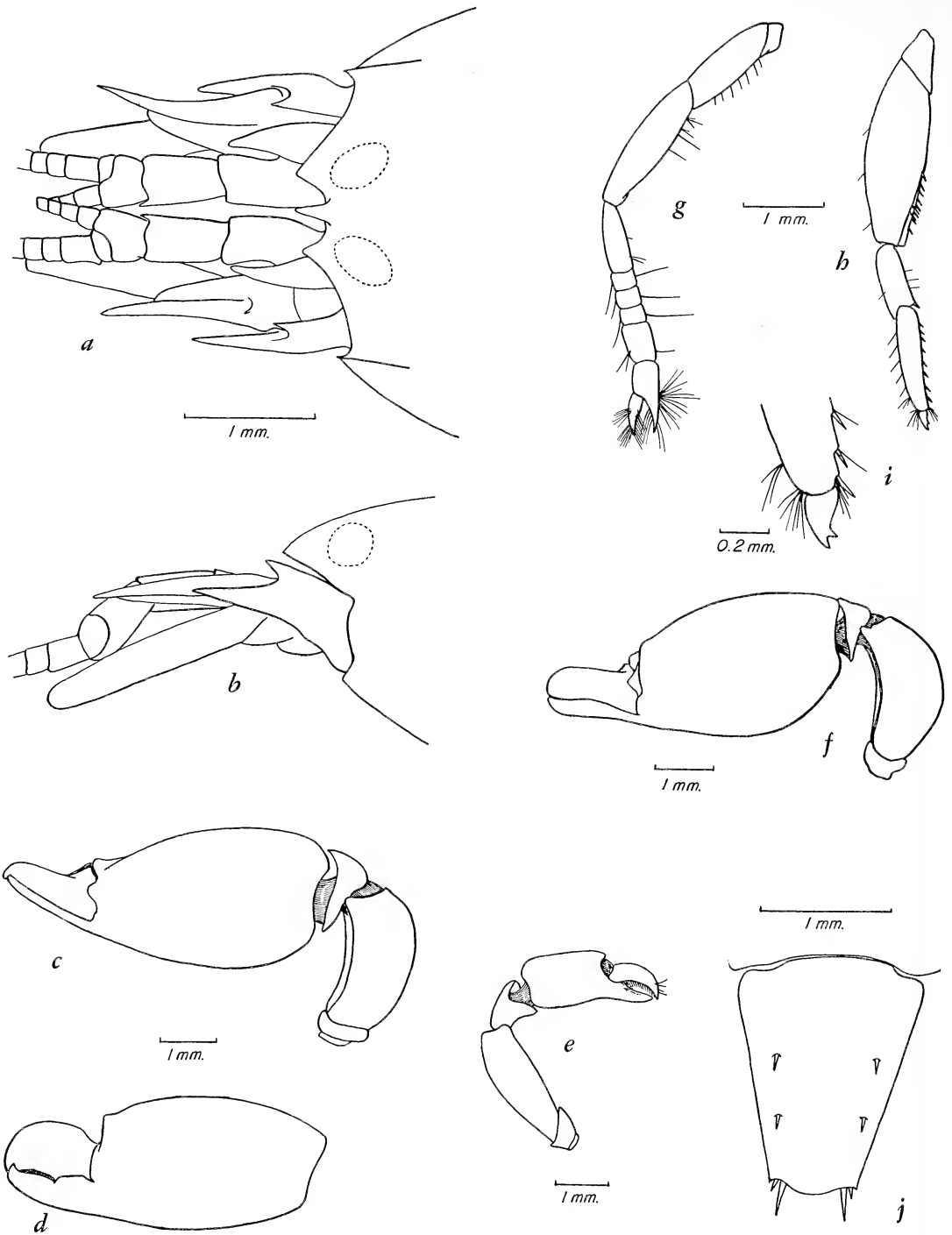


FIG. 2. *Synalpheus tubilli* sp. nov. *a, b*, Anterior region, dorsal and lateral aspects (assymetry of scaphocerites are as found in specimen); *c*, large cheliped, female, lateral aspect; *d*, same, superior face; *e*, small cheliped, female; *f*, large cheliped, male; *g*, second leg; *h*, third leg; *i*, third leg, dactylus; *j*, telson.

Orbital hoods and rostrum depressed and rounded in lateral view.

Antennular peduncle with first article slightly longer than second; second article about twice length of third article. Stylocerites heavy, with slightly rounded tips not reaching to end of first antennular article. Lateral spine of basicerite reaching almost to middle of second antennular article. Stylocerite with lateral spine well developed (that of right side distorted on type specimen), reaching to end of antennular peduncle; blade reduced, narrow and reaching only to end of second antennular article. Carpocerite markedly longer than antennular peduncle.

Large chela inflated, subcylindrical in section, 2.4 times as long as broad, tapering strongly to fingers. End of palm above dactylar articulation unmarked by any prominences. Fingers occupying distal quarter of entire length of chela, twisted from axis of palm; dactylus high, narrow, with superior edge rounded. Merus short, less than half length of chela, heavy, twice as long as broad, and strongly curved, with superior margin more strongly curved than inferior; superior margin not terminated in angle, but curved towards dactylar articulation.

Small chela small but heavy, with palm 1.6 times as long as broad, and 1.7 times as long as fingers; fingers tapering, slightly broadened proximally. Merus about as long as that of large cheliped, almost as long as small chela proper; superior margin curved but not as strongly as that of large cheliped; inferior margin straight.

Carpal articles of second leg with ratio: 10:2.5:2.5:2.5:6.

Third legs with merus heavy, three times as long as broad, with inferior distal margin bearing numerous short spines which are usually concealed in normal side view by larger outer (or posterior) ridge. Carpus as long as merus is broad, superior margin ending in rounded tooth, inferior margin terminally armed with single weak spine. Propodus 0.56 as long as merus, 4.5 times as long as broad,

armed with 9 weak spines. Dactylus less than 0.2 length of propodus, with strong taper and small ungui.

Telson 2.7 times as long as broad at posterior margin, with anterior margin twice as broad as posterior; lateral margins slightly convex in middle, terminated by slight subacute angles; posterior margin with low convexity.

DISCUSSION: In the nine specimens in the collection little variation is present except for the large chela and the armature of the merus of the third legs. In the larger specimens the length of the finger in respect to the chela is like that of the type, but in some of the smaller specimens the fingers occupy up to 0.32 the length of the chela; the fingers of the small specimens are also more slender, being as much as 2.6 times as long as broad. It should also be noted that the merus of the allotype is more strongly curved than that of the type. The merus of the third legs bears from 3 to 9 spinules, with the small number being on the smaller specimens.

It is also interesting that of this small collection, two males and one female (ovigerous) bear parasitic isopods on their abdomens.

This form is plainly related to *S. pachymeris* Coutière (1905a: 873) and *S. bituberculatus* de Man (1910: 294), and less closely to *S. coutierei* Banner (1953: 36) of the Coutierei group (see description under the name *S. biunguiculatus* (Stimpson) in Coutière, 1898: 230). The last species differs from the first two and from this form in that the merus of the third legs is unarmed. This form differs from the first two species in that the margin of the palm above the dactylar articulation is unarmed and the palm itself is inflated, while in both others the palm is more slender and bears one (*S. pachymeris*) or two (*S. bituberculatus*) rounded projections above the dactylus. There are also slight differences in the armature of the anterior carapace, but it is unlikely that these are of significance. In *S. pachymeris* and *S. bituberculatus* (but not in *S. pachymeris cargadosi* Coutière) the stylocerites are longer than the

first antennular article, but they are shorter in this form. Coutière regarded the number of spinules on the merus of the third legs as important in his description of his variety *S. p. cargadosi* (1921: 417), but neither in de Man's species, nor in Coutière's original description (where he described *pachymeris* as a variety of *S. biunguiculatus* = *S. coutierei*), any more than in these specimens, were the number of spinules constant between individuals.

Unfortunately the name *tuthilli* used in the genus *Alpheus* will have to be put in synonymy in a subsequent paper; this is another attempt to express thanks to Dr. Leonard D. Tuthill, friend and former editor of *Pacific Science*, for the help he has given me.

ALPHEUS Fabricius

Megacheles Group

Alpheus lanceostylus sp. nov.

Fig. 3a-b

Alpheus species 1, Banner, Pacific Sci., 10(3): 338, 1956.

TYPE: 28 mm. male collected at Pearl and Hermes Reef, Hawaiian Archipelago (27°N., 146°W.), by U. S. Navy Ship "Dranga" in 1927. Bernice P. Bishop Museum No. 2737.

PARATYPE: An ovigerous female 22 mm. long without chela collected from Saipan, Marianas (probably from the reef flat west of Cape Nafutan—exact data are lost), by A. H. Banner in 1945.

DESCRIPTION: Rostrum acute, reaching beyond end of first antennular article, broad at the base, dorsally only slightly rounded. Orbitorostral borders slightly concave. Orbital teeth strong, similar in shape to rostrum and about half as long.

Antennular peduncle with the second article 1.6 times the length of the visible portion of the first article, 1.2 times the length of the second article, and 1.3 times as long as broad. Stylocerite acute and reaching to middle of second antennular article. Scaphocerite broken on right side, left side with broad squamous portion reaching almost to tip, and tip slightly

exceeding end of third antennular article. Carpoperite reaching slightly beyond end of scaphocerite. Lateral spine of basicerite not heavy, and reaching to level of tip of rostrum.

Merus of large cheliped with inner face 1.5 times as long as maximum breadth distally; superior margin terminating in subacute tooth; inferior external margin irregular but not bearing spines; inferior internal margin bearing 10 small movable spines and terminating distally in strong acute tooth. Ischium bearing 4 inferior spines and a strong superior tooth. Carpus bearing a rounded tooth on superior internal distal margin. Chela heavy, compressed, almost as broad distally through the fingers as proximally, 2.9 times as long as broad. Superior crest of palm terminating distally in strong acute tooth, interrupted by shallow and poorly defined transverse groove, and proximally merging with surface of chela. Superior groove shallow and flattened. Palmar crest broadly rounded and poorly defined proximal to transverse groove. Palmar groove broad and rounded. Inferior crest distinct only distally and ending in strong tooth. Inferior depression deep but rounded. Shoulder distinct but not abrupt. (For explanation of terms see Banner, 1953, fig. 17e). Fixed finger strongly curved. Dactylus closing across end of chela, thin with high sharp crest, and strongly curved; superior margin without marked lobes, inferior margin with what appears to be an extra rounded tooth. Cheliped bearing only scanty setae except near fingers where setae are somewhat heavier.

Small chela lacking in both type and paratype.

Carpal article of second legs with ratio 10:7:4:3:5.

Third legs with ischium bearing movable spine; merus 6.6 times as long as broad, unarmed; carpus unarmed and 0.5 length of merus; propodus bearing 7 weak spines, 0.7 as long as merus; dactylus slender, curved, with single superior serration.

Telson 1.4 times as broad proximally as distally, 2.5 times as long as tip is broad, with

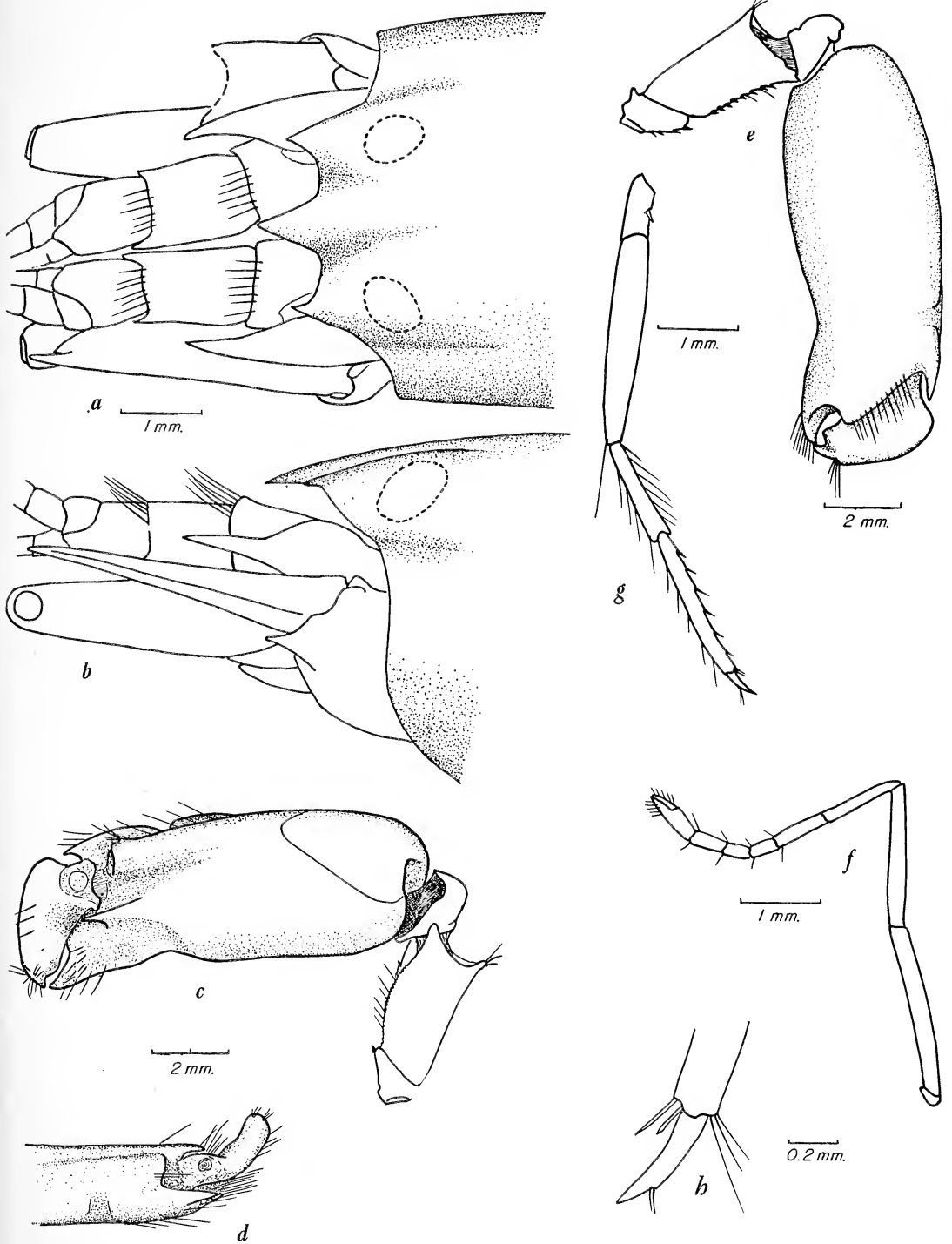


FIG. 3. *Alpheus lanceostylus* sp. nov. *a, b*, Anterior region, dorsal and lateral aspect; *c, d*, large cheliped, lateral and medial aspect; *e*, large chela, tip, superior aspect; *f*, second legs; *g*, third legs; *h*, third leg, dactylus.

lateral margins almost straight. Anterior dorsal spinules 0.3, posterior 0.6, of the length from articulation to tip.

DISCUSSION: The only difference noted between the incomplete specimen from Saipan and the type is that the propodus of the third legs carries 9 instead of 7 spines.

This species plainly belongs to the *Megacheles* group, and to the *A. hailstonei* Coutière complex (see Banner, 1953, p. 51 *et seq.*). However, it can be sharply separated from all others of that group (including *A. staphylinus* Coutière) by a series of characters, which include the broad second article of the antennular peduncle, the long stylocerite, and the nature of and direction of closure of the dactylus of the large cheliped. Other characteristics will separate it from one or more of the complex, as the presence of ischial spines will separate it from *A. hailstonei hailstonei* Coutière and *A. brachymerus* (Banner); the armature of the dactylus from several others, etc. (*op. cit.*, p. 55).

It is difficult to state which of the known species of the complex is most closely related to the new species. On the basis of the anterior carapace, large chela, and third leg it appears to be closest to *A. hailstonei paucispinata* (Banner).

Alpheus collumianus medius Banner

For synonymy, see Banner, Pacific Sci. 10(3): 340, 1956.

LOCALITIES: 2 specimens, Station Y-215, Tomil Harbor, Caroline Archipelago; collected by R. W. Hiatt. One specimen, Jarvis Island, Line Islands, Itaska Expedition; collected by Toomey, Ahia, and Graf, 1935. One specimen, Wake Island (19°18'N., 166°35'E.), collected by C. H. Edmondsom, Tanager Expedition, 1923.

DISCUSSION: Of the two specimens from Tomil Harbor, Yap, one was similar to the type in all respects, but the other, also similar, showed assymetry in the basicerites, with one normal for the subspecies and the other like that of *A. c. inermis* Banner (1956:342).

The one specimen from Midway was also very similar to the type specimens except that its only remaining second leg had the carpus divided into six rather than five articles. The ratio of these articles was 10:2:9:4:4:7, showing that the extra article was the short one between the first and second articles.

Alpheus seurati Coutière

Fig. 4

Alpheus seurati Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 881, pl. 75, fig. 20, 1905.

LOCALITY: 1 specimen from Jarvis Island, Line Islands; collected by Toomey, Ahia, and Graf, Itasca Expedition, 1935.

DISCUSSION: This sole specimen of the species agrees almost perfectly with the description and figures of Coutière, although it lacks the small chela.

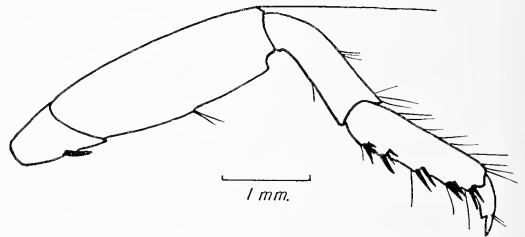


FIG. 4. *Alpheus seurati* Coutière. Third leg.

This species is plainly most closely related to *A. collumianus* Stimpson and within *A. collumianus* to the two subspecies, *A. c. medius* and *A. c. inermis* Banner (1956: 340). Coutière points out that the form of the anterior carapace, the large chela, the second legs, and the telson are like *A. collumianus* (actually, more like *A. c. medius*); the differences lie in the stylocerite—which is like that of *A. c. inermis*—and in the third legs, where the merus is broadened and lacking an acute distal tooth, but bears rather a rounded protuberance. He also points out several other characteristics that differ, but these, like the relative lengths of the second legs and the presence or absence of spines on the carpus of the third legs, are

variable characteristics, at least between the present subspecies.

I believe, therefore, that if the two subspecies are acceptable this species, too, should be made a subspecies of *A. collumianus*; however, I have deferred the action until more specimens can be examined.

Macrochirus Group

Alpheus buikau nom. nov.

Fig. 5a-e

Crangon nanus Banner, Pacific Sci. 7(1): 90, figs. 30, 31, 1953.

Alpheus nanus Banner, Pacific Sci. 10(3): 345, 1956.

nec *Crangon nanus* Krøyer, Naturhist. Tidsskr. 4(3): 231, 1842.

LOCALITIES: 13 specimens, Station 827, USNM 194726, Nado Island, Likiep Atoll, Marshall Islands; collected by S. V. MacNeil, 1952. One specimen, Station 2252, Ngaru-maoa Island, Raroia Atoll, Tuamotu Archipelago; collected by Maxwell Doty, Sept. 3, 1952.

DISCUSSION: It has been necessary to apply a new name to this species, which was named when the genus was called *Crangon* instead of *Alpheus*, because of Krøyer's use of *Crangon nanus* in 1842 for a species no longer in *Crangon* (or *Crago*) in 1953. The new name is from the Hawaiian, and means "confusion" or "mixed-up mess."

This group of specimens presents three points worthy of discussion. First, while the chelae on all of the females are like those described from Hawaii, the three males in the collection, all between 10 and 11.5 mm. in length, present an overgrowth of the fingers of the large and small chelae similar to that reported below for *A. paragracilis* Coutière. In the large chela the dactylus is very elongate, acute, and curved; the fingers occupy a large proportion of the length of the chela. The inferior internal margin of the merus only bears two feeble spinules, fewer than those reported in specimens in the Marianas and

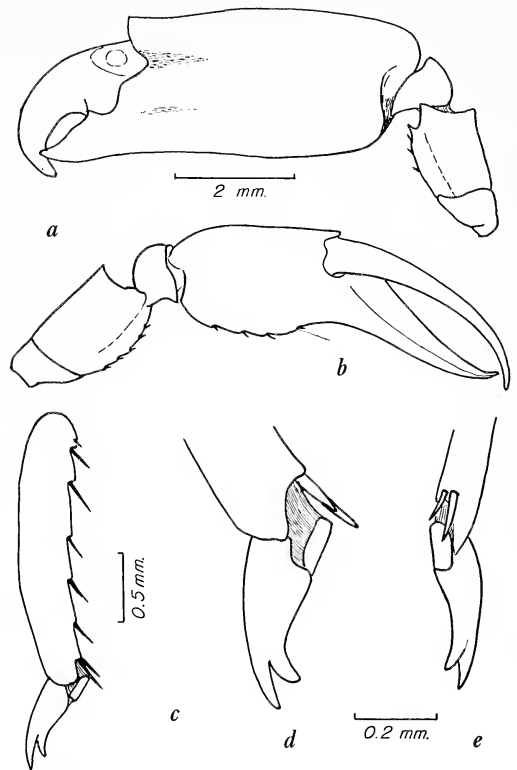


FIG. 5. *Alpheus buikau* nom. nov. a, b, Large and small chelipeds, showing overgrowth of fingers; c, third leg, merus and dactylus, anterior or medial aspect; d, e, third leg, dactylus, posterior and inferior aspects.

Arno. The small chela of the males also has the fingers elongate and curved; the merus is armed with two strong spines and three weaker spinules; the inferior margin of the palm bears two strong spines and two weaker spines, a characteristic not observed in previous specimens. This development of the chelae in the largest specimens is similar to that found for *A. paragracilis*. Unfortunately, neither this series of specimens, nor those from other islands, present a picture of gradual development as is found for *A. paragracilis*; however, a few other larger males, like those from Arno, do have a tendency towards the longer dactyli.

Second, is the peculiar development of an extra chitinized piece proximal to the dactylus and inferior to the distal end of the merus of

the third to fifth legs. This piece is borne by the tendon that reaches to the "heel" of the dactylus and is ordinarily obscured by the spines at the end of the dactylus if the animal dies with the dactyl straight or flexed towards the propodus. In many of these specimens, however, the dactylus was bent back on the propodus in death, so that the extra plate is apparent. The extra piece fits into an emargination of the inferior distal end of the propodus when the dactylus is straight or flexed. Other specimens of this species were re-examined and it was found that this development was carried by specimens from all areas studied. Moreover, specimens of the closely related *A. paragracilis* were also found to have the same structure.

Third, the outer uropods of these specimens bear several broad teeth on the distal articulation, and the inner uropod on its outer distal margin bears several small spines; neither of these characteristics was found in the specimens from Hawaii. This difference is not considered worthy of taxonomic emphasis.

The single specimen from the Tuamotus differs from the Hawaiian specimens in two minor ways. First, the rostrum is slightly shorter instead of slightly longer than the orbital hoods; second, the third and fourth carpal articles of the second legs are 1.3 and 2.0 times as long as broad instead of being broader than long. This latter characteristic may be important, but one specimen is not adequate for drawing such a conclusion.

Alpheus paragracilis Coutière

Fig. 6a-d

For synonymy, see Banner, Pacific Sci. 10(3): 345, 1956.

LOCALITIES: 1 specimen, Station Y-252, Yap Island, Caroline Archipelago, under small rocks on outer reef; collected by R. W. Hiatt, 1946. Nine specimens, Midway Island, Hawaiian Archipelago; collected by Y. Spicer, 1941.

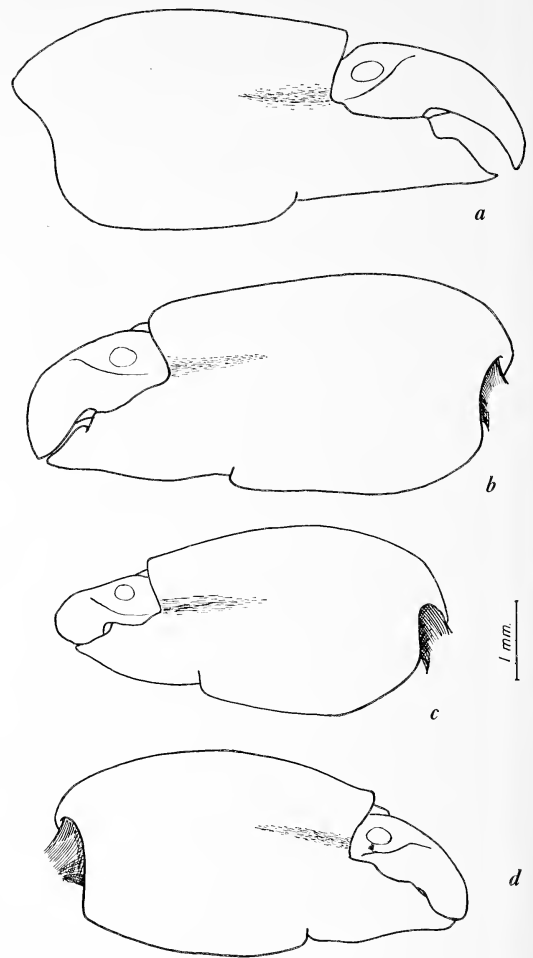


FIG. 6. *Alpheus paragracilis* Coutière, variation in the large chela. a, Male, 11.4 mm. long; b, male 10.8 mm. long; c, female, 11.4 mm. long; d, male, 9.6 mm. long. All drawn to the same scale.

DISCUSSION: These specimens present an interesting series on the change of form of the large chela with growth. The smaller males, less than 9.0 mm. long, and the females of all sizes have similar chelae, about twice as long as broad, and about 3.5 times the length of the fingers; the fingers of the dactylus are short, heavy, and rounded distally. However, on the largest male in the collection, 11.4 mm. long, the chela is 2.4 times as long as broad, and only 2.3 times the length of the fingers, and the dactylus is long, thin, curved and acute on the end. Between these two condi-

tions are found intermediate males, progressing from rounded condition of the immature forms to the acute form of the oldest male. It is also noteworthy that the chelae in the males are 1.5 times the length of those of the females of the same size.

In other collections examined and reported upon in previous papers, including those from Hawaii, this condition was not seen.

Alpheus macrochirus Richters

For synonymy, see Banner, Pacific Sci. 11(2): 198, 1957.

LOCALITIES: 2 specimens, Washington Island, Line Islands, in coral, Whippoorwill Expedition; collected by C. H. Edmondson, August, 1924.

Alpheus edmondsoni (Banner)

Crangon edmondsoni Banner, Pacific Sci. 7(1): 78, fig. 26, 1953.

LOCALITY: 1 specimen, Station 2063, One-roa Island, Caroline Archipelago, from surge channel, on outer reef beyond *Litbothanmion* ridge; collected by Morris, Doty, and Herre, August 6, 1952. (Specimen without chelae, therefore identification questionable.)

Alpheus ventrosus Milne-Edwards

For synonymy, see Banner, Pacific Sci. 10(3): 345, 1956.

LOCALITIES: 2 specimens, Station Y-214, Tomil Harbor, Yap Island, Caroline Archipelago, in *Pocillopora* at 3.0 feet; collected by R. W. Hiatt, 1946. Eight specimens from racimose coral heads east side Tomil Harbor, Station Y-215; other data as above. Two specimens from Kaneohe Bay, Oahu, Hawaiian Archipelago; collected by A. H. Banner, August 24, 1955.

DISCUSSION: The pair of specimens, male and female, from Hawaii are included in this paper because of their unusual color pattern. Wherever I have collected this species in the Pacific the color has been the same, a basic orange red, with spots and sometimes stripes of deeper red. This pair, from the same head

of *Pocillopora meandrina* var. *nobilis* Verrill, had in life a ground color of white with a tinge of pinkish yellow, and carried a series of paired irregular dark reddish-brown spots on either side of the middorsal line, three pairs on the carapace, and one pair on each abdominal somite. Similar but smaller spots were found at the bases of the abdominal pleura. Only the large and small chelae had the color usually characteristic of this species. The female carried larvae, recently hatched but still clinging to the pleopods, of pale violet color. No morphological differences were found between these and the normally colored specimens.

Obesomanus Group

Alpheus lutini Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 346, 1956.

LOCALITIES: 1 specimen at Y-214, 2 at Y-215, collection data as in *A. ventrosus* above.

Alpheus phrygianus Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 346, 1956.

LOCALITY: 1 specimen from Palmyra Island, Line Islands, in coral; collected by C. H. Edmondson on Whippoorwill A Expedition, August, 1924.

Crinitus Group

Alpheus frontalis H. Milne-Edwards

For synonymy, see Banner, Pacific Sci. 10(3): 357, 1956.

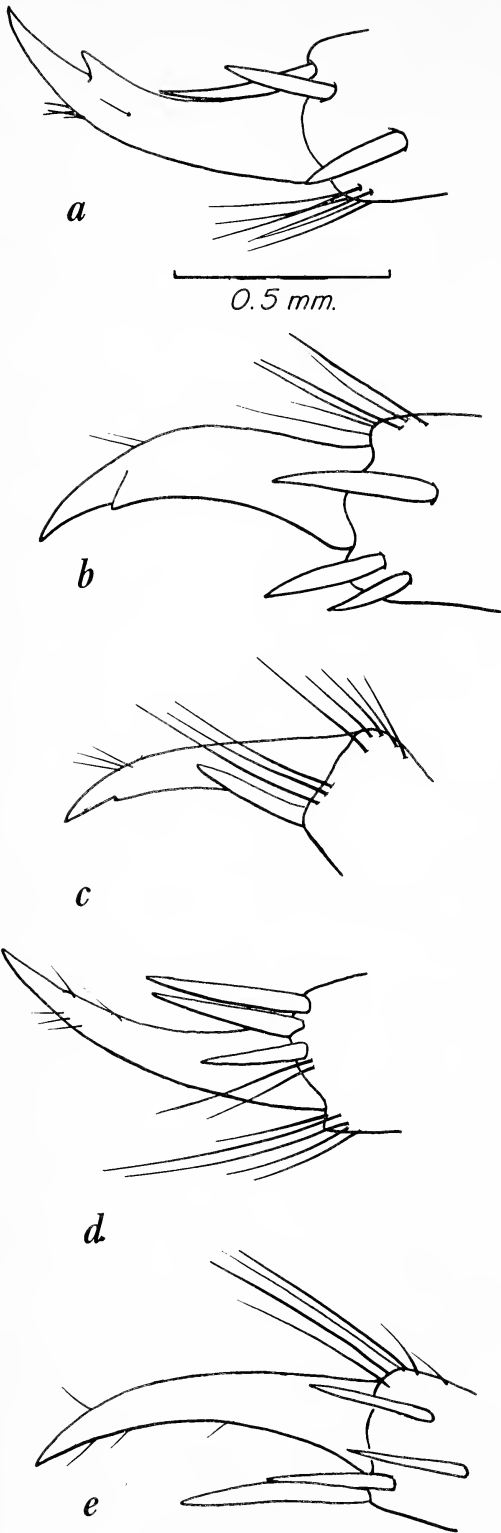
LOCALITY: 2 specimens, Station 1963 from Hamahomo Island, Tuamotu Archipelago, in algal tubes, under rocks, near shore; collected by J. E. P. Morrison, July 21, 1952.

Diadema Group

Alpheus diadema Dana

Fig. 7a-e

For synonymy, see Banner, Pacific Sci. 10(3): 357, 1956.



LOCALITIES: 2 specimens, Midway Island, Hawaiian Archipelago; collected by Y. D. P. Spicer, 1941. Six specimens, Ahoelaka ("Sand Island"), Kaneohe Bay, Oahu, Hawaiian Archipelago, under coral heads; collected by A. H. Banner, August, 1955.

DISCUSSION: In the group of specimens from Kaneohe Bay listed above an interesting variation occurs in the dactyli of the third, and to a lesser extent, the fourth legs. In most of the specimens from Hawaii these dactyli are either simple like the neotype (Banner, 1953, fig. 43j) or with a very small thickening or shoulder similar to those shown in Figure 7c, d. However, in this group of specimens from Kaneohe Bay, three specimens, male and female, have a definite and well-developed secondary unguis (Fig. 7a); the other specimens from the same locality had the secondary unguis developed as a shoulder only (Fig. 7b). There are no other noteworthy variations in either group of specimens. In the whole series of specimens it is the third legs that have the greatest development of the secondary unguis, and usually the fourth have but a slight thickening at most; moreover, often the accessory tooth or shoulder is not of uniform bilateral development.

The extensive collections of this species from the central Pacific area were spot checked for this characteristic, and it was found that most specimens were of intermediate development, similar to the conditions shown in Figure 7b-d. The extreme development, similar to the conditions shown in Figure 7a and e, were both rare.

Obviously, no significance should be attached to this variation.

An error in the redescription (Banner, 1953: 119) should be corrected. In describing the dactylus of the third legs, the text states: "Dactylus simple . . . as long as merus." In-

FIG. 7. *Alpheus diadema* Dana, variation in the dactyli of the third legs. a, Male, 19 mm. long, Kaneohe Bay, Hawaii; b, female, 24 mm. long, same locality; c, male, 15.5 mm. long, Tutuila, American Samoa; d, male, 18 mm. long, Midway Island; e, male, 17 mm. long, Tongatabu, Tonga. All drawn to the same scale.

stead, it should read: "Dactylus simple . . . as long as merus is broad."

Alpheus lanceoloti Coutière

Fig. 8a-k

For synonymy, see Banner: 1958: 167.

LOCALITIES: 13 specimens, some ovigerous; Ahoalaka ("Sand Island") Kaneohe Bay, Oahu, Hawaii; collected from silty sand flats at tide level by A. H. Banner. Maximum length about 20 mm.

DISCUSSION: These specimens agree well with the original description by Coutière on the general configuration and most details; there are, however, some differences. The rostral front in general agrees with Coutière's description and figures (1905a: 900, pl. 63, fig. 39) but some variation occurs: the rostrum may be slightly longer, the rounded rostral ridge may not reach any further back than the middle of the orbital hoods, the frontal margin at either side of the rostrum may be definitely concave instead of almost straight, and finally the line or ridge at the inner margin of the orbital hoods is usually lacking. ("Le rostre est . . . séparé des voûtes orbitaires par un sillon. . .") Slight and variable differences are similarly found in the proportions of the antennular peduncle and thoracic legs. In the large chela, as in the specimen already reported from Onotoa, the merus bears movable spines instead of teeth as shown by Coutière; moreover, the ischium of the same appendage bears three or four movable spines. The greatest difference is in the small chela of the male, which Coutière shows to be slender, with the fingers equalling the palm in length, while in these specimens the fingers are 1.2 times as long as the palm, slightly expanded in the middle, hooked on the end, and bear a fringe of setae, similar to a "balaeniceps-form," except that it does not cross over the superior face of the chela. The small chela of the females and immature males is similar to that drawn by Coutière. Coutière may have overlooked the sexual dimorphism. The small chela of the male from Onotoa was

similar to the form described by Coutière. It should be noted that the large chela is laterally compressed, approaching the condition found in the *Rapax* group, but twisted, so that in these figures, and presumably those of Coutière, the compression is not shown.

In life the specimens had a basic light "sandy color," similar in hue to their environment; the chromatophores on their abdomens were in irregular and imperfectly defined bands. Their eggs were bright green.

These specimens were found burrowing into the coherent fine sand of a broad sand flat. While their burrows were not traced, from the depths of the excavations necessary to capture the shrimp it is estimated that they penetrate into the sand about 12-15 inches. In the same environment, but burrowing more deeply, are found *A. rapax* (Fabricius) and a callianassid shrimp.

The figures are included to complete the series of figures of Hawaiian species.

Brevirostris Group

Alpheus rapax Fabricius

Figs. 9a-d, 10b

For synonymy, see Banner, Pacific Sci. 10(3): 358, 1956.

LOCALITIES: About 40 specimens, Kaneohe Bay, Oahu, in shallow burrows on the inshore mud flats, intertidal zone; two specimens from deep sand burrows on Ahoalaka ("Sand Island") low in the intertidal zone, Kaneohe Bay, Oahu, Hawaii; collected by A. H. Banner, 1955, 1956.

DISCUSSION: These specimens seem to be of two different size ranges according to their habitats; those from the shallow burrows (possibly up to 6 inches deep in the mud flats, with *A. platyunguiculatus* (Banner) occupying deeper burrows reaching into buried coral heads) were mature individuals with the carapace lengths up to 7.6 mm., while the two from the deep burrows in the fine sand of Ahoalaka were found from 12 to 18 inches down (with *A. lanceoloti* Coutière in shallow

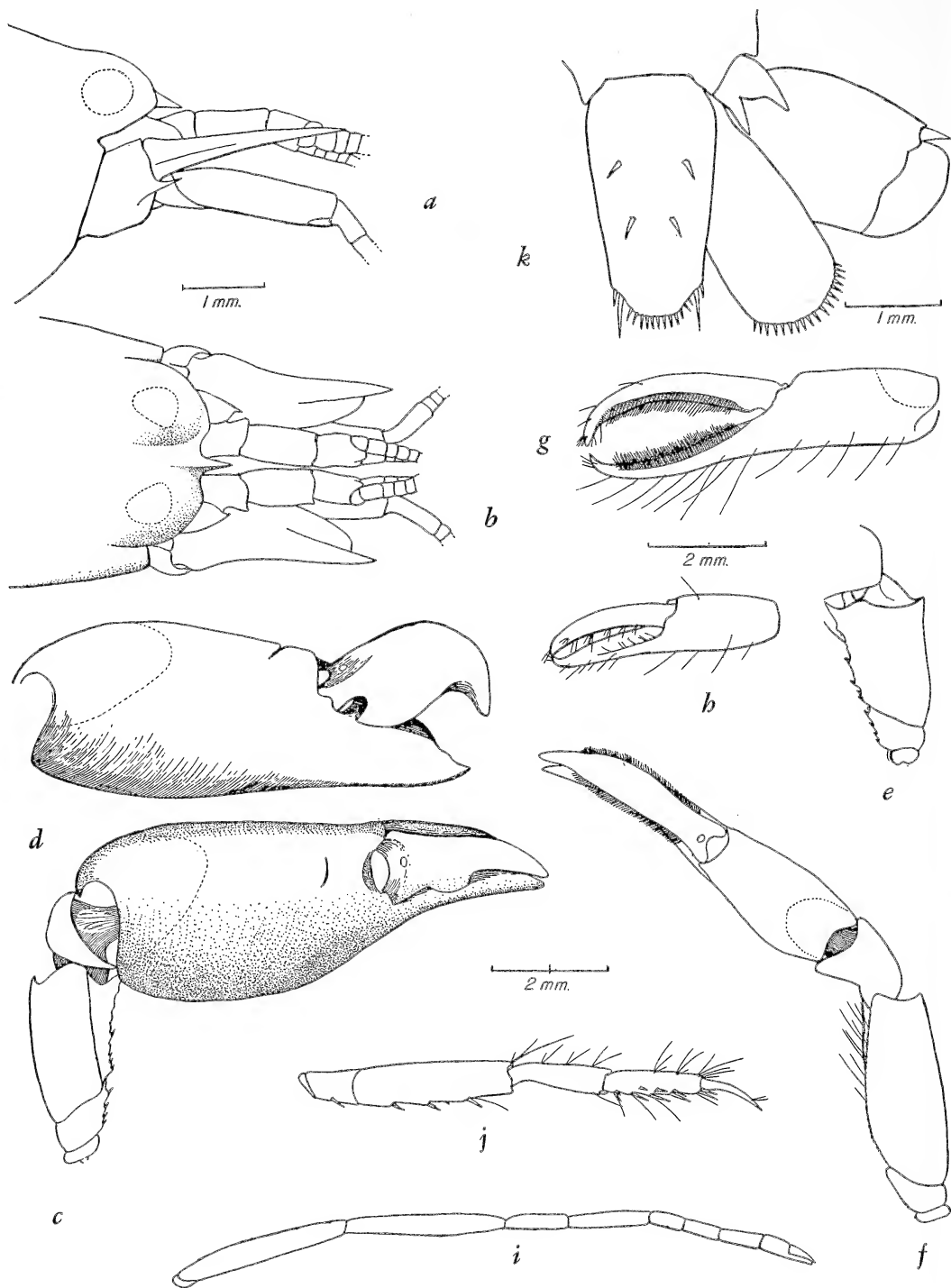


FIG. 8. *Alpheus lanceoloti* Coutière. *a, b*, Anterior regions, dorsal and lateral aspects; *c*, large cheliped; *d*, large chela, inferior aspect; *e*, large cheliped, merus, medial aspect; *f*, small cheliped, male; *g*, small chela, male, inferior aspect; *h*, small chela, female; *i*, second leg; *j*, third leg; *k*, telson and uropods.

burrows) and were almost twice that size (carapace length of 13.5 mm., total length to 32 mm.). Because of this difference in size and habitat the individuals were carefully studied to see if any specific differences occurred between them. The large specimens were found to fall well within the range of variation of the small specimens. The difference in size may be due to the difference in habitat. The difference in the depth of burrows may be due to the underlying substrate of coral in the mud flats which prevents them from excavating their burrows as deeply as they can in the pure sand of the bar.

The variation in a group of 30 specimens, including the 2 large specimens, was tabulated with the following results.

Antennular peduncle: Second article from 1.4 to 2.5 times the length of the first. Third article from 0.6 to 1.1 times the length of the first.

Scaphocerite: Usually slightly to definitely longer than both carpocerite and antennular peduncle.

Carpocerite: Usually equal or subequal in length to the antennular peduncle; in two specimens, otherwise normal, equal in length to the scaphocerite, definitely longer than antennular peduncle.

Large chela: Total length usually 1.5 to 1.8 times breadth. Fingers usually 0.4 to 0.7 length of palm.

Small chela: Palm 1.2 to 1.5 usually 1.4, times as long as broad in males, 1.1 to 1.8, usually 1.3, times as long as broad in females.³ Fingers 1.5 to 1.8, usually 1.7–1.8, times the length of palm in males, 1.4 to 1.8, usually 1.4–1.6, times length of palm in females.

Carpus, second legs: Second article 0.7 to 1.0 times length of first article, with most 0.8 times.

In one specimen a very peculiar large and small chela was noted. In this specimen the

³ In my original description of the Hawaiian specimens (1953: 128, top line, left column) there is an error for the palm was 1.5, not 2.5, times as long as broad.

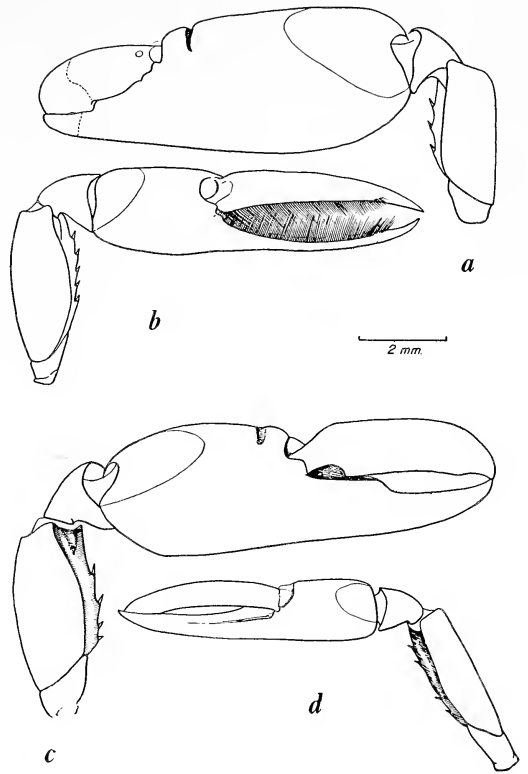


FIG. 9. *Alpheus rapax* Fabricius. Aberrant large and small chelae. *a, b*, Normal large and small chelae of male; *c, d*, aberrant large and small chelae, male. All drawn to same scale.

fingers of the large chela were 1.1 times the length of the palm, and the small chela was much thinner than usual, and not *balaeniceps*-shaped as would be expected for a male. (Fig. 9*c-d* contrasts these chelae with normal male chelae of approximately the same size.) All other characteristics are like those of the typical *A. rapax*. A similar condition has been previously reported. De Haan (1850: 178, pl. 45, fig. 4) described a new species, *A. digitalis*, separated from *A. rapax* only by the great elongation of the dactylus of the large chela. Coutière (1898*b*:248) examined the type of this species and two other species of the genus described on the basis of similar characteristics, and came to the conclusion that these were examples of regeneration where the development was arrested "à un stade

moins profondément 'évolué' que sa forme habituelle," and that *A. digitalis* was a synonym of *A. rapax*. I believe a more logical explanation of this condition may be found in the process of either the normal replacement of a lost large chela, or the rather unusual replacement of both chelae. In the normal replacement of the large chela during successive molts, the small chela grows larger and takes on the appearance of the small chela; the condition drawn may be an intermediate stage where the small chela is regenerated, and the growing large chela has its size but not its final characteristics. In the replacement of both chelae, Darby (1934: 349, *et seq.*) reported that if the timing of loss of the individual appendages was controlled, they were replaced not by normal large and small chelae but by chelae of "intermediate" development.

Finally, many, but not all, of these specimens have the inferior external margin of the merus of the small cheliped bearing extremely fine and irregular movable spines or serrations; under ordinary magnification these are not noticeable, and even under 100 diameters of magnification it could not be discerned whether these projections were articulated. This, too, was not found in the regenerating chela mentioned above.

Alpheus platyungiculatus (Banner)

Fig. 10a

Crangon platyungiculata Banner, Pacific Sci. 7(1): 130, fig. 47, 1953.

LOCALITIES: 8 specimens, the largest a 34 mm. ovigerous female, all collected from silt-buried coral heads in the intertidal mud flats behind the shoreward reefs of Kaneohe Bay, Oahu, Hawaii. Collected by A. H. Banner.

DISCUSSION: Since the collection of the five specimens upon which the original description was based, continuing search has been made for more specimens of this species. As explained in the original description, these shrimp appear to be confined to burrows in the muddy to sandy areas where the burrows can reach down through the loose substrate

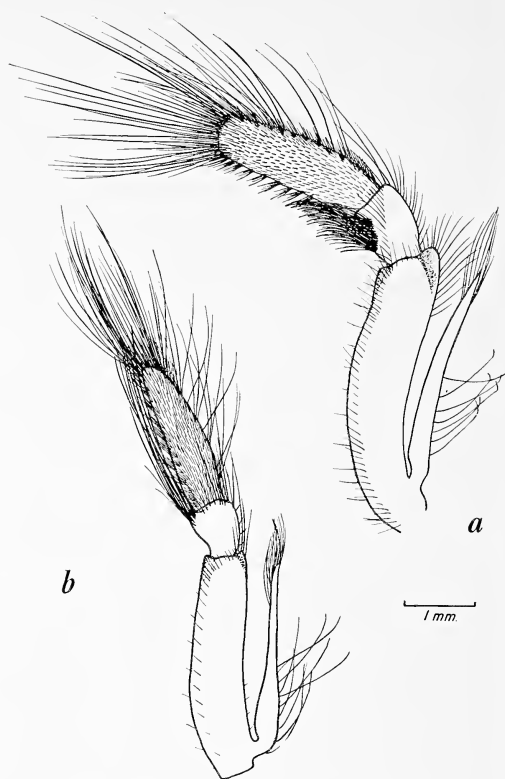


FIG. 10. *Alpheus platyungiculatus* (Banner) and *Alpheus rapax* Fabricius, third maxillipeds, medial aspects. a, *A. platyungiculatus*; b, *A. rapax*. Drawn to the same scale.

into buried coral heads. A section of inshore reef was found where the buried coral was loose and breakable; in this area these specimens were found, together with *A. rapax* (Fabricius). When only shallow holes were dug, several inches deep to the top of the imbedded coral, only *A. rapax* was found; when the imbedded coral itself was broken up from a depth of 8 inches or a foot, both *A. platyungiculatus* and *A. rapax* were found. It appeared that the *A. rapax* was probably carried down from the sides of the excavation.

In the examination of these specimens an excellent specific characteristic was found to separate this species from *A. rapax*. In *A. platyungiculatus* the middle article of the 3rd maxilliped bears a dense tuft of hairs, the longest reaching about one-third the length

of the ultimate article (Fig. 10a); in *A. rapax* this article bears a smaller group, not a tuft, of hairs, the longest of which reaches to the end of the ultimate article. In a few specimens of *A. platyunguiculatus* the tuft is not fully developed, but all lack the long setae of *A. rapax*.

Alpheus platyunguiculatus was separated from related species, especially from *A. sauvensis* de Man, on the basis of a series of minor differences in the proportions of the appendages.⁴ This series of specimens was closely examined in those points of distinction, the results of which are given below:

	TYPE SPECIMEN	RANGE OF THIS SERIES
Ratio of lengths of first two antennular articles . . .	1:1.3	1:1.4-1:2.0
Large cheliped		
Merus, length ÷ breadth . . .	2.5	2.2-2.8
Number of meral spines . . .	2	2-5
Chela, length ÷ breadth . . .	2.3	2.1-2.6
Chela, finger length ÷ palmar length	0.5	0.4-0.7
Small Cheliped		
Merus, length ÷ breadth . . .	2.6	2.0-2.8
Spines	4	2-5
Chela		
Palm, length ÷ breadth . . .	1.5 female 1.6 female	1.5 sole male 1.3-1.6 females
Finger length ÷ palmar length	1.2 male 1.2 female	1.25 male 1.25-1.50 females
Second legs, ratio of first two carpal articles	1:2.3	1:1.85-2.3
Third legs		
Merus, length ÷ breadth . . .	4.0	4.3-5.0

This range of variation destroys the value of most of the criteria set forth for the separation of *A. sauvensis* and *A. platyunguiculatus*; it also casts some doubts on the value of couplets used in de Man's key to this group. However, de Man (1908:110) specified that

⁴ In the tabulation on p. 132 of the original description the reference to the stylocerite should be to the scaphocerite, and in the comparison to *A. djeddensis* in the paragraph preceding the tabulation the text should read "small chela" instead of "third chela."

the dactyls of the third to fifth legs in his species were simple and rounded, and in all these specimens they are definitely flattened. Moreover, de Man did not describe the tuft of dense hairs on the penultimate joint of the third maxillipeds, and he did describe the terminal setae of the last article of this appendage as being over twice as long as the article, while in this species they are not even as long as the article. I believe, therefore, that this species is valid.

Edwardsii Group

Alpheus bastardi Coutière

Alpheus bouvieri var. *bastardi* Coutière, Soc. Ent. de France, Bul., 1898(5): 133, fig. 1a, 1898.

Alpheus bastardi Coutière, Fauna and Geog., Maldive and Laccadive Archipelagoes 2(4): 907, pl. 85, fig. 45, 1905.

LOCALITIES: 1 specimen, Station Y-111, Tomil Harbor, Yap Island, Caroline Archipelago, from holes in intertidal zone, rocky beach; collected by R. W. Hiatt, 1946.

DISCUSSION: This single specimen, a female, agrees perfectly with the short description and figures of Courtière. Unfortunately there is no male with which to confirm the identification.

Alpheus crassimanus Heller

Fig. 11a-e

For synonymy, see Banner, Pacific Sci. 11(2): 204, 1957.

LOCALITIES: 3 specimens from Station Y-111, collection data as above. One specimen, Station 2015, Otikaheru Island, Tuamotu Archipelago, on coral stones, under surface of muddy sand, near shore of brakish enclosed lagoon; collected by J. E. P. Morrison, July 29, 1952.

DISCUSSION: Most of the previous studies on this species have indicated that the small chela of the male not only has the dactylus subspatulate and fringed with long setae, but also that the palm bears sculpturing (see de Man, 1911, p. 417; Bate, 1888: pl. 99, fig. 2;

Coutière 1899: fig. 293). Yet the illustrations showed slight differences in the sculpturing (contrast Bate, fig. 2k to Coutière, *loc. cit.*). In contrast, the specimens reported from Hawaii (Banner, 1953: 134) did not show the sculpturing, nor did those reported from Arno

and Onotoa (Banner, 1957: 204; 1958: 168).

The three specimens from Yap indicate a possible reason for this difference. One of the specimens is an ovigerous 22 mm. female, which shows a slight trace of sculpturing in a shallow, ill-defined depression located longitudinally on the upper surface of the palm. The male of the same size has the characteristic dactylus of the adult male, yet the palm, like that of the female, bears only a slight longitudinal depression. However, in the 27 mm. male the palm is strongly sculptured. It is very roughly triangular in cross section, with the upper medial and lateral faces bearing extensive depressions that are quite well delimited (although not as definite as the corresponding depressions on the large chela); these are connected across the superior margin by a rounded, saddlelike transverse groove. On the inferolateral margin there is a strong shoulder; the inferior surface of the chela is flattened and demarked by abrupt but rounded margins; the inferolateral shoulder does not continue on the inner face.

Specimens from Hawaii were re-examined, and while the smaller males show almost no trace of the sculpturing, the largest male available (24.6 mm. long, collected in the mud flats at Heeia, Kaneohe Bay, Oahu in about plus 1 to 2 ft. tide zone) shows sculpturing similar to that of the 22 mm. Yap specimen.

Inasmuch as specimens less than 20 mm. long are often ovigerous, and inasmuch as specimens up to 44 mm. long have been reported (de Man, 1902: 880), it appears that the younger, but mature, males bear the subspatulate dactylus but may be entirely lacking in the sculpturing of the palm, while larger males develop the sculpturing. It is likely that the point of transition between the two forms may be around the body length of 25 mm., although this size may vary in different geographic areas. For example, none from Hawaii appear to reach the necessary size, while the specimen reported by de Man from Makassar (*loc. cit.*) evidently had the sculpturing at a body length of 25 mm.

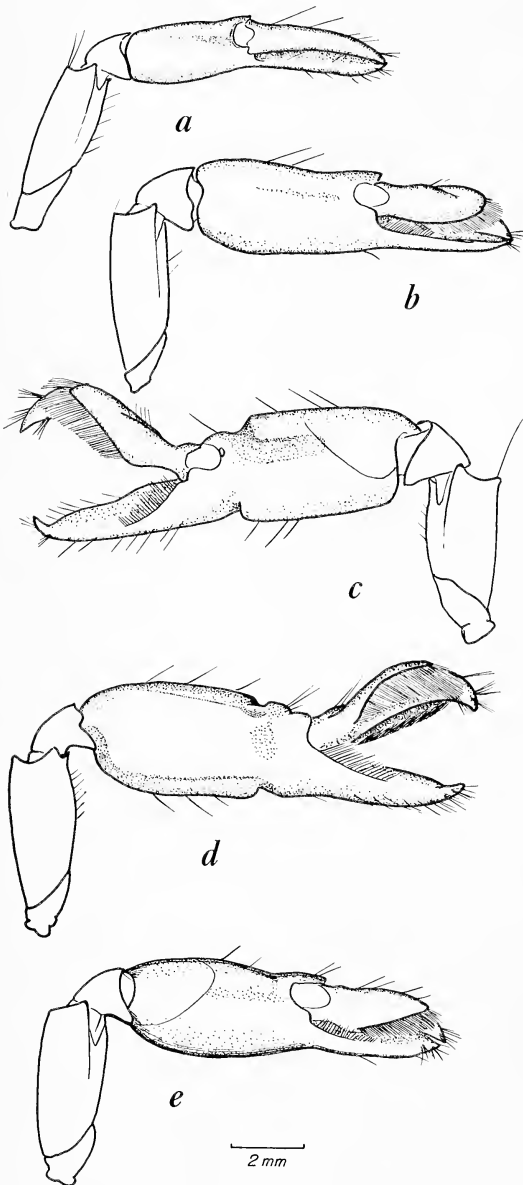


FIG. 11. *Alpheus crassimanus* Heller. Variation in form of small chelae. *a*, 22 mm. ovigerous female; *b*, 22 mm. male; *c*, 27 mm. male, lateral aspect; *d*, same, medial aspect; *e*, 24.6 mm. male. Specimens shown in *a-d* from Yap, *e*, from Hawaii; all drawn to same scale.

It may be that this is the wrong conclusion to draw from these specimens. Certainly two male specimens are not enough to prove or disprove the relationship. Only when a series of specimens of different body lengths are available can it be safely said that this is or is not a growth difference.

It should also be noted that the merus of the larger chelipeds of the 22 mm. female and the 27 mm. male bear a small acute tooth at the termination of the inferior internal margin, while the 22 mm. male, like those from Hawaii, lack this tooth.

The one specimen from the Tuamotus is a smaller male and similar in the form of the small chela to those from Hawaii.

Alpheus strenuus Dana

For synonymy, see Banner, Pacific Sci. 11(2): 204, 1957.

LOCALITY: 1 specimen, Station Y-122 from Tomil Harbor, Yap Island, Caroline Archipelago, in shallow burrows, intertidal zone; collected by R. W. Hiatt, 1946.

Alpheus pacificus Dana

For synonymy, see Banner, Pacific Sci. 10(3): 362, 1956.

LOCALITY: 2 specimens from Midway Island, Hawaiian Archipelago; collected by Y. D. P. Spicer, 1941.

Alpheus malabaricus (Fabricius) *mackayi* subsp. nov.

Fig. 12a-n

Astacus malabaricus Fabricius, System. Ent. p. 415, 1775.

Alpheus malabaricus Fabricius, Sup. Ent. System., p. 405, 1798.

Alpheus malabaricus Henderson, Zool. Soc. London, Trans., II, 5: 434, pl. 40, figs. 1-3, 1893. [Species reestablished and redescribed.]

Alpheus malabaricus de Man, Siboga Exped. 39a¹ (2): 429, 1911. [New subspecies with separate synonymy.]

Alpheus malabaricus Barnard, South African Mus., Ann., fig. 142 l-n, 1950.

Crangon species, McKay, Canad. Field-Nat. 61(4): 135, pl. 1, 1947.

TYPES: Holotype, an ovigerous female 37.8 mm. long; allotype, a male 27.7 mm. long; both collected by Donald C. G. MacKay in Wailupe fish pond, Oahu, Hawaii.

DESCRIPTION: Orbital hoods and rostrum protruding far beyond anterolateral margins of carapace. Orbital hoods inflated, high, rounded; rostrum short, not reaching beyond anterior margin of orbital hoods, carina short, rounded, not reaching to middle of orbital hoods; interorbital area behind termination of carina flat, anteriorly abruptly demarked from convexity of orbital hoods.

Antennular peduncle with second article about 2.4 times as long as broad, about twice length of visible portion of first article and not quite 3 times length of third article. First article terminating in high setose crest on superior margin; basicerite broad, flat, with small anterior tooth not reaching to end of first article. Basicerite with acute lateral tooth. Scaphocerite reaching to beyond end of antennular peduncle, squamous portion broad, slightly narrowing distally, and exceeded by the lateral spine; lateral spine curved inward at tip. Carpocerite reaching to end of lateral spine of scaphocerite.

Large chela of male and female of similar proportions, and almost identical size in spite of difference in body lengths. Merus with outer face 1.7 times as long as broad; superior margin ending distally in slight projection; inferior internal margin terminating in strong acute tooth, otherwise unarmed. Carpus of usual form. Large chela 2.4 times as long as maximum width, tapering towards fingers, with maximum width of fingers 0.66 as wide as palm; fingers strong, occupying the distal 0.3 of chela (about half as long as palm). Palm with rounded depressed areas on either face, both roughly triangular; superior margin of palm ending in shoulder overhanging shallow, rounded groove that connects de-

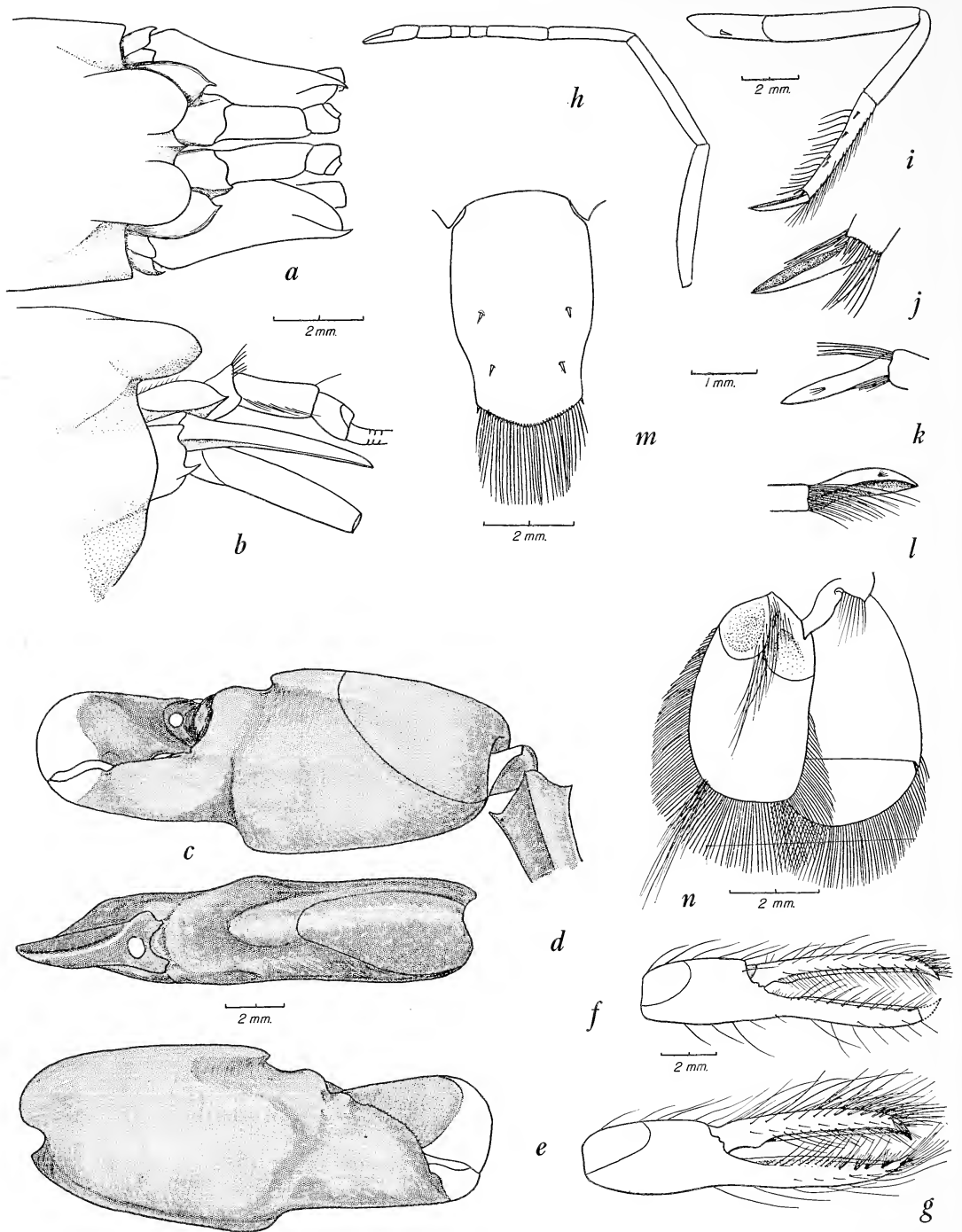


FIG. 12. *Alpheus malabaricus* (Fabricius) *mackayi* subsp. nov. *a, b*, Anterior regions, superior and lateral aspects, setae not shown; *c, d, e*, large chela, lateral, superior and medial aspects; *f*, small chela, male; *g*, small chela, female; *b*, second leg; *i*, third leg; *j, k, l*, dactylus, third leg, anterior, superior and posterior aspects; *m*, telson; *n*, uropod, showing proximal concavities.

pressed areas on either face; inferior margin terminating, almost right angled, in strong shoulder on outer face.

Small chelae also similar in both sexes. Merus unarmed on inferior internal margin. Palm slender, rounded, without sculpturing. Fingers 1.4 times length of palm in female, 1.7 times length of palm in male, straight except for slightly hooked tips, both movable and fixed fingers rounded on outer portion of opposing faces, bearing a sharp cutting edge on inner margin; dactylus bearing a low rounded tooth proximal to cutting edge.

Carpal articles of second legs with the ratio: 10:7.6:2.0:2.3:4.3; chela, in same ratio, 1.7.

Third and fourth legs with ischium bearing weak spine; merus 6 times as long as broad, unarmed; carpus 0.6 as long as merus, without distal teeth or projections; propodus 0.75 as long as merus, bearing 6 feeble spines and numerous long setae; dactylus 0.3 as long as merus, strongly curved in superior view, roughly triangular in cross section, with both superior faces somewhat convex, inferior face broad and flattened. Fifth leg with brush on propodus strongly developed.

Telson 2.4 times as long as posterior margin is broad, 1.3 times as broad anteriorly as posteriorly; in dorsal view, anterior 0.6 with slightly convex margins, without taper, then tapering abruptly to posterior portion with parallel margins; in lateral view, middle of lateral margin strongly depressed; tip strongly arcuate. Dorsal spinules feeble; inner pair of posterolateral spinules so slender that they can be confused with terminal setae; terminal setae numerous and heavy; posterior margin also armed with series of minute spinules. Outer uropod with spine on shoulder slight. Inner uropod with a shallow but well-demarcated basin to accommodate depressed lateral margin of telson.

DISCUSSION: These specimens agree very well with the species *A. malabaricus* as re-described by Henderson, and with the subspecies described by de Man (*loc. cit.*), except in the length of the rostrum and the relative

proportions of the small chela; apparently all are similar in form of the dactylus of the third legs, in the general shape of the large chela, etc. However, all specimens of *A. malabaricus* except that described and figured by Barnard from South Africa (*loc. cit.*), have longer rostrums, and in none are the fingers as short when compared to the palm. Both reported subspecies have fingers on the small chela that are gaping instead of straight. The habitat of these specimens—the thick soft mud of a fish pond—and those reported by Henderson from India are also similar.

Because of their great similarities it is not logical to consider these specimens as other than a geographically isolated subspecies; it may be that when other specimens are found between Hawaii and India intergrading specimens will be found.

The type locality, Wailupe fish pond, no longer exists. It was filled in and is now used for homesites, the area being called Wailupe Peninsula. Presumably the subspecies exists elsewhere in the Hawaiian Islands, but it has not yet been found in other areas.

THUNOR Armstrong

Thunor microscaphis sp. nov.

Fig. 13*a-i*

Thunor sp. Banner, Pacific Sci. 10(3): 367, fig. 23*a-e*, 1956.

TYPE SPECIMEN: A 9.5 mm. male from Station 827, Likiep Atoll, Marshall Islands, USNM 194726; collected by S. V. MacNeil.

DESCRIPTION: Specimen with cephalothorax preponderant, abdomen reduced, only slightly more than equal in length to carapace.

Anterior carapace distorted in specimen with folds and wrinkles permitting the eyes to be partially exposed. Rostrum obtuse, short, not reaching beyond anterior margin of orbital hoods, and bearing low, rounded carina reaching to slightly past middle of orbital hoods. Orbital hoods large, inflated, evenly rounded anteriorly.

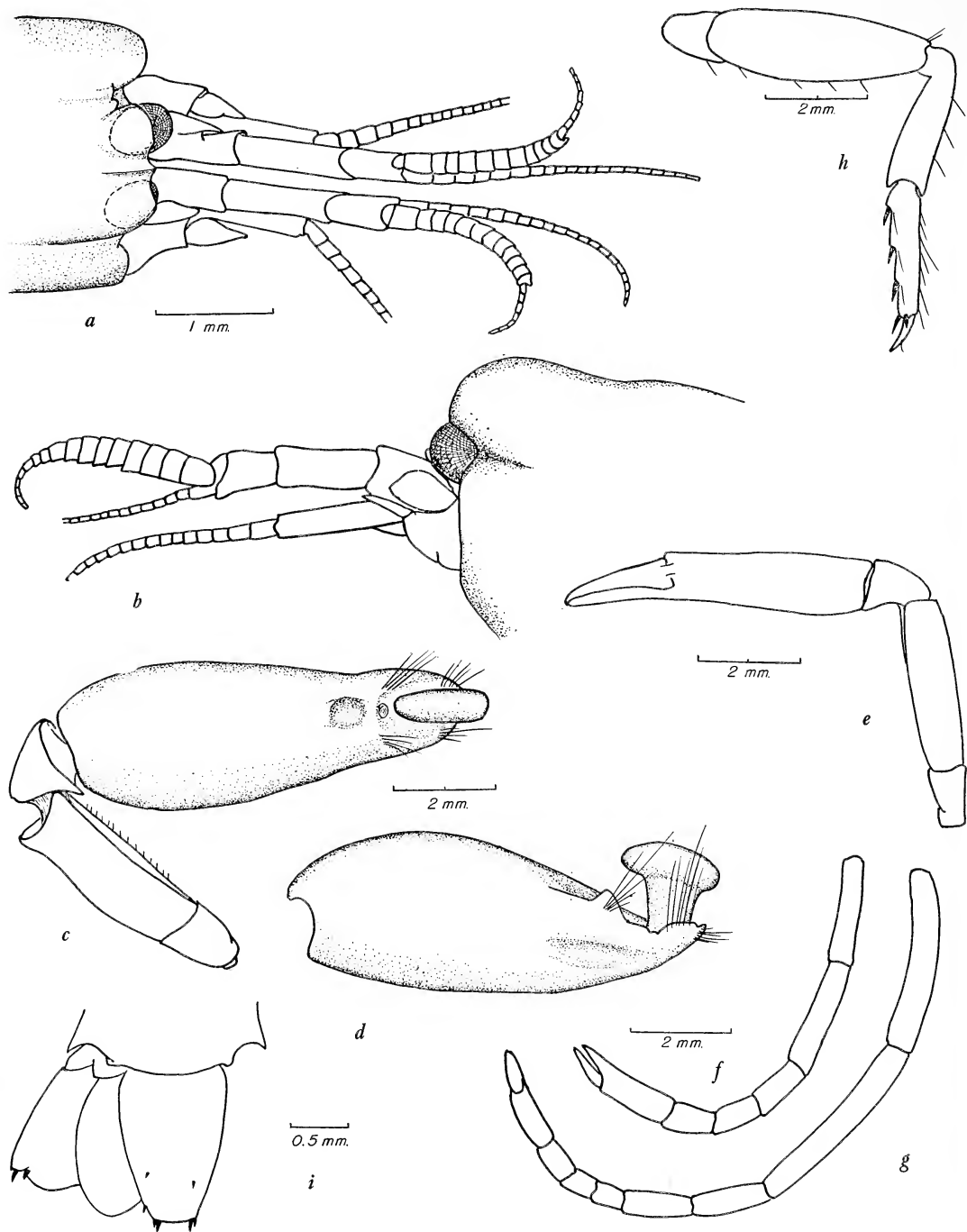


FIG. 13. *Thunor microscephis* sp. nov. *a*, *b*, Anterior regions, superior and lateral aspects; *c*, *d*, large cheliped; *e*, small cheliped; *f*, second leg, left, carpus to dactylus; *g*, second leg, right, ischium to dactylus; *h*, third leg; *i*, telson and uropods.

Antennular peduncle with second article 1.7 times length of first article; third article subequal to first; second article 3.5 times as long as broad. Stylocerite assymmetrically developed, with that on left almost rounded anteriorly and reaching about 0.7 the length of first article; that on right anterior irregular (but rounded) reaching only a little more than 0.5 length of first article.

Scaphocerite reduced to bract which reaches on left to end, on right to slightly beyond end of first antennular article. Basicerite unarmed. Carpocerite reaching 0.6 length of second antennular article. Antennal flagellum elongate.

Large chela 2.7 times as long as broad, with fingers occupying the distal 0.2; margins mostly regular and strongly tapering. Distally chela with a deep pit proximal to articulation of dactylus to accommodate protruding margin of dactylus; lateral and proximal to articulation of dactylus is located a shallow depression with poorly defined margins. Fixed finger very short. Dactylus hammer-shaped, with distal margin swollen and rounded, proximal portion broad and thin. Carpus of usual form. Merus about 0.4 length of chela, with outer face 3.5 times as long as broad; distally unarmed; inferior internal and external margins sharp; inferior internal margin bearing 13 slight and feeble spines.

Small chela 5 times as long as broad, with the simple fingers occupying the distal 0.35. Merus 0.55 length of chela, 0.25 as long as broad, unarmed.

Second legs assymetrical, with left as long as body, and right a little over half as long. Carpal articles of right legs with ratio: 10:9:4:5:6; left leg with first article slightly shorter, relatively.

Third leg with ischium unarmed; merus unarmed, 3.2 times as long as broad; carpus with distal angles rounded; propodus bearing 3 single inferior spines and paired spines distally; dactylus simple and curved.

Outer uropod bearing a single lateral spine without articulation, inner unarmed. Telson

3.5 times as long as tip is broad, 1.8 times as broad anteriorly as posteriorly; sides slightly curved. Dorsal spines abnormal, with anterior left about 0.7 length posterior from articulation, posterior left located on margin; anterior right posterior to corresponding left, posterior right missing.

DISCUSSION: This single specimen appears to be of the same species as the two fragmentary specimens previously described but not named from Saipan (Banner, *loc. cit.*). A number of slight differences are found between the two forms: the length of the interorbital carina, the proportion of the articles of the antennular peduncle, the ratio of the carpal articles of the second leg (only one second leg remained on the two Saipan specimens), the armature of the propodus of the third legs, and the proportions and armature of the telson. These differences, most of them in parts that have been found to be variable in *T. idiocheles* (Courtière) and *T. ratbbunae* (Schmitt), as well as in related species of the *Obesomanus* group of *Alpheus*, are probably without significance. Another difference between the two lies in the development of the antennal peduncle: in the male specimen from Saipan the scaphocerite reaches to the middle of the second article of the antennular peduncle, and the carpocerite reaches to the end of the same article, while in the female from Saipan the development of these is shorter and more degenerate than that found in the male. As this male is similar to the Saipan female, the difference is obviously not sexual dimorphism, but may show the variability of the development of this appendage; however, the two Saipan specimens may be of different species. A final difference is found in the merus of the large chela, which in this specimen bears 13 feeble spines, and in the Saipan specimen bears a few bristles in corresponding locations. Opposed to these slight and seemingly insignificant differences are many and great similarities, as can best be seen by comparing the figures of the two forms.

This species plainly belongs to *Thunor* if

that genus is to be accepted, for it lacks the anal tubercles and the articulation of the outer uropod; in addition the specimens lack the ocular beak and in two of the three specimens the cardiac notch is lacking.

Within the genus, *T. microscaphis* is best distinguished from *T. idiocheles* by the form of the large chela, for in this species the dactylus is formed like a two-headed hammer, and the superior surface of the chela bears a marked depression to accommodate the superior projection of the dactylus when that article is flexed. In *T. idiocheles*, the dactylus of the large chela lacks this superior projection and there is no corresponding depression of the palm. From *T. rathbunae* this species is distinguished by the presence of a small rostrum as well as by the form of the large chela and the relatively greater length of the small chela.

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Botanical Novelties on the Island of Niihau, Hawaiian Islands
Hawaiian Plant Studies 25¹

HAROLD ST. JOHN²

IN 1947 and again in 1949 the writer was so fortunate as to be able to make botanical explorations on the island of Niihau, a remote, high island of the principal group of Hawaiian Islands. A lengthy account of its flora is in preparation. It seems desirable now to put on record the new botanical discoveries made on that island or in connection with the investigation of its flora.

The holotypes of the new species are in the Bernice P. Bishop Museum, Honolulu, (BISH), unless otherwise specified.

GRAMINEAE

Panicum Heupueo sp. nov. (subgenus
Panicum)

Fig. 1

NOM. VERN.: "heu pueo" (= fine hairs on the owl); also called, "hakonakona," perhaps in error, as that is the established name of *P. torridum* Gaud.

DIAGNOSIS HOLOTYPI: Breviter annuum erectum 16–34 cm. altum plerumque e basi

¹This is the twenty-fifth of a series of papers designed to present descriptions, revisions, and records of Hawaiian plants. The preceding papers have been published in B. P. Bishop Mus., Occ. Papers 10(4), 1933; 10(12), 1934; 11(14), 1935; 12(8), 1936; 14(8), 1938; 15(1), 1939; 15(2), 1939; 15(22), 1940; 15(28), 1940; 17(12), 1943; Calif. Acad. Sci., Proc. IV, 25(16), 1946; Torrey Bot. Club, Bul. 72: 22–30, 1945; Lloydia 7: 265–274, 1944; Pacific Sci. 1(1): 5–20, 1947; Brittonia 6(4): 431–499, 1949; Gray Herb., Contrib. 165: 39–42, 1947; Pacific Sci. 3(4): 296–301, 1949; 4(4): 339–345, 1950; B. P. Bishop Mus., Occ. Papers 20(6), 1950; Pacific Sci. 6(1): 30–34, 1952; 6(3): 213–255, 1952; 8(2): 140–146, 1954; Polynesian Soc., Jour. 63(1): 27–34, 1954; B. P. Bishop Mus., Occ. Papers 21(15), 1955; Brussels Jard. Bot. de l'État Bul. 27(1): 49–54, fig. 2, 1957.

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unicauliferum sed supra basem culmis bifurcatis cum ramis subaequalibus, internodis superioribus villosis inferioribus glabris, internodis plantarum parvarum quam vaginam brevioribus sed plantarum magnarum ad bis longioribus quam vaginam, vaginis 15–29 mm. longis valde nervosis pustulato-albiciliatis, pilis 0.2–0.4 mm. longis, laminis 4–10 cm. longis 2–4 mm. latis planis linearibus acutis albo-villosis in ambis lateris, paniculis 2–8 cm. longis 5–30 mm. latis densis in culmis omnibus terminalibus in basi vaginatis, ramulis adscendentibus valde adpressis sed post florendis ramulis superioribus paene divergentibus, rhachide ad basim sparse piloso sed ad apicem scabro, ramulis scabris, spiculis 1.2–1.5 mm. longis elliptico-ovoideis acutis glabris pallidis scariosis viridi-nervosis, gluma prima 1.9 mm. longa 1.2 mm. lata 3-nervata lanceo-ovata, gluma secunda 1.7 mm. longa 1.4 mm. lata late elliptica acuta 7-nervata, lemma sterilis 1.8 mm. longa 1.1 mm. lata late elliptica acuta, palea sterilis 1.1 mm. longa 0.5 mm. lata elliptica membranacea in basi involuta, lemma fertilis 0.9–1 mm. longa 0.6 mm. lata ovata cartilaginea lucida alba deinde brunneo-plumbaginea indistincte 5-nervata concava marginibus involutis, palea subconcava clausa 3-nervata, antheris 0.4 mm. longis oblongis, stigma dendritica.

DESCRIPTION OF ALL SPECIMENS: Short-lived annual, erect, 10–53 cm. tall, mostly 1-stemmed from the base, but above it the culms repeatedly bifurcate, with subequal branches; internodes villous on upper part, glabrous on lower; on small plants the internodes shorter than the sheaths but on larger ones the internodes as long as twice the length of the sheaths; leaf sheaths 15–48 mm. long, strongly nerved, pustulate white villous;

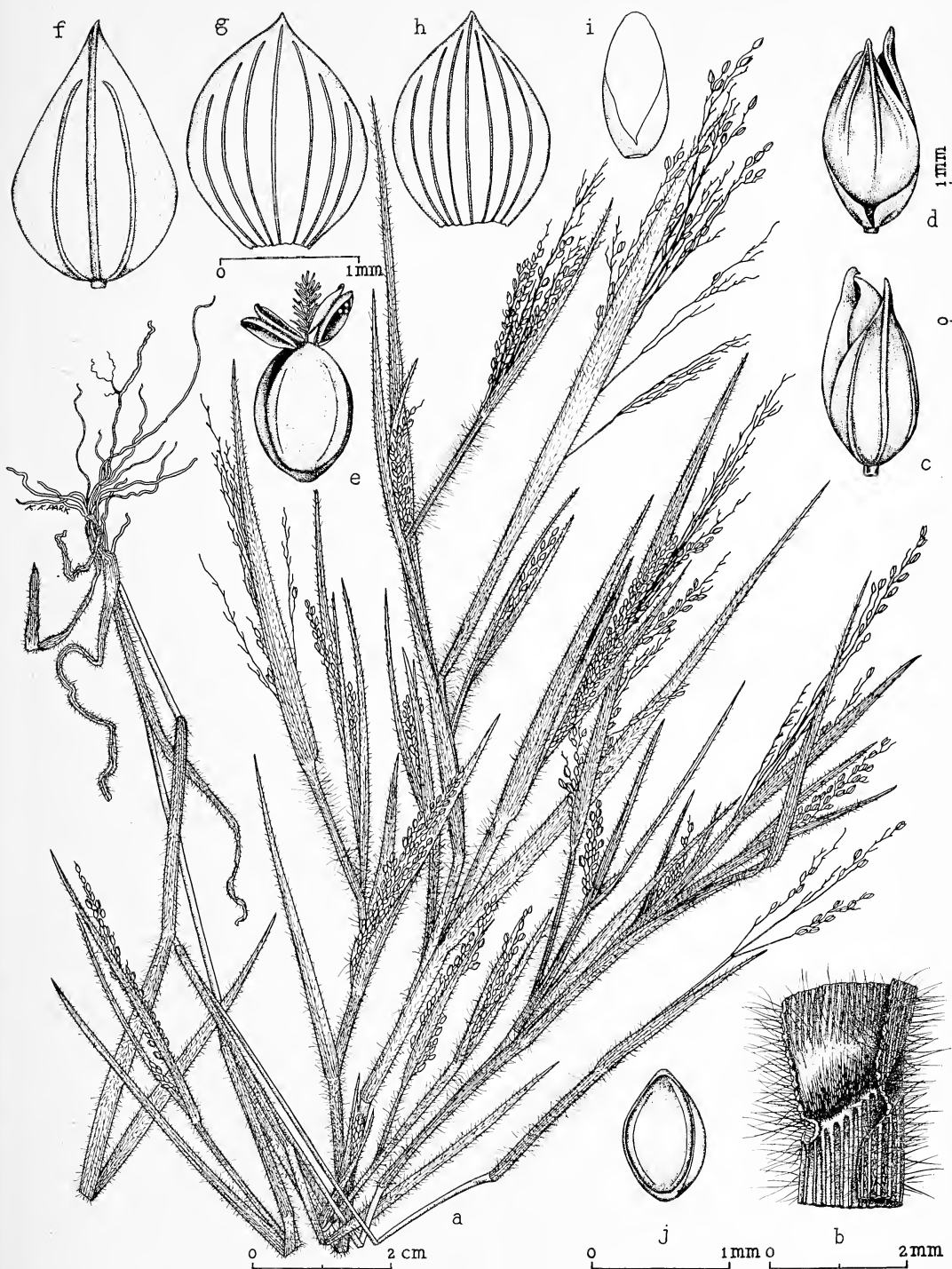


FIG. 1. *Panicum Heupueo*, from the holotype: *a*, habit $\times 1$; *b*, blade and sheath $\times 10$; *c*, spikelet $\times 20$; *d*, spikelet $\times 20$; *e*, floret $\times 20$; *f*, first glume, dorsal view, $\times 20$; *g*, second glume, dorsal view, $\times 20$; *h*, sterile lemma, dorsal view, $\times 20$; *i*, sterile palea, ventral view, $\times 20$.

ligule a narrow membrane, pilosulous ciliate with hairs 0.2–0.4 mm. long; blades 3–13 cm. long, 2–6 mm. wide, flat, linear, acute, white villous on both sides; panicles 2–15 cm. long, 3–50 mm. wide, dense, terminal on all branches, enfolded at base by the leaf blade or sheath, the ascending branches closely appressed, but after anthesis the upper ones slightly diverging; the rhachis sparsely pilosulous towards the base, but towards the apex scabrous; branchlets scabrous; spikelets 1.2–1.5 mm. long, elliptic ovoid, acute, glabrous, pale scarious, with greenish nerves; first glume 1.9 mm. long, 1.2 mm. wide, 3-nerved, lance-ovate; second glume 1.7 mm. long, 1.4 mm. wide, broadly elliptic, acute, 7-nerved; sterile lemma 1.8 mm. long, 1.1 mm. wide, broadly elliptic, acute; sterile palea present, 1.1 mm. long, 0.5 mm. wide, elliptic, membranous, enfolded at base; fertile lemma 0.9–1 mm. long, 0.6 mm. wide, ovate, cartilaginous, shining, white, then brownish lead-colored, faintly 5-nerved, concave, the margins inrolled; palea gently concave, enclosed, 3-nerved; anthers 0.4 mm. long, oblong; stigma dendritic.

HOLOTYPE: Niihau, Kii, between basalt rocks, on rocky knoll, 100 ft. alt., April 2, 1949, *H. St. John* 23,666 (BISH).

SPECIMENS EXAMINED: Kii, with same data, *St. John* 23,665; 23,670.

The new species is a member of the subgenus *Panicum* (formerly *Eupanicum*) but it is not here assigned to a section. Neither the treatment of the genus in North America by Hitchcock and Chase nor the world treatment by Pilger in the second edition of Engler's "Pflanzenfamilien" has any section into which this species will fit. It comes closest to agreeing with the characters of section *Capillaria*, but it disagrees in several characters.

The most closely related species is *P. Fauriei* Hitchc. of the islands of Hawaii, Maui, Molokai, and Oahu. This species differs in having the sheaths appressed puberulous, the ligule a membrane with pilose hairs 1 mm. long; the blades 0.8–3.5 mm. wide,

mostly involute, and below appressed puberulous; the panicle rhachis and branchlets ascending villosulous; the spikelets 1.8–2.1 mm. long, and the fertile lemma 1.2 mm. long. In contrast, *P. Heupueo* is distinguished by having the sheaths villous; the ligule a very narrow membrane pilosulous ciliate with hairs 0.2–0.4 mm. long; blades 2–6 mm. wide, flat, villous above and below; panicle with the rhachis below sparsely pilosulous, above scabrous, the branchlets scabrous; the spikelets 1.2–1.5 mm. long; and the fertile lemma 0.9 mm. long.

Panicum radiatius nom. nov.

Paspalidium radiatum Vickery, N. S. Wales Natl. Herb., Contr. 1(6): 332–334, 1950; non *Panicum radiatum* R. Br., Prodr. Fl. Nov. Holl. 192, 1810 which is *Digitaria tonsa* D. K. Hughes, Kew Bul. 313, 1923.

The genus *Paspalidium* was described in the *Flora of Tropical Africa*, vol. 9, by Stapf. It was published in 1917 in the key only, then in 1920 a description of the genus and of the two species followed. The genus was validly published, but not contrasted with the related genera or discussed. It now has been accepted and enlarged, especially in Australia, but little has been added to substantiate its generic status. The spikelets are biseriate on 1-sided lateral spikes, but in detail are like those of species in the enormous genus *Panicum*. A revision of the Australian species has been announced by S. T. Blake, so a disposition of the other species should await that treatment. However, the structure of the spikelet agrees well with that of *Panicum* and the inflorescence seems to show a reduced state derived from a panicle, so it is here maintained that the best assignment for the species introduced to Hawaii is in the genus *Panicum*. A new name is proposed because of the existence of an earlier homonym in *Panicum*.

Niihau: Short grass that appeared on its own on Niihau, November 1, 1939, *G. C. Munro*; Kiekie, 50 ft. alt., cultivated pasture

grass, *St. John* 23,661. The Munro collection had once been determined as *Paspalidium caespitosum* C. E. Hubbard.

CYPERACEAE

Eleocharis calva Torr. var. *australis* (Nees) comb. nov.

Fig. 2

E. palustris (L.) R. & S. var. *australis* Nees, Acad. Caes. Leop. Nat. Cur., Nov. Act. 19, Suppl. 1: 96, 1843 (as *E. palustris* R. Br. β *Australis* Nees).

Scirpus nudissimus Steud., Soc. Linn. de Normandie, Bull. II, 9: 280, 1875, *synon. nov.*

E. palustris sensu Hbd., Fl. Haw. Is. 474, 1888, and of C. N. Forbes, B. P. Bishop Mus., Occ. Papers 7(5): 48, 1920; not of (L.) R. & S.

E. calva sensu Fernald & Brackett as to Oahu plant, Rhodora 31: 68–70, 1929; not of Torr.

E. macrostachya sensu Svenson as to Oahu plants, Rhodora 41: 57, 1939; not of Britt. NOM. VERN.: "kohekohe."

Niihau: Loe Lake, 2 miles N. of Puuwai, marshy border of temporary flood-water lake, 10 ft. alt., plants up to 12 dm. tall, basal sheaths red, *St. John* 23,598.

Hillebrand (1888: 474) apparently did not encounter this plant in the Hawaiian Islands, but included it doubtfully in his *Flora of the Hawaiian Islands*, upon the report of Meyen's collection by Kunth (1843: 96). It seems strange that Hillebrand did not find this species. Quite a number of collections of it are now known and some of them were previous to Hillebrand's time in the Islands (1850–71). The collections are as follows:

1825: James Macrae (Herb. Lindley)

1831: Maio, in Oahu insula, F. J. F. Meyen (Vienna Herb.)

1842: Oahu, U. S. Exploring Expedition (Gray Herb.)

1920: Oahu, Kaimuki, creeping in the mud, March 26, 1916, C. N. Forbes 2360.0 (Bishop Mus.)

1927: Oahu, O. Degener 9,002 (N. Y.)

1949: Niihau, Puuwai, H. St. John 23,598 (Bishop Mus.)

1950: Niihau, "tohotohe," September, Henry Judd (Bishop Mus.)

In 1929 Fernald and Brackett (p. 68) identified this with *Eleocharis calva* Torr., occurring from Quebec to Alberta and Washington, south to Florida, Oklahoma, and Mexico, and also in Manchuria. It is close to this species because of the close, red sheaths, the linear-lanceoloid spikes with a single basal sterile scale. This primarily American species has the plant loosely stoloniferous to slightly caespitose; culms 1–6.5 dm. tall, 0.5–1.5 mm. in diameter; lower and median fertile scales 1.8–3 mm. long, oblong to ovate, reddish to pale brown; anthers 1.3–1.7 mm. long; achenes 1–1.4 mm. long, 0.7–1 mm. broad; style base 0.2–0.4 mm. broad at base, conical; perianth wanting or of 1–4 delicate bristles usually equaling or slightly exceeding the style base. The local *E. calva* var. *australis* has the plant short stoloniferous but densely caespitose in habit; culms 1–12 dm. tall, 1–3 mm. in diameter; lower and median fertile scales 3–4 mm. long, lance-ovate, castaneous between the hyaline margin and the pale midrib; anther 2 mm. long; achenes 1.7–1.9 mm. long, 1.2–1.3 mm. wide; style base 0.4–0.6 mm. wide, deltoid-ovoid; perianth of 4 stout bristles, retrorse barbellate and nearly or fully as long as the achene. The Hawaiian plant seems clearly separable from *E. calva*.

In 1939 Svenson in his monograph reduced *Scirpus nudissimus* Steud. He called it a "nomen subnudum" (Rhodora 41: 57, 1939) but there is no such designation in our present International Code. There is the term "nomen nudum" for names published without any description. Steudel's description was as follows:

"5. Le *S. nudissimus*, Steud., se compose d'une tige terminée par un épi grêle, d'ou son nom spécifique; mais Steudel ajoute: nisi forte *Eleocharis palustris*, var?" This original publication included two items of descrip-

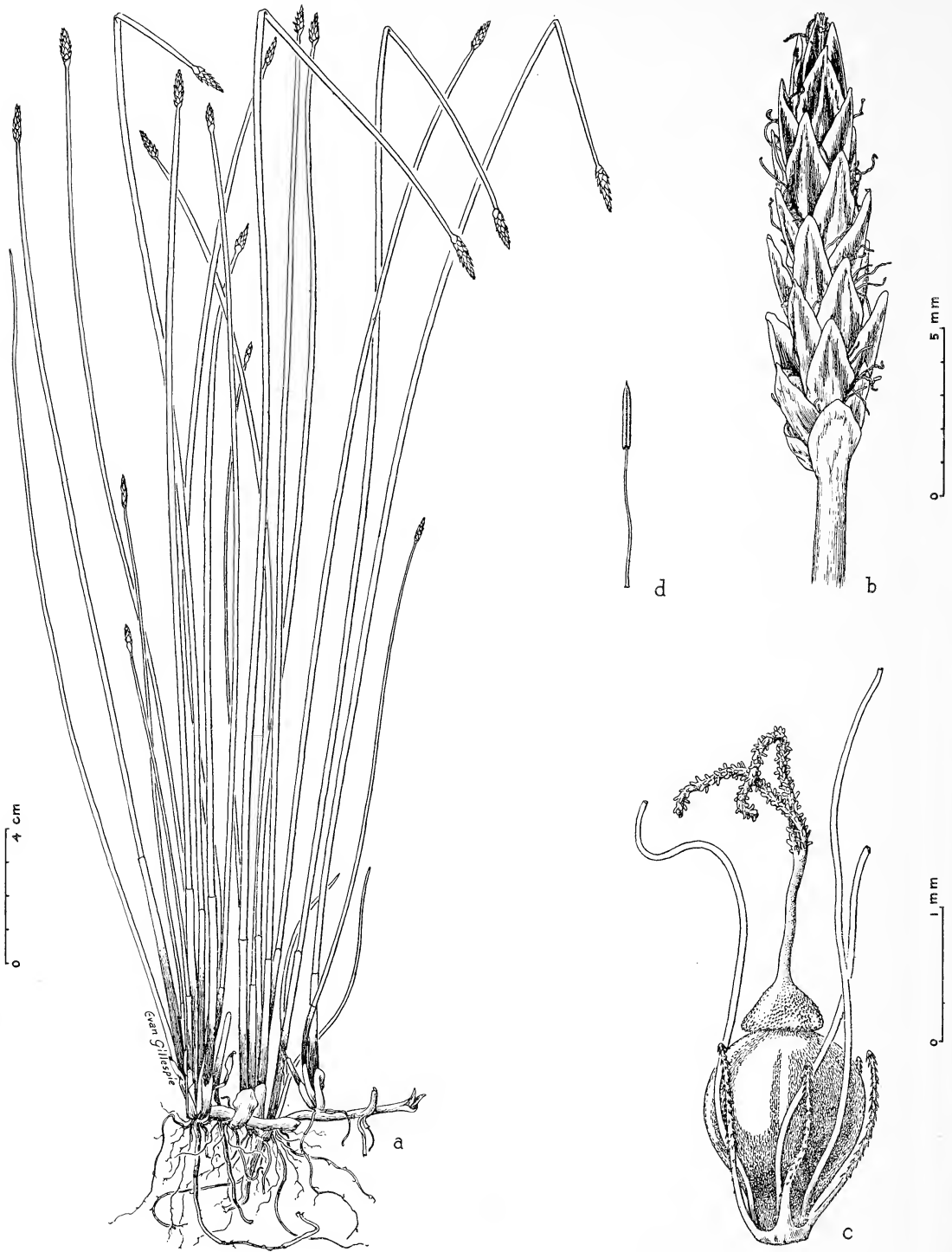


FIG. 2. *Eleocharis calva* var. *australis*, from St. John 23,598: *a*, habit $\times \frac{1}{2}$; *b*, spike $\times 5$; *c*, achene $\times 20$; *d*, stamen $\times 5$.

tion: spikelet slender; plant appearing like a variety of *Eleocharis palustris*. If this plant (see Fig. 2) is compared with *E. palustris* (see Rhodora 31: pl. 181, figs. 1-4), it will be seen that the spikelets are much more slender.

Svenson also refers to *E. macrostachya* the Oahu plant described from the collection by Meyen. This was published as: "E. palustris R. Br. (β Australis Nees squamis spicae acutiusculis albis tenuibus nervo medio pallide viridi litura cuspidato fusco cincto.)."

In Oahu insula, Maio 1831, Meyen; ex eadem insula Macrae in Herb. Lindl."

Both *Scirpus nudissimus* Steud. and *Eleocharis palustris* var. *australis* were referred by Svenson to *E. macrostachya* Britt. This species, occurring from Illinois to British Columbia, south to Louisiana, California, and Michigan, is recognizable by having culms compressed, soft, very flat after pressure; lowest sterile scales 2-3; achenes averaging 1 mm. wide; bristles 5-6 (or -8, or 0) very delicate, often overtopping the achene and style base, the teeth slender. On the other hand, the Hawaiian *E. palustris* var. *australis* has the culm terete, soft, little flattened under pressure; lowest sterile scale 1, encircling the base $\frac{3}{4}$ way; achenes 1.2-1.3 mm. wide; the 4 bristles stout, nearly or quite equalling the achene body, with stout retrorse teeth.

It is also related to *E. palustris* (L.) R. & S., and more closely to its var. *major* Sonder which occurs from Labrador to British Columbia and south to Pennsylvania, Iowa, Wyoming, and California. This var. *major* has the sheaths 3-30 cm. long, comparatively loose; culms 5-19 dm. tall; spikelets 0.7-2.6 cm. long, 2.5-7 mm. thick, lanceolate to ovoid, $\frac{1}{2}$ as wide as long; basal scales 2-3; lower and median fertile scales 3.2-5.5 mm. long; bristles 4, slender, commonly reaching to the middle of the style base; style base lanceoloid-conic, much higher than broad. The Hawaiian var. *australis* has the sheaths 3-8 cm. long, close; culms 1-12 dm. tall; spikelets 1.3-1.7 mm. long, 2.5-3.5 mm. thick, narrowly linear-lanceoloid, $\frac{1}{4}$ as wide

as long; basal scale 1; lower and median fertile scales 3-4 mm. long; the 4 bristles stout, nearly or quite equalling the achene; style base deltoid-ovoid, as wide as long. In any other group, this isolated Hawaiian kind, having significant characters that separate it in the keys from the American and Eurasian species, in this instance from *E. palustris*, *E. calva*, and *E. macrostachya*, and even by its truncate, indurate, apiculate sheaths from subseries *Palustres*, a natural conclusion would be that it too should be classed as a species. However, consideration should be given to the commentary on the subseries *Palustres* by the recent monographer of the genus, H. K. Svenson (1939: 55, 59).

In the eastern United States . . . the entities are clear; in Europe and in the western United States, the situation seems to be chaotic. The *Palustres*, chiefly of holarctic distribution, have probably spread out in post-glacial time, achieving a variation comparable with that of *Rubus* or *Crataegus*. In Western United States, with its natural barriers and diversified terrain, numerous intergrading geographical races have developed, the most noteworthy of which I have illustrated by drawings and photographs. It would be perfectly easy to describe more species in this group, adding to the plethora of intangible species, but I have made little or no change. In my mind, there is even some question whether more than a single good species of the *Palustris* group exists in northwestern Europe, and whether in Europe these are not environmental responses to sea-strand, meadow, and bog, which parallel the variation of *E. palustris* in western America. Although I have spent an inordinate amount of time on this group and have seen a vast amount of material, the problems do not appear to be close to solution. . . . The *Palustris* group appears to be equally complex in Asia. . . .

He gives many details of the variability or plasticity of *E. palustris* and its relatives in Europe.

Realizing these facts, it does not appear wise to give the Hawaiian *Eleocharis* specific rank, even though there is a name available

for transfer. The plant is related to *E. palustris*, but that natural group has the spikelet with 2-3 sterile basal scales. Since the Hawaiian plant has, like *E. calva*, the single basal scale, the similar linear-lanceoloid spikes, the similar shaped achene and style base, and prominent red basal sheaths, it appears to be most closely related to that species. The differences between the two are tabulated a few pages back. When evaluated, these morphological differences are of some significance, but in the subseries *Palustres* with its variable or merging taxa distributed well around the northern hemisphere, the best method of classification seems the ultraconservative. It is concluded that the Hawaiian plant is a local, endemic variety, allied to *E. calva*, and best placed as a variety of it. Hence, the combination for it as a variety of that species is here made.

Now that abundant and complete material of this plant from Oahu and Niihau is at hand, it is possible to tabulate its characters, and re-evaluate its distinctions. Knowing the high endemism in the Hawaiian flora (92 per cent or more), one could easily take the view that with any clear differences, this plant could well be classed as an endemic Hawaiian species. It was collected as early as 1825 when there were few adventives present. It has been collected five times since then. Though it is not common, it must be remembered that it is a lowland plant of fresh marshy habitats. Most of the collections on Oahu were in present or former cultivated lands—taro patches. It was thus a weed in the taro patch. Most weeds are adventives, but in wet cultivations the percentage of native plants persisting in the taro patch, cranberry bog, or rice paddy is much higher than in dry land agricultural fields. On Niihau it was not in agricultural land, but by the edge of a small lake on the coastal plain bordering the mountainous upland. Flood waters make a lake that may last for several months, then for the remainder of the year the spot is parched and completely dry and alkaline. There is no taro

cultivation anywhere in the vicinity. From the habitat and the manner of its occurrence, it seemed to the collector to be a native plant on Niihau. It may also be a native of Oahu, persisting only in existing or former taro patches. On a small island like Oahu, with a large population depending on taro as the basic crop, nearly all natural fresh ponds and swamps were converted into taro patches. Also, almost every lowland alluvial spot to which irrigation water could be conducted, was made into a taro patch. Thus, even in aboriginal times, the swampy habitats, natural to *Eleocharis*, were converted to intensively cultivated taro patches. Since the discovery and westernization of the islands, these lands on Oahu have in part been used continually as taro patches, but in recent times more largely occupied for sugar cane plantations or for house lots. The *Eleocharis* is now rare on Oahu, but well preserved on Niihau, and visible there for a few months after heavy southerly winter rains.

It is also significant that the deep red basal sheaths were gathered by the native Hawaiians on Niihau and plaited to form ornamental geometrical patterns, mostly small triangles, near the border of the pliant, fine mats called "pawehe" to distinguish them from the pure white ones called "makaloa," made solely of the stems of *Cyperus laevigatus* and lacking the red, ornamental inlay. It appears that the "pawehe" mats were made only on Niihau. Aylmer F. Robinson wrote (in a letter of July 26, 1952), "I believe the art is very old, and indigenous, though right now I do not think of any proof of it." There are in the Bishop Museum several of these mats, but none of the older ones are definitely dated. One was probably made at least as long ago as early in the 19th century. Hence, from the early occurrence on Oahu and Niihau, from the artistic use in fine matting by the natives, and from its distinctive morphology, it is concluded that *Eleocharis calva* var. *australis* is a variety endemic to the Hawaiian Islands. Since it has not been illustrated, and since

most of the older collections are incomplete or immature, an illustration made from the Niihau collection, *St. John 23,598*, is included.

PALMAE

Pritchardia Aylmer-Robinsonii sp. nov.

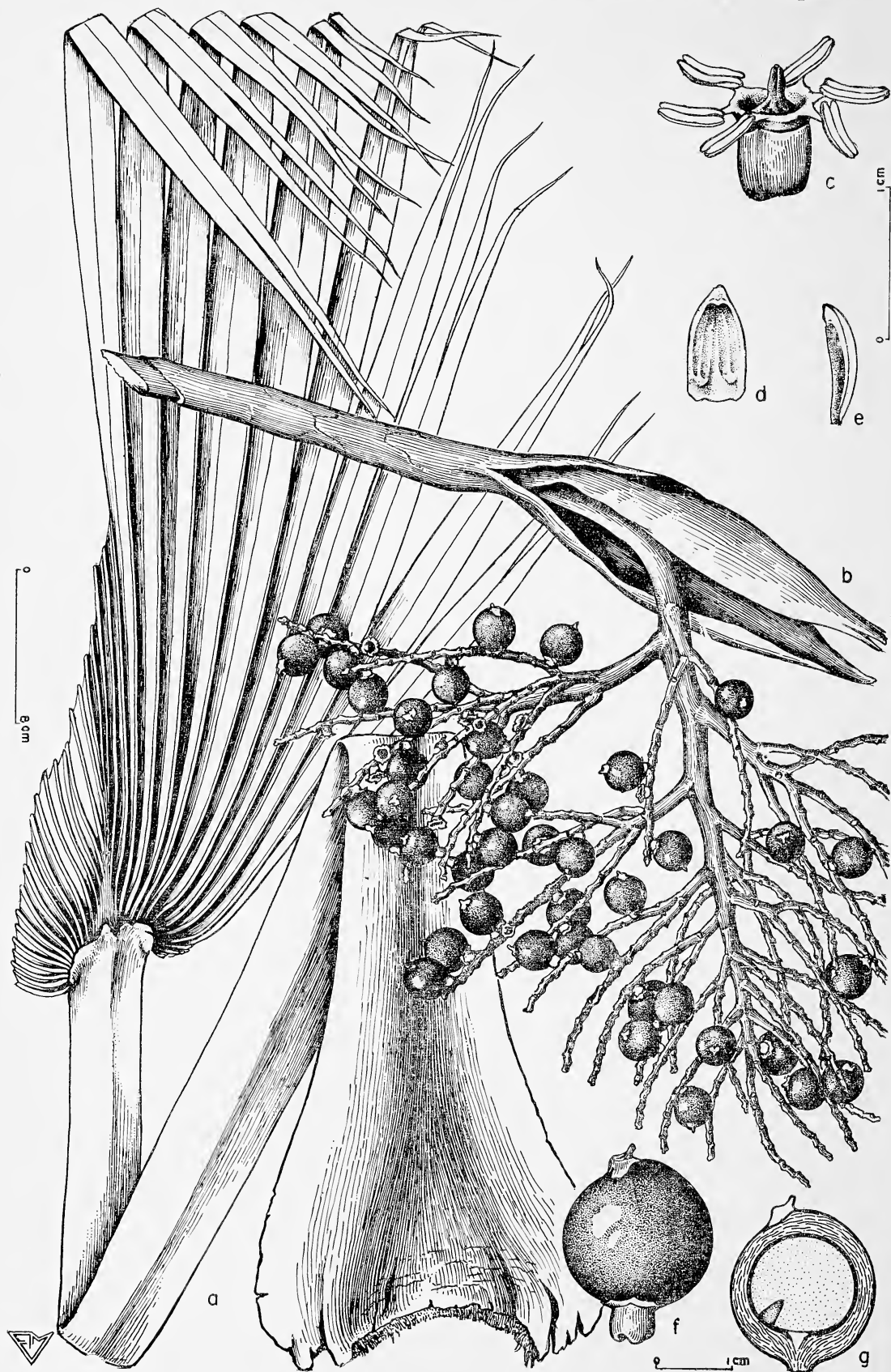
Fig. 3

NOM. VERN.: "wahane," or occasionally "hawane."

DIAGNOSIS HOLOTYPI: Arbor, stirpe unica erecta 7 m. alta, 2 dm. diametro, summa turbinata densa 35–40-folifera, foliis adscendenti-divergentibus, deinde foliis marcidis pendentibus, petiolis 92 cm. longis in basi 19 cm. latis in apice 3.7 cm. latis clariter viridibus glabris, scutello 2–4 cm. longo glabro valde obliquo late obtuso apice anguste acuminato fugaceo, laminis 1 m. longis clariter viridibus et in maturis in lateribus ambis glabris, segmentis multis per 4 dm. partitis apicibus bilobatis tenuibus pendulis sensim diminuentibus acutisque, paginis ambis cum nervulis transversis minute striatis, segmentis centralibus in basi 17 mm. latis, segmentis imaturis complicatis infra in costis et petiolis dense fusco-lanatis, pilis omnibus similibus gracilibus et implicatis vel cum lepidiis paucis permixtis, spadiceis glabris apicibus liberis expansis 15–20 cm. longis anguste ellipticis concavis, inflorescentiis geminatis 6–9 dm. longis glabris, pedunculis 40–55 cm. longis, paniculis 25–30 cm. longis, 25–30 cm. diametro ovoideis, ramis secundariis ferentibus 2–9 ramulis floriferis 4–13 cm. longis 2–4 mm. diametro glabris, bracteis et alabastris in exemplare desunt, calycibus 4 mm. longis minime tridentatis subcylindricis, nervis obscuris sed in apicibus ad dentibus manifestis et convergentibus, petalis 7.5 mm. longis 3.8–4 mm. latis ellipticis in basi truncatis intra cum impressio antherarum sulcatis caducis, circulo staminali extra calycem 1–1.5 mm. exserto et distento, filamentis rotatis parte libera 1.5–2 mm. longa, antheris 4.5 mm. longis divergentibus anguste oblongis ob-

tusis et emarginatis, ovario sulcato apici conico, stigmati trigonali truncato, fructibus orbicularibus 18–20 mm. diametro nigris duris, pericarpis 2.5–3.5 mm. crassis, mesocarpis grumosis et fibrosis pallidis, endocarpis 0.5 mm. crassis brunneis, testis levigatis atrobunneis, endospermiis albis osseosis, perianthiis fructiferis 3.5–4 mm. longis 4–5 mm. latis subcylindraceutis a latere compressis.

Tree with single erect trunk 7 m. tall, 2 dm. in diameter; crown turbinate, dense with the numerous (35–40) leaves, ascending, spreading, then on withering becoming pendent, and the inflorescences making the same descending, semicircular course of movement; petiole 92 cm. long, 19 cm. wide just above the base, 3.7 cm. wide at apex, after expansion bright green, glabrous; scutellum 2–4 cm. long, glabrous, very oblique, broadly obtuse with a narrow acuminate, fugaceous apex; blade parted into numerous segments, measuring 1 m. from the ligula to the apex, bright green and glabrous on both sides long before maturity; segments parted for about 4 dm., rather thin and drooping, deeply parted into two, gradually tapering acute tips; both surfaces finely striate with oblique transverse veinlets; central and largest segments 17 mm. wide at their disjunction points; young unexpanded leaves having the back of the petiole and the costae of the lower blade surface densely lanate with a fawn-colored coat, the hairs fine and tangled, uniform or mixed with a few lepidia; spadices glabrous, the free expanded tips 15–20 cm. long, narrowly elliptic, concave; inflorescences paired, 6–9 dm. long, glabrous; peduncle 40–55 cm. long; panicle 25–30 cm. long, 25–30 cm. in diameter, ovoid; secondary branches bearing 2–9 floriferous branches, these 4–13 cm. long, 2–4 mm. in diameter, slightly zigzag between the nodes, glabrous; bracts and buds not collected; calyx 4 mm. long, perceptibly 3-toothed, subcylindric, nerves obscure but their tips visible and converging towards the calyx teeth; petals 7.5 mm. long, 3.8–4 mm. wide, elliptic, the base truncate, the apex



subacute, thick and coriaceous, within longitudinally furrowed by the impress of the anther sacs, caducous; staminal ring exerted 1–1.5 mm. beyond the calyx and wide flaring; filaments diverging almost horizontally, the free part 1.5–2 mm. long; anthers 4.5 mm. long, divergent, narrowly oblong, obtuse and emarginate; ovary with the exposed tip conical, furrowed and ridged below; stigma trigonous, truncate; fruit spherical, 18–20 mm. in diameter, black, hard; pericarp 2.5–3.5 mm. thick; mesocarp grumous and fibrous, pale, endocarp 0.5 mm. thick, brown; seed coat smooth, dark brown; endosperm white, bony; fruiting perianth subcylindric, 3.5–4 mm. long, 4–5 mm. wide, laterally compressed.

HOLOTYPE: Niihau, Mokouia Valley, south ridge of, knoll, protected by basalt boulders, 875 ft. alt., August 15, 1947, *H. St. John* 22,813 (BISH).

This new species of palm was the most interesting find made during the visit to Niihau, and is a vivid reminder of the various other indigenous plants that doubtless formed a scrub or forest growth on the uplands, before their destruction by grazing animals. First a single palm tree was seen, at the head of the entrenched lower part of Haa Valley at 250 feet altitude. It was rooted in a rugged rocky talus just below the cliffs forming the cirque-like head wall. The trunk was about 15 meters tall and 30 centimeters in diameter, and it projected high above the cliff walls. The crown was unhealthy, and there were no inflorescences, probably due to a large hole bored into the trunk near the apex, probably by some animal. The next specimens were seen on the south divide of Mokouia Valley at 875 feet altitude, on the top of a prominent summit. Here in a forbidding jumble of great basalt boulders was one tree, healthy, and in flower and fruit, and it furnished the type specimens. At its foot were several seedlings with good leaves, but scarcely any trunk de-

veloped as yet. The crown of the large tree was dense and it bore many inflorescences in flower and fruit. The writer shinned up the trunk, 7 meters tall, grasped a lower leaf and hung there to rest, but then was too tired to scramble into the crown. He cut off a leaf, inflorescences with flowers and ones with fruits, then slid exhausted down the trunk. More specimens could have been obtained by felling the tree, but to do that to a rare survival near extinction would have been vandalism. A third grove was shown to the collector on the lower north slope of Kapaka Valley which is the next major valley northeast of Mokouia Valley, and debouching on the plain about one eighth mile east of Puu Alala. Here, rising out of a tangle of *Prosopis chilensis* trees, was a small clump of the *Pritchardia*, several smaller ones and two mature trees reaching about 7 and 10 meters in height. The native guide who knew the island thoroughly did not know of any other existing trees. These few survivors were in localities where the rugged and steep rocky slopes gave them some protection from the grazing sheep and cattle. Even so, the species is on the point of extinction.

The new species is named in compliment to Aylmer F. Robinson, in recognition of his keen interest in and wide knowledge of the natural productions of Niihau. His suggestions made the time in the field much more productive, and he has kindly reviewed both the botany and the Hawaiian names in this report. It is a pleasure to name this Niihau tree for Mr. Robinson.

The report by David Samuel who visited Niihau on January 29, 1778, with Captain Cook, that he saw "two or three palm trees," might have referred to the new species of *Pritchardia*, or to *Cocos nucifera*. From the vague nature of his statement, it is not now certain what palm he saw. His words are quoted by Handy (1940: 153).

FIG. 3. *Pritchardia Aylmer-Robinsonii*, from the holotype: a, leaf $\times \frac{1}{4}$; b, fructescence $\times \frac{1}{4}$; c, flower $\times 2$; d and e, petals $\times 2$; f, fruit $\times 1$; g, fruit in longitudinal section $\times 1$.

AMARANTHACEAE

Nototrichium sandwicense (Gray ex Mann)
Hbd. var. *niibauense* var. nov.

Fig. 4

DIAGNOSIS HOLOTYPI: Frutex 1–3 m. alta, laminis 5.7–15.8 cm. longis, 2.8–9.1 cm. latis, spicis 2–6 cm. longis recurvatis pervillosis et floribus clausis, bracteis rhachidis 2–2.5 mm. longis, bracteis florum 2.3–2.7 mm. longis, sepalis 3–3.5 mm. longis obscure plurinervis dense albo villosis in omnibus partibus excepta margine, antheris 0.5 mm. longis cellulis connectis.

DESCRIPTION OF ALL SPECIMENS: Shrub 1–3 m. tall, as much as 2 cm. in diameter at base; petioles 8–25 mm. long; blades 5.7–15.8 cm. long, 28–91 mm. wide, ovate, obtuse, abruptly cuneate and short decurrent, above short appressed pilosulous, below whitened by the appressed pilose tomentum; peduncles 3–30 mm. long, 2-bracted; spikes 2–6 cm. long, 8–10 mm. in diameter, recurving and the tips pendent, the axis pilose, with glabrous, scarious lanceolate bracts 2–2.5 mm. long, these exposed after the shedding of the fruits; flowers almost hidden by the abundant silky villosity, the paired bracts persisting below the flower 2.3–2.7 mm. long, sparsely pilose or villous; the four sepals 3–3.5 mm. long, broadly lanceolate, densely white villous except near the margins; stamens $\frac{3}{5}$ the length of the perianth; filament ring prominent, dark; anthers 0.5 mm. long, oblong-ellipsoid, the cells joined; ovary subglobose; utricle 1.5 mm. long, cylindrical, transparent; seed 0.5 mm. long, brown, obliquely elliptic.

HOLOTYPE: Niihau, first valley west of Kaali Cliff, top of steep basalt talus, 100 ft. alt., shrubs 1–2 m. tall, August 16, 1947, *H. St. John* 22,830 (BISH).

SPECIMENS EXAMINED: Niihau, Mokouia Valley, basalt rock beneath *Prosopis* tree, 700 ft. alt., March 30, 1949, *H. St. John* 23,589. It was also observed by the writer, but not collected, on Kaali Cliff.

The holotypic collection is abundant and with abundant flowering and fruiting spikes, but not a whole leaf was left on the plant. Some insects had eaten of the foliage, till the leaves were reduced to a mere lacework. The second collection, made after a heavy winter rain, has lush new growth and unharmed leaves. A branch of this is shown on the illustration (Fig. 4) and may be classed as a paratype.

No Hawaiian vernacular name for this species was known to the informant, Kalani Niau. Being a large and conspicuous shrub, a specimen was taken to the village and shown to the best informed, older native Hawaiians, but none knew a name for it. This is regretted, for as a perusal will show, the natives of Niihau still remember the Hawaiian vernacular names for almost all of the native plant species, and they have given Hawaiian names to most of the well-established adventive and cultivated species.

These are the first available collections of *Nototrichium* from the island of Niihau, so it is not surprising to have them turn out to be undescribed. There is an earlier record by Forbes (1913: 21) of this species from Niihau in his account of the Stokes collections. This early collection is lost. It is not now to be found in the Bishop Museum, and it does not appear in their card index of the herbarium as ever having been inserted in the collection.

The closest relative seems to be var. *longespdatum* Hbd. from Molokai (and perhaps formerly from Maui). This differs by having smaller blades, the principal ones 4–6 cm. long and 2.5–4.2 cm. wide; shorter spikes 2.5–5 cm. long, usually straight, less hairy, and with the flowers well exposed; bracts of the rhachis 1.5–2 mm. long; floral bracts 1.5–2 mm. long; sepals 2.7–3.2 mm. long, strongly 5–9-nerved, villous at base, the hairs diminish and becoming few on the pilose back, the apex and broad margins glabrous; anthers 0.2 mm. long, the cells separate, much diverging towards the base. On the other hand var. *niibauense* has the



FIG. 4. *Nototrichium sandwicense* var. *niibauense*: a, habit $\times 1$; b, inflorescence $\times 1$; c, flower $\times 8$; d, utricle $\times 8$; e, funiculus and seed $\times 8$; figs. b, c, d, e from holotype; fig. a from St. John 23,589.

blades 5.7–15.8 cm. long, 2.8–9.1 cm. wide; spikes 2–6 cm. long, recurving and with pendent tips, and so villous that the flowers are almost concealed; bracts of the rhachis 2–2.5 mm. long; floral bracts 2.3–2.7 mm. long; sepals 3–3.5 mm. long, obscurely several nerved, densely white villous except near the margin; anthers 0.5 mm. long, the cells joined.

In Mann's Enumeration (1867: 200) was also published *Ptilotus Sandwicensis* Gray ex Mann, var. β *Kavaiensis* Gray ex Mann. Sherff has recently (1951: 16), following Hillebrand (1888: 373), taken up this as *Nototrichium sandwicense* var. *kauaiense*. In Hillebrand's time the rules of nomenclature were less precise and, as was customary, authors assumed the right to "correct" the spelling of names of taxa, particularly those derived from geographic place names. Hillebrand changed all previously published names like: *maviensis*, *kavaiensis*, *owhybensis*, and *wabuensis* to *mauiensis*, *kauaiensis*, *hawaiiensis*, and *oahuensis*. The recent international codes of nomenclature (Amsterdam 1935, Stockholm 1950, and Paris 1954) do not permit this free alteration of validly published scientific names (1954 code: art. 73). Unless it can be proved that the original author made a typographical error or a mistake in spelling, his scientific name must be retained as published. Once-current geographic names are not now erroneous, even though a different spelling of the geographic name has been officially adopted and standardized. In latinizing the Hawaiian name Kauai, Gray chose to render the letter u by the Latin v, and he had good precedent for this course. Hence, even though Sherff in his revision of the genus has adopted the spelling *kauaiensis*, one must in conformity with the rules return to the original spelling: *Nototrichium sandwicense* var. *kavaiense*. It is given a neuter ending, because the varietal name must agree in gender with that of the genus, in this case it being neuter.

Since it has not been illustrated, there is included here a drawing made from the holo-

type: Kauai, Hanapepe, Mann & Brigham 590 (GH), of *N. viride* Hbd. var. *viride* (Fig. 5).

LEGUMINOSAE

Abrus precatorius (L.) L. forma *luteoseminalis* forma nov.

Seminibus pallide luteis. Seeds pale yellow.

NOM. VERN.: "pukeawe lenalena" (=Yellow Pukeawe). On the larger Hawaiian Islands the vernacular name "pukeawe" is applied to the native shrubs in the genus *Styphelia*.

HOLOTYPE: Niihau, Nonopapa, 20 ft. alt., in scrub on dry limestone flat, seeds pale yellow, August 13, 1947, *H. St. John* 22,768 (BISH).

The typical form of the species with black-ended scarlet seeds occurred near by, but in one section of the thicket all the plants produced wholly seeds that were of a pale yellow color. This is not a common form of the species, and seems to have been mentioned previously only by Pollacci (1918: pl. 18, fig. 10). The new name is from the Latin *luteus*, yellow, *seminalis*, pertaining to a seed, in allusion to the seed color.

Erythrina sandwicensis Degener var. *sandwicensis* forma *sandwicensis*

E. sandwicensis Degener, Fl. Haw. fam. 169c: 12/5/'32, with fig.

E. monosperma Gaud., Voy. Freyc. Uranie, Bot. 486, 93, (1826) [=1830]; and Atlas pl. 114, 1826–30; not *E. monosperma* Lam. (1786) = *Butea monosperma* (Lam.) Taubert.

Corollas orange, or varying from yellow to scarlet; seeds bright red.

The name *E. sandwicensis* Degener was merely a renaming of the long known common lowland tree first called *E. monosperma* Gaud., this name having proven invalid, being a later homonym. Hillebrand, Rock, and other Hawaiian authors had accepted this tree as indigenous in both Hawaii and Tahiti, and listed as a synonym *E. tabitensis* Nad., described from a locality at 700–800 meters

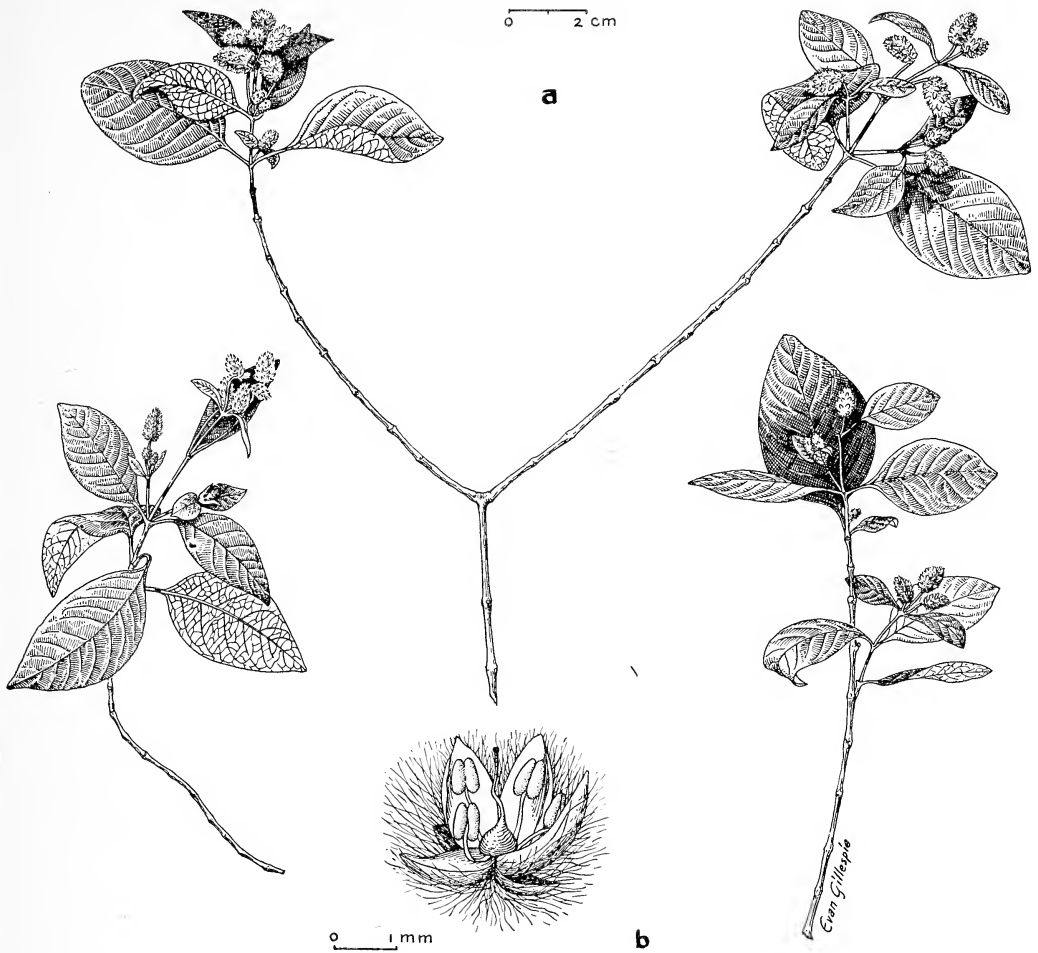


FIG. 5. *Nototrichium viride* var. *viride*, from isotype: a, habit $\times \frac{1}{2}$; b, flower $\times 8$.

in the mountains of Tahiti. Degener gives the new name *E. sandwicensis*, and his publication is valid, though it is not well documented. He says merely, not *E. tabitensis*, giving no differentiating characters to separate his newly named species from the Tahitian one. Later, Krukoff (1939: 226–227) discussed the relationship between *E. sandwicensis* Degener and *E. tabitensis* Nad. "The rediscovery of the very rare *E. tabitensis* in Tahiti seems to be essential for ascertaining the nomenclatural status of the Hawaiian plant now known as *E. sandwicensis*. I have seen Nadeaud 499 (type of *E. tabitensis*), deposited at Geneva. It consists of a single inflorescence

with small flower buds, two flowers, one pod, one seed, and no leaflets. From this available material it is impossible to decide whether or not the plant is specifically distinct from the plant native to Hawaii."

The writer had studied the original description of *E. tabitensis* Nad. It is detailed and 12 lines long. The following characters seem diagnostic. They are, in translation: lateral leaflets cordate, acuminate, glabrous; calyx 4-toothed; keel broad, rounded, emarginate; stamens monadelphous; seeds orange. After the writer studied the collections of *Erythrina* in Paris and Geneva, he was able to complete the description of *E. tabitensis* Nad. and to

establish it as distinct from the Hawaiian *E. sandwicensis* Degener (see St. John, 1955: 293-299).

Degener gives under his new name, *E. sandwicensis*, a list of synonyms and usages, but the earliest and the basic one is *E. monosperma* Gaud., the first name given to the Hawaiian "wiliwili" tree. This is confirmed by the fact that Degener gives a type locality: "In insulis Sandwicensibus (Alt. 350-400 hex.)." This is a quotation from the single locality given by Gaudichaud for his new *E. monosperma*. Hence, Degener's concept rests primarily on that of Gaudichaud. Gaudichaud obtained a specimen and this was illustrated in his atlas in detail, showing stem, leaves, buds, flowers, fruit, seeds, and details. He mentions the plant in his phytogeographic discussion (1827: 93) where he describes the second region, where, after leaving the lowland cultivated areas, and entered as one begins to ascend and to encounter the first indigenous plants, but he gives no further details here, other than the vernacular name, "ouiliwiri." His brief description (1830: 486) is here quoted:

"1. *Erythrina monosperma*. Pl. 114.

E. arborea; *inermis*; *foliis late ovato-reniformibus*, *obtusis*, *subtus calycibusque molliter fuscenti-tomentosis*; *fructibus monospermis*.

In insulis Sandwicensibus (Alt. 350-400 hex.)."

There are trees or branches of trees of the "wiliwili" that are unarmed, but usually there are numerous branches beset with short spines, so the unarmed branches are not diagnostic. The smaller pods may be 1-seeded, but much more characteristically the pods are several-seeded. Gaudichaud's description omits mention of the color of flower or fruit, but in the Explanation of Plates in his Atlas (1826-30: 21) for plate 114, fig. 9, he states, "Graine rouge foncé. . . ." Thus we know that his specimen was red-seeded, but the color of flower was not recorded. The flowers are fleshy, and are borne in heavy, dense

racemes, so that even today, with the best drying methods using artificial heat, it is expected to have the flowers fade to dull brown.

Degener (1932: family 169c) describes his *E. sandwicensis*, as with, "Standard . . . orange-red to rarely yellow or even white . . . ; wings greenish yellow . . . ; keel greenish yellow. . . ." This seems a composite description of the plant population that he included in the species, but it is clear that he included the common form of the species which has the corollas orange or shading from yellow to scarlet. In some, the bases of the corollas are greenish, but the predominant colors are as stated above. This color form is also the biological type of the species, and the writer here chooses it as the nomenclatural type. In the Bishop Museum the specimens of this forma *sandwicensis* for which there is record of the color, have it given as follows: orange, orange, orange, red, green and pink. Various other botanists in Hawaii have published accounts of the tree now called *E. sandwicensis*, and below are quoted their descriptions of the flower colors. Mann wrote (1867: 185) flowers "red, much the color of red coral, with some yellow, showy." Mrs. Sinclair said (1885: pl. 18 with text), "The flowers vary in colour from pale yellow to orange scarlet. There is no perceptible difference in the trees, but the natives say the wood of those with scarlet flowers is slightly harder and more durable than the other. . . ." Her colored plate shows the corolla orange blending to scarlet, the seeds bright red. Hillebrand (1888: 99) stated, flowers "pale red or orange, rarely yellow." Rock recorded (1913: 191) the "flowers pale yellow or brick red. . . ." Then later (1919: 49), flowers "brick red, orange or pale yellow." He later repeats this same description (1920: 183). Degener's flower description has already been quoted. Nearly all of these writers agree that the tree has flowers that are orange or yellow shading to scarlet. This is the kind here selected as the type form. The other ones with different flower colors are here described as color

forms, and one new seed color is distinguished. C. Judd (1920: 96) stated that the "blossoms vary in color from an orange scarlet to pale yellow." There is an early collection from Niihau, Foot of Plateau, S. E., January 1912, *J. F. G. Stokes*. This now has faded, brown flowers, and is without color notes. However, the native informants on Niihau reported that the majority of the trees had orange flowers and red seeds.

One of these color forms was marked in the herbarium by Dr. Rock with a name as a new variety. We refrain from adopting this name of his, since in his three publications on the subject he did not publish it, and apparently has not done so elsewhere. It seems that he decided not to publish it. In any case, the writer treats the plant not as a variety but as a forma.

E. sandwicensis Degener forma *alba*, forma nov.

Floribus albis. Corollas white.

HOLOTYPE: Oahu, between Koko Crater and Makapuu, level plain, alt. 30 m., tree 6 m. tall, flowers white, April 19, 1931, *E. P. Hume* 187 (BISH).

E. sandwicensis Degener forma *lutea*, forma nov.

Floribus luteis vel luteo-viridibus. Corollas yellow, greenish yellow, or yellowish green; seeds red.

HOLOTYPE: Niihau, Apana Valley, 400 ft. alt., rocky dry gulch, tree 6 m. × 2 dm., flowers yellowish green, seeds red, August 14, 1947, *H. St. John* 22,806 (BISH). Vernacular name: "wiliwili."

SPECIMENS EXAMINED: Molokai, Kamalo, Kapulei Ridge, arid rocky region, common, June 25, 1928, *O. Degener* 7,216.

Maui, East Maui, Ulupalakua district, fl. greenish yellow, August 26, 1948, *Karl H. Korte*.

Lanai, Mauna Lei, July 13, 1910, *J. F. Rock* 8,118; Paomai, yellow flowered, September

14, 1913, *G. C. Munro* 39, and 94, these last two probably being duplicates.

All but one of these collections are leafless, as this is the common condition at anthesis.

E. sandwicensis Degener var. *luteosperma*, var. nov.

Seminibus luteis, corollis pallide viridibus. Seeds dull yellow; corollas pale green.

HOLOTYPE: Niihau, Nonopapa, 20 ft. alt., thicket on dry flat, tree 7 m. × 2 dm., fl. pale green, seeds dull yellow, August 13, 1947, *H. St. John* 22,769 (BISH). Vernacular name: "wiliwili lenalena."

No other collections of this are known. Since it has distinctive color characters of both flower and seed, it is classed as a variety.

ARALIACEAE

Cheirodendron trigynum (Gaud.)
Heller var. *Hillebrandii* Sherff

Panax ovatum H. & A., Bot. Beechey Voy. 84, 1832. (See Fig. 6.)

Not found by any recent collector, its record being from a collection by Lay and Collie of the Beechey Voyage (Hooker and Arnott, 1832: 84). It is certainly extinct now. This collection, the holotype of *P. ovatum*, is in the herbarium at Kew. A complete revision of the genus *Cheirodendron* in Hawaii has just been published by Sherff. In this he mentions (1954: 3, 4) *Panax? ovatum* H. & A. and discusses (1954: 28) its placement. He repeats the descriptive characters given by Hooker and Arnott, but does not definitely place the species or key it. He tentatively suggests (1954: 27) that it is a synonym of *C. trigynum* (Gaud.) Heller var. *halawanum* Sherff. Because the holotype of *P. ovatum* was a sterile specimen, one cannot be positive as to its identity. However, Sherff's placement of it in var. *halawanum* does not seem to be justified. This variety, known from abundant collections on Oahu, Molokai, and Lanai, has the petioles 4–10 cm. long; the lateral petiolules 7–34 mm. long; the terminal petiolules 17–42

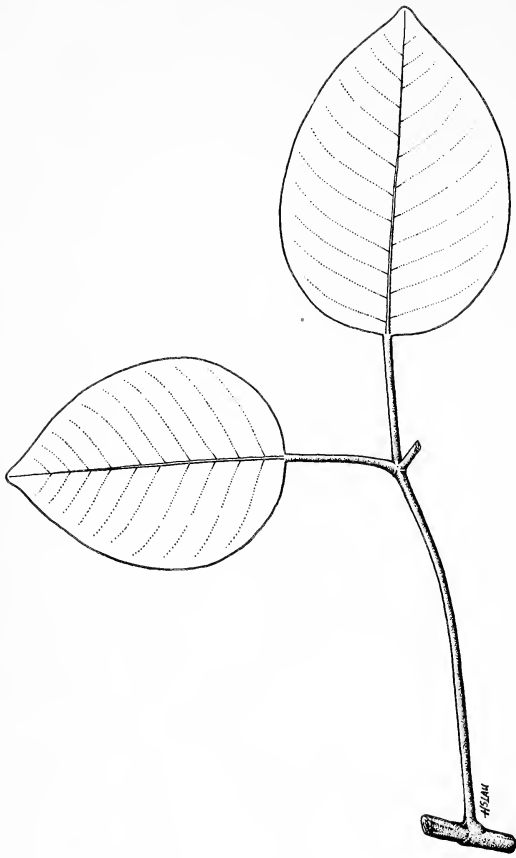


FIG. 6. *Panax? ovatum*, from holotype: a, leaf $\times \frac{1}{2}$.

mm. long; the leaflets when dried, thinnish, obsoletely to sharply 1-9-denticulate, and the lateral ones 28-63 mm. wide, and the terminal ones 44-75 mm. wide. *P. ovatum* H. & A. has, on the other hand, the petioles 7.5-11 cm. long; the lateral petiolules 22-30 mm. long; the terminal petiolules 26-38 mm. long; the leaflets when dried, thick chartaceous to subcoriaceous, entire, the lateral ones 50-60 mm. wide; and the terminal ones 55-65 mm. wide. This is the third species that was described in the group that is now called *Cheirodendron*. The type specimen is well preserved and is available in the Kew herbarium. The writer studied it there in 1954. The accompanying drawing shows a leaf from this holotype. It is not clear why Sherff did not examine it, as it

is available at Kew, and he studied and cited other specimens from the Kew herbarium.

It is possible that *P. ovatum* H. & A. is a species endemic to the island of Niihau, but there seems no chance of establishing that now, as the native forest has vanished and this species has not been found there by any of the recent collectors. The island of Kauai is nearest to Niihau, being only 9 miles distant. There are, according to Sherff, four species and six varieties of *Cheirodendron* on Kauai. None of them has foliage matching that of the Niihau tree. The next closest island, Oahu, is about 120 miles away. Though all described taxa have been checked, it seems that it is most like a variety that occurs on both mountain ranges of Oahu, *C. trigynum* var. *Hillebrandii* Sherff. This variety usually has the leaflets serrate and elliptic or elliptic-lanceolate to elliptic-ovate. However, there are some collections of it with entire and broader leaflets, ovate, entire, abruptly obtuse, and with long petiolules. These exactly match the holotype of *P.? ovatum* H. & A. When and if fertile material of the Niihau plant is found, the taxonomic placement can be reviewed. Till then the best placement seems to be as a synonym of *C. trigynum* (Gaud.) Heller var. *Hillebrandii* Sherff.

Reynoldsia sandwicensis Gray

NOM. VERN.: "ohe'ohe."

The only record of this is in the publication by C. N. Forbes (1913: 23) on the collection by J. F. G. Stokes. The species is listed without comment. The specimen is not now in the Bishop Museum nor does it appear in the card catalogue of the herbarium as ever having been inserted there. When exploring Niihau in 1947 the writer did not see the tree. It was one of the four native trees reported by Forbes, so its rediscovery was much desired. When asked, the guide K. Niau immediately replied that he knew the "ohe'ohe," that it was now very rare. He said there was only one living tree left, and he then led the way on August 13th to a spot on a steep side

of upper Kanaha Valley. At the site which he knew, there was now no sign of a tree, it having died and the soft stems having rotted away since the guide's last visit to the spot. Without doubt it is now extinct on Niihau. The record is a credible one, as the tree once, and to some degree still, makes a scattered arborescent growth on the low, very dry sections of all of the Hawaiian Islands. In the revision of the genus by Sherff (1952: 7), he states, "I have seen as yet no specimens from Kauai, Niihau, or Kahoolawe."

SOLANACEAE

Solanum Nelsoni Dunal var. *Nelsoni*

- S. Nelsoni* Dunal in DC., Prodr. 13: 123, 1852.
S. laysanense Bitter, Nat. Ver. Bremen, Abh. 16(3): 432-435, pl. 4, fig. A-D, 1900.
S. nelsoni Dunal var. *typicum* F. Br., in Christopersen & Caum, Bernice P. Bishop Mus., Bul. 81: 35, 1931.
S. nelsoni Dunal var. *intermedium* F. Br., 1. c. 35-36.
S. nelsoni Dunal var. *caumii* F. Br., 1. c. 36.
S. nelsoni Dunal var. *acuminatum* F. Br., 1. c. 36.

NOM. VERN.: "akia."

Niihau, south end, sand country; also cliff at, November 1, 1939, G. C. Munro; Kawaewae, under *Prosopis* thicket, 75 ft. alt., *St. John* 22,731; Leahi, in coral sand near beach, 10 ft. alt., *St. John* 23,621.

Two isotypes of *S. laysanense* as well as the holotypes and the paratypes of the varieties of *S. Nelsoni* described by Dr. F. B. H. Brown and all the specimens in the Bishop Museum have been studied. The shrubs are all similar; the flowers are identical; the fruits essentially so, though the collectors recorded a few as with red berries, while the majority recorded black berries. The berries recorded as red when fresh are now black when dried. There is some apparent variation in the size of the berries, but as they were juicy, then were pressed, the variation does not seem significant. The seeds are identical. The leaves vary

in shape from cordate to orbicular, ovate, or elliptic; the base from cordate to rounded, truncate, or cuneate; the apex from obtuse to acute; the margin from entire to slightly or markedly sinuate. The measurements of the hairs meet or overlap, and the leaf shapes are variable and difficult to define. Upon these characters the species and varieties listed have been described. The larger the leaves, the more apt they are to be acute at apex and with sinuate margins. An isotypic sheet of *S. laysanense* shows some blades subcordate at base, as well as ones rounded or cuneate. The holotype of *S. Nelsoni* var. *acuminatum*, Caum 68 from Nihoa I., has most of the blades sinuate, a key character, but several adult leaves on the same branch are entire. The same is true on an isotype, while on a second isotypic sheet, most of the blades are entire, while only a few show a slight waviness in the margin. The holotypes and isotypes of var. *Caumii* and var. *intermedium* are relatively constant to the characters alleged. *S. Nelsoni*, as shown by a photo of the holotype, David Nelson, from the Sandwich Islands, and by the several recent collections from Molokai, is relatively constant in its cordate, entire blades, but one sheet of several collected by Rock, March 1910, from Momomi (=Moomomi) beach, Molokai, shows both leaves with cordate bases and ones with rounded bases on the same stem. *S. Nelsoni* var. *intermedium* was keyed as having the leaves cordate to subacute at the base, and the several specimens show stems with leaves that are cordate, rounded, or subcuneate at base.

At hand are two unmounted collections with numerous duplicates. These would be classified as *S. Nelsoni* or its var. *typica*. *St. John* 19,962 from Moomomi, Molokai, consists of 22 separate plants or branches. Mostly these show small, cordate, entire blades, but four bear also some leaves that are shallowly sinuate. *St. John* 22,731 from Kawaewae, Niihau, consists of numerous sheets with a total of 50 branches. These all have the leaves cordate or ovate-cordate, obtuse or subacute, and

most of them entire. Four of them have some of the blades slightly sinuate, and one has a single large leaf strongly sinuate. From this review of the characters of the leaves, the writer is convinced that the shapes and shallow lobing of the leaves mentioned are mere fluctuations in a single population and usually on the same individual branch. Hence, the specific and varietal names based upon plants showing these characters are here reduced to the synonymy of *S. Nelsoni* Dunal.

Early there was described another variety, *S. Nelsoni* var. *thomasiaefolium* Seem. (Jour. Bot., Brit. and Foreign 1: 209, 1863), based upon a collection by T. Nuttall on Ato'i (=Kauai). This may well be the greatest extreme among the lobed-leaved plants. At hand is a photo of the type in the British Museum. Three years after publishing the variety Seeman again listed it (1866: 174) and repeated this original account; "foliis cordato-ovatis sinuato-lobatis, lobis (5-7) obtusis vel cordatis integris. . . This has quite the look of *Thomasia solanacea*, Gay, and would probably be described as a new species by anyone not having seen the evident transition there is in some specimens of what Nuttall has called *S. rotundifolium* and A. Gray justly considers identical with the original *S. Nelsoni*, Dun., preserved at the British Museum. In these specimens some of the leaves have a tendency to become sinuato-lobate, whilst again several leaves of my var. *thomasiaefolium* are cordate and entire." The photo of the holotype confirms this, that there are several leaves that are cordate and entire, but mostly they are strongly sinuately lobed, with two large, sinuate lobes on a side, cut half-way to the midrib. Seeman well states the inconstancy in this group of the characters of leaf shape and lobing, and the writer has stated his observations on the same points. However, no recent collections or any others seen show blades with the deep rounded lobes like those of var. *thomasiaefolium*. It is a marked extreme, and no intermediates have been seen that fill in the gap. Hence, until the variety is again

collected and more knowledge can be gained of its variability and occurrence, it seems best to accept var. *thomasiaefolium* as a variety, peculiar to Kauai. The writer and his several assistants searched for it in December, 1947, on the sandy shores of Kauai without success.

The treatment of this group by Dr. F. B. H. Brown (1931: 37) raises a question of typification. He gives a generalized description for *S. Nelsoni* Dunal (as *nelsoni*), then a detailed one for each of the four varieties, including var. *typicum* F. Br., new var. As var. *typicum* he recognized the plants with cordate, entire leaves. For this he cites only two collections, both in the Bishop Museum, and both from Moomomi, Molokai: *J. F. Rock*, March 1910, sheet A (which lettering was added to Rock's label in a later hand, apparently Brown's); and *C. N. Forbes* no. 613.Mo. No type was designated in the publication, but in the Bishop Museum the specimens are marked: the *Rock* sheet A is marked in Brown's writing, "Type of Descript."; the *Forbes* 613.Mo. is marked in Brown's writing, "Type! of amplif. descript."; and there is a third, unlisted, sheet, *Forbes* 604.Mo., marked in Brown's writing, "Type of amplif. descript." On checking Forbes's field number book, it is evident that both of his numbers written by him on his labels were wrong, that his collection of this *Solanum* from the sand dunes at Moomomi was no. 607.Mo., and that both of his sheets should be corrected to so read, as does an unmounted duplicate. Thus Brown, in describing *S. Nelsoni* Dunal var. *typica* F. Br., published no choice of a type in the bulletin, which was issued by Christophersen and Caum, but in the herbarium he marked as type three sheets collected in 1910 and 1915 by two different collectors. Not every possible detail concerning the selection of types is covered in the International Code of Botanical Nomenclature, but the practice is established and legalized. It is clearly improper to choose either the Forbes or the Rock collections to be the type of var. *typica* (now called var. *Nelsoni*). The type must be the same specimen

described as *S. Nelsoni* Dunal, that is the specimen in the British Museum collected "in insulis Sandwich," by David Nelson in 1788. There is a photo of this in the Bishop Museum. It has small, cordate, entire leaves, like the ones described by Brown for var. *typica*.

CUCURBITACEAE

Sicyos niibauensis, sp. nov.

Fig. 7

NOM. VERN.: "pua o Kama" (=the flower of Chief Kama; or perhaps merely a modification of "kaukama" =cucumber).

DIAGNOSIS HOLOTYPEI: Liana annua herbacea, caulibus ad 10 m. longis supra arbores frutesque scandentibus vel decumbentibus gracilibus pallide viridibus deinde glabratiss, novellis puberulentis pilis in initio glandulosis, pilis in nodis persistentioribus, internodis 6–20 cm. longis cirrhis oppositifoliis cum pedunculo rigido 8–30 mm. longo puberulento 2- 3-partitis, partibus 7–15 cm. longis ad basim puberulis ad apicem glabris dense spiralis, foliis multis, petiolis 13–50 mm. longis scabro-puberulentis, laminis subvariabilis sed frequentissime 4.5–11.5 cm. longis 4.2–14 cm. latis suborbicularibus tenuiter 3-lobatis digitatis cum sinibus late U-formatis 3–15 mm. profundis apicibus acutis basi profunde cordata membranaceis supra pustulato-scabris pallide viridibus cum nervis pallidioris infra dense pustulato-scabris et in nervis scabro-puberulentis marginibus subintegris nervis palmatis 3-fidis, nervis lateralibus dichotomis, ramis juvenalibus fortioribus cum laminis 6.7–9.5 cm. longis 6.2–11.3 cm. latis suborbicularibus 3–5-lobatis lobis 2.5–4 cm. longis sinibus late U-formatis marginibus subintegris vel paucementatis et remote apiculato-denticulatis, paniculis masculis 1.5–9.5 cm. longis glanduloso-puberulentis, pedunculo 12–70 mm. longo, pedicellis 2.7 mm. longis gracilibus, alabastris 2–3 mm. diametro forte depresso-suborbicularibus pallide lutescentibus vel albis, perianthiis in flore 8–8.5 mm. diametro

tubo 1.5 mm. longo subrotato, lobis 5 inaequalibus 3–3.5 mm. longis 1.8–2.2 mm. latis late lanceo-ovatis extra capitato-glanduloso-puberulentis intra minute ita, columna staminali 1.5 mm. alta, 5 antheris 1 mm. longis hippocrepiformis, inflorescentiis femineis capitatis axillaribus, pedunculis 10–15 mm. longis 9–13-floriferis capitato-glanduloso-puberulentis, corollis epigynis patelliformis vel subrotatis extra minute capitato-glanduloso-puberulentis et intra etiam minute ita, tubo 1.2 mm. diametro, lobis 1 mm. longis elliptico-ovatis, stylo 1 mm. longo glabro, lobis stigmatis 3 ligulatis recurvatis, ovario 3–5 mm. longo anguste turbinato tertia infera nuda vel sparse hirsutula, parte supera velata cum incrementis multis digitatis vel spatulatis dense hirsutis pilis in initio minute capitato-glanduloso, capitatis in fructu 12–17 mm. diametro globosis dense hirsutis, fructibus 6–7 mm. longis 5–6 mm. latis 2–3.5 mm. crassis late lanceolatis infra albo-puberulentis supra velata cum incrementis adscendentibus 1.5–3 mm. longis digitatis vel spatulatis integris vel furcatis dense catenulato-glanduloso-hirsutis, seminibus solitaribus 3.9 mm. longis 3.5 mm. latis 1.9 mm. crassis lenticularibus marginibus rotundatis, testis pallide luteis vel brunneis duris lucidis, hilo 1.9–2 mm. longo elevato cartilagineo albo simili ad duam partem labias in linea formata.

Annual climbing herbaceous vine; stems climbing as much as 10 m. over trees or bushes, or decumbent, slender, pale greenish, at length glabrate; young shoots puberulent and the hairs at first glandular, the hairs persisting longer near the nodes; internodes 6–20 cm. long; tendrils oppositifolious, with a stout rigid, common stalk 8–30 mm. long, puberulent, forking into 2 or 3 tendrils 7–15 cm. long, puberulous towards the base, glabrous towards the tip, closely coiling; leaves numerous; petioles 13–50 mm. long, scabrous puberulent; blades slightly variable in form, but the commonest shape 4.5–11.5 cm. long, 4.2–14 cm. wide, suborbicular, shallowly palmately 3-lobed, the broad U-shaped sinuses

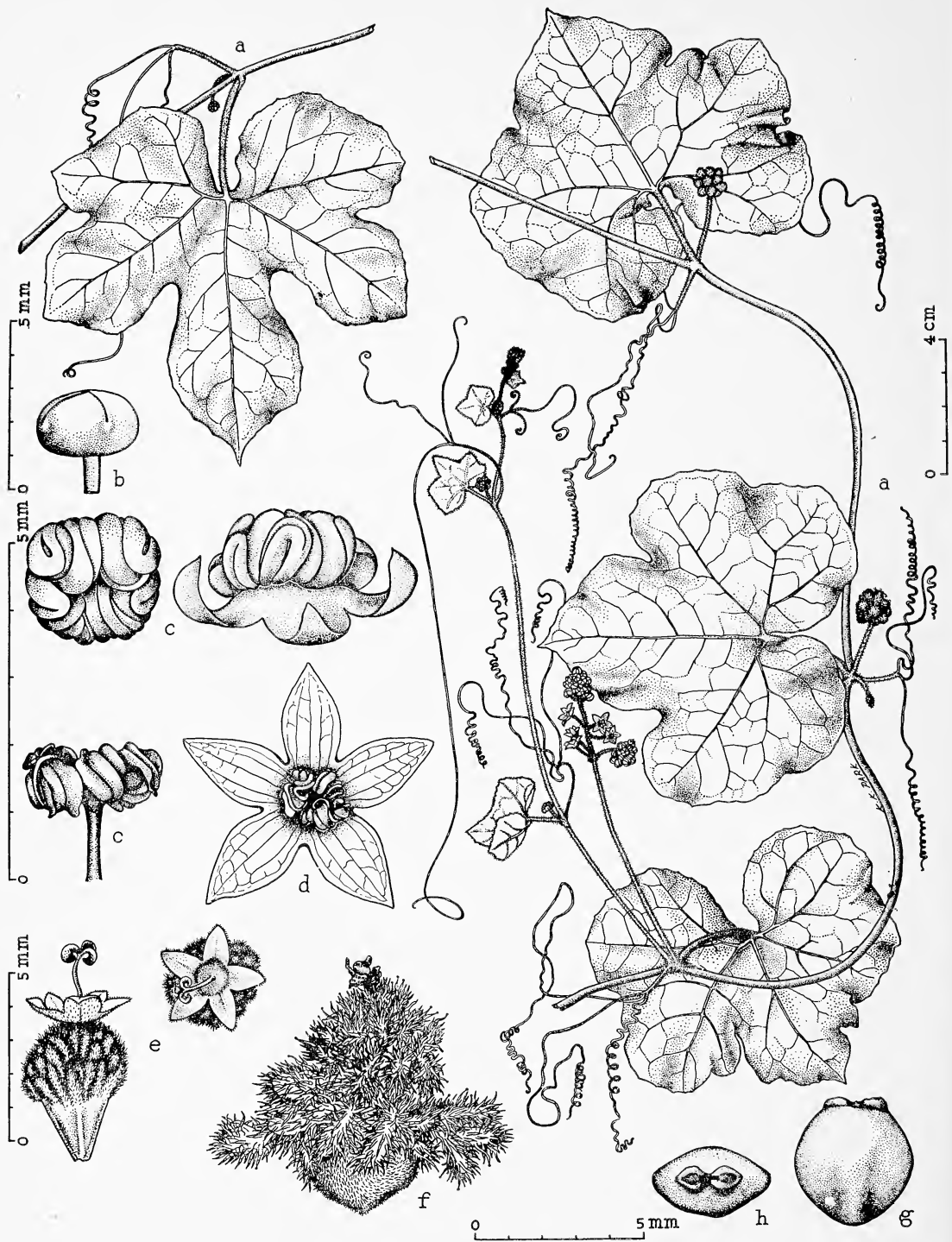


FIG. 7. *Sicyos niibauensis*, from holotype: *a*, habit $\times \frac{1}{2}$; *b*, staminate bud $\times 5$; *c*, anthers $\times 10$; *d*, staminate flower $\times 5$; *e*, pistillate flower $\times 5$; *f*, fruit $\times 5$; *g*, seed, lateral view, $\times 5$; *h*, seed, apical view, $\times 5$.

3–15 mm. deep, the apex acute, the base deeply cordate, texture membranous, above pustulate scabrous, pale green, the veins lighter green, below densely pustulate scabrous and on the veins scabrous puberulent, the margins appearing subentire but under a lens seen with a few veins ending in minute apiculate projections, palmately 3-nerved from the base, the lateral veins forking; blades of more vigorous juvenile branches 6.7–9.5 cm. long, 6.2–11.3 cm. wide, suborbicular 3–5-lobed about halfway to base, the sinuses 2.5–4 cm. deep, wide U-shaped, the margins subentire or few-dentate and remotely apiculate denticulate; staminate panicle 1.5–9.5 cm. long, glandular puberulent; peduncle 12–70 mm. long; pedicels 2–7 mm. long, slender; bud much depressed suborbicular, 2–3 mm. in diameter, pale yellowish or whitish; perianth in anthesis rotate, 8–8.5 mm. in diameter, the tube 1.5 mm. long, almost rotate, the five lobes unequal, 3–3.5 mm. long, 1.8–2.2 mm. wide, broadly lance-ovate, capitate glandular puberulous without, minutely so within; staminal column 1.5 mm. tall; the five anthers 1 mm. long, hippocrepiform; pistillate inflorescences capitate, axillary; peduncles 10–15 mm. long, capitate glandular puberulent; pistillate flowers 9–13 in a head; corolla epigynous, shallow saucer-shaped or almost rotate, minutely capitate glandular puberulous without and even more minutely so within; the tube 1.2 mm. in diameter, the lobes 1 mm. long, elliptic ovate; style 1 mm. long, glabrous; stigma lobes 3, recurving, ligulate; ovary 3–5 mm. long, narrowly top-shaped, the lower third naked or but sparsely hirsutulous, the upper two-thirds covered with many fingerlike or thick spatulate processes and each of these densely shaggy hirsute, the hairs at first minutely capitate glandular; fruiting heads 12–17 mm. in diameter, globose, densely hairy; fruits 6–7 mm. long, 5–6 mm. wide, 2–3.5 mm. thick, broadly lanceolate, the lower part white puberulent, the upper part covered with ascending processes which are 1.5–3 mm. long,

thick fingerlike or spatulate, simple or forked and densely shaggy catenulate gland-tipped hirsute; seed single, 3.9 mm. long, 3.5 mm. wide, 1.9 mm. thick, lenticular, the edges rounded, the testa pale yellow or brownish, hard, smooth, shining, the hilum 1.9–2 mm. long, raised, cartilaginous, white, shaped like two pairs of slightly open lips in a line.

HOLOTYPE: Niuhau, 1 mile W. of Kii, 50 ft. alt. (also common on Kaali cliff), grassy, sandy flats, elongate vine climbing *Prosopis* tree, leaves, pale green, veins lighter, staminate flowers white, March 29, 1949, *H. St. John* 23,567 (BISH).

The closest known species is *S. pachycarpus* H. & A. of Oahu which has the petioles glabrate; blades shallowly 5-lobed; fruits 2.3–2.8 mm. wide and 1–1.8 mm. thick with the upper part glabrous; seed 2.8 mm. wide, and the hilum 0.8 mm. long. *S. niuhauensis* differs by having the petioles scabrous puberulent; blades shallowly palmately 3-lobed; fruits 5–6 mm. wide, 2–3.5 mm. thick, and the upper part covered with ascending fingerlike processes, densely glandular hirsute; seeds 3.5 mm. wide, and the hilum 1.9–2 mm. long.

LOBELIACEAE

Delissea niuhauensis, sp. nov.

Fig. 8

DIAGNOSIS HOLOTYPE: Frutex, caule 1–2 cm. diametro glabro, cicatricibus 9–10 mm. latis 4–5 mm. altis aggregatis stramineis depresso-scutelliformis, fasciculis 8–11 exsertis in ellipso disponitis, internodis reductis ad oras inter cicatrices congregatis, foliis glabris in fasciculo terminali denso aggregatis, petiolis plerumque divergentibus 2–4 cm. longis sed in sicco 1–1.5 mm. diametro, laminis 5.5–7.5 cm. longis 3.4–5 cm. latis chartaceis late ovatis apice acuto marginibus crenatis nervis lateralibus ad apicem diffuse ramosis, costa paulo recurvata sed lateribus foliae adscendentibus, inflorescentiis axillaribus multis tam numerosis quam petiolos obscurantur, cymis



FIG. 8. *Delissea niibauensis*, from holotype: a, habit $\times \frac{1}{2}$; b, flower $\times 2$; c, corolla $\times 2$; d, stamens and stigmas $\times 2$; e, fruit $\times 2$; f, seed $\times 20$; g, h, leaves of *D. undulata*, from holotype, Paris, $\times \frac{1}{2}$.

17–19-pluri-floriferis divergentibus sive deflexis, pedunculis 11–16 mm. longis nudis, bracteis ad 1 mm. longis hirsutulis deinde subglabratibus, pedicellis 3–8 mm. longis glabris aggregatis in cyma condensa, axile 8–15 mm. longa, hypanthiis 3–4 mm. longis ellipsoideis truncatis, dentibus calycorum 0.8–1.3 mm. longis deltoideis obtusis crassis foliaceis hirsutulis, alabastris 18–20 mm. longis subarcuatis apice in 55° decurvato, corollis in flore 22–25 mm. longis glabris subcylindricis curvatis in basi 2–2.5 mm. diametro supra majoribus in fauce 3.5–4 mm. diametro, gibbo proximo 1 mm. alto asymmetrico-conico obtuso reflexo et e basi 10 mm. distante, gibbis lateralibus binis dimidiis et ad basem proximioribus, tubo corollae 10 mm. longo, labia supra bilobata sino 8–10 mm. longo, lobis 1.7–1.8 mm. latis ligulatis subito diminuendibus ad apicem obtusam decurvatis, labia infera subaequaliter trilobata sinibus 7–9 mm. profundis, lobis 1.5–1.7 mm. latis subiter ad apicem subacutam contractis, lobis corollae intra sparse papillois, columna staminalis 17–21 mm. longis paene decurvatis glabris pallidis, antheris superis 8–8.5 mm. longis glabris, antheris inferis binis 6–8 mm. longis in apice penicillatis pilis hispidois 1.5–2 mm. longis albis, stigmatibus exsertis 1–1.3 mm. convexis, ovario 1.5 mm. longo ellipsoideo, baccis 6–7 mm. diametro globoso-turbinatis apophysatis subviridescentibus, seminibus 1.4–1.5 mm. longis 0.7–0.9 mm. latis 0.2–0.3 mm. crassis ellipticis compressis cum jugis transversis sinuosis parallelis in parte muriculatis, marginibus e raphi prominenti crassi straminei, lateribus brunneis.

Shrub, apparently erect and single stemmed, stature unknown; stem 1–2 cm. in diameter below the lowest leaf, glabrous, the surface covered with the crowded straw-colored leaf scars 9–10 mm. wide, 4–5 mm. high, depressed shield-shaped, the 8–11 bundle scars protruding, in a broad ellipse complete except at top; internodes inconspicuous, merely pale brown protruding rims between the crowded leaf scars; leaves glabrous, numer-

ous, in a terminal dense plume, the petioles mostly diverging; petioles 2–4 cm. long, when dried 1–1.5 mm. in diameter; blades 5.5–7.5 cm. long, 3.4–5 cm. wide, chartaceous, broadly ovate, the apex acute, the margin crenate, lateral veins 7–9 on a side, arched ascending, becoming diffusely branched near the tip, the midrib gently recurved, the sides of the leaf upturned, so that the blade will not lie flat; inflorescences axillary, numerous, forming a mass so dense as to obscure the petioles; cymes 17–19-more-flowered, divergent or deflexed; peduncle 11–16 mm. long, naked; bracts subtending the pedicels nearly 1 mm. long, at first hirsutulous, later subglabrate; pedicels 3–8 mm. long, glabrous, crowded on the condensed cyme with the axis 8–15 mm. long; hypanthium 3–4 mm. long, truncate, ellipsoid, apparently green; calyx teeth 0.8–1.3 mm. long, deltoid, obtuse, thick foliaceous, hirsutulous; bud 18–20 mm. long, gently arcuate, the apex decurved at 55° from the axis of the ovary and corolla base; corolla in anthesis 22–25 mm. long, glabrous, curved subcylindric, at base 2–2.5 mm. in diameter, gradually slightly enlarging upwards to the throat where 3.5–4 mm. in diameter; proximal protruding knob 10 mm. from the base of the corolla, asymmetric conic, obtuse, pointed backwards, 1 mm. high, the two lateral knobs about half as large and slightly nearer the pale corolla base; the dorsal suture in late anthesis parted to the knob, so the tube only 10 mm. long; corolla 2-lipped; upper lip 2-lobed, the lateral sutures split down only 8–10 mm., the lobes strap-shaped, 1.7–1.8 mm. wide, abruptly narrowed to the obtuse tip, decurved below the column which is exerted through the upper suture; lower lip subequally 3-lobed, the sutures 7–9 mm. deep, the lobes 1.5–1.7 mm. wide, strap-shaped, abruptly contracted to the subacute tip, all corolla lobes sparsely papillose within; staminal column 17–21 mm. long, gently decurved, glabrous, pale; upper anthers 8–8.5 mm. long, glabrous; two lower anthers 6–8 mm. long, the apex penicillate,

the stiff hairs 1.5–2 mm. long, white; stigmas briefly short exerted (for 1–1.3 mm.), low rounded, with a central crease; ovary 1.5 mm. long, ellipsoid; berry 6–7 mm. in diameter, globose-turbinate, apophysate, greenish; seeds 1.4–1.5 mm. long, 0.7–0.9 mm. wide, 0.2–0.3 mm. thick, elliptic, flat, with strong wavy parallel transverse ridges, the eminences rounded or muriculate, the raphe forming a prominent, thickened, straw-colored margin, the flat faces dull brown, but the color in places masked by the pale epidermis.

HOLOTYPE: Niihau, *W. T. Brigham* (distributed by *Mann & Brigham*), (BISH).

SPECIMENS EXAMINED: Kauai ou Nihau (=Niihau), 1851–55, *J. Remy 300 bis* (GH; and photo in BISH).

H. Mann, Jr., commented (1867: 180) on this Remy collection, "more probably Niihau—where it was also found by Mr. W. T. Brigham." Rock (1919a: 357) observed that, "The plants from Niihau collected by Remy are much more robust, the stems being nearly 5 cm. in diameter." The three sheets of the type collection, by Brigham, in the Bishop Museum, contain seven branches, all of them sections split longitudinally from the heavy and densely flowered stems. The longitudinal stem sectors were flattened in pressing, so that one cannot be sure of their original diameter. A revised estimate is 1–2 cm. at the base of the lowest leaves.

The occurrence of a *Delissea* on Niihau is very noteworthy, for the lobelias in general and all of the species of *Delissea* in particular, occur in moist forests, usually in the rain-forest. That a *Delissea* was twice collected between 1850 and 1865 by different botanists is an indication of the occurrence then on the uplands of a moist forest. Brigham, then the director of the Bishop Museum, is quoted by Forbes (1913: 25) as saying, "this is the only *lobelia* that he saw on the island, and that it was more plentiful over the area where it occurred than perhaps any other lobeliaceous plant occurring in an equal area on the [Hawaiian] group." The species is certainly ex-

tinct now, having vanished when domestic grazing animals destroyed the native forest.

Delissea undulata, collected by Gaudichaud in 1819 was described by him (1829: 457 and pl. 78). His description in Latin consists of 12 words, only 9 of which are descriptive. His own type specimen, now in Paris, gives the locality Iles Sandwich. No more precise localization has been found. A photograph of his type specimen has been published by Rock (1919: 201) and this shows a specimen in fruit and flower, and with slender, linear-lanceolate blades, coarsely and irregularly sinuate dentate. Though with broader leaves, a collection by Hillebrand, August 1870, dry pali of Olualu (Olowalu) gulch, West Maui, was photographed by Rock when in Berlin and this excellent photograph is in the Bishop Museum. It is similar to the generalized drawing published by Gaudichaud (1826–30, Atlas: pl. 78). The plant has broader, less deeply lobed blades, but it appears to be of the same species, *D. undulata* Gaud., and it was so determined by Rock.

There is a *D. undulata* Gaud. var. *serrulata* Wawra, described from fruiting material, Wawra 1,943, from Waihee, Maui. Rock (1919: 353) reduced this to the synonymy of the species and cited Wawra's specimen which he had studied in Vienna. This may well belong in the synonymy of *D. undulata*, but in lack of flowers it cannot be placed with certainty. It appears, then, that the *D. undulata* Gaud. was probably collected by Gaudichaud in the adjacent mountains when the "Uranie" was anchored at Lahaina, Maui. *D. undulata* Gaud. has the blades linear-lanceolate, coarsely and irregularly sinuate-dentate, and apparently much larger, while *D. niihauensis* has the blades broadly ovate, crenate, and 5.5–7.5 cm. long.

D. fallax Hbd., apparently the closest relative, has the blades 7–23 cm. long, 2.3–5.8 cm. wide, narrowly elliptic, apiculate, serrate; petioles 3–13 cm. long; calyx lobes subulate, glabrous; corolla 15–17 mm. long, with a single, inconspicuous dorsal knob;

anthers 4.5–6 mm. long; penicillate brush 1–1.3 mm. long; berry 10–12 mm. in diameter. In contrast, *D. niibauensis* has the blades 5.5–7.5 cm. long, 3.4–5 cm. wide, broadly ovate, crenate; petioles 2–4 cm. long; calyx teeth deltoid, hirsutulous; corolla 22–25 mm. long, with one conspicuous dorsal and two lateral knobs; anthers 6–8.5 mm. long, the penicillate brush 1.5–2 mm. long; berry 6–7 mm. in diameter.

Rock (1919a: 353, 357) lists two of his own collections, 3,950 and 10,053, from the western side of the island of Hawaii, simple stalked trees more than 30 feet high, and relates his surprise at finding these on Hualalai, Puuwaawaa, and Pulehua. A similar specimen, *Forbes 263.H*, from Kanahaha, Kona, Hawaii, has recently been described as *Cyanea argutidentata* E. Wimm. Its only two mature flowers scarcely show the single gibbous corolla hump, but it is evident on the flowers of other collections of what is considered the same species, all from Kona, Hawaii: Puuwaawaa, *Rock 3,950*; Pulehua, Mauna Loa, *Rock 10,053*, and Kanehaha (=Kanahaha) *Forbes 264.H*; and Hanehane, *Forbes 196.H*. For the latter there is a drawing showing the single, proximal gibbous swelling at the apex of the corolla tube, and recording the swelling as red, while the lower part of the corolla as white, the upper part with reddish dots, the corolla lobes, filament tube apex, and stigmas pea green. Since this population has the technical characters, the following transfer is proposed.

Delissea argutidentata (E. Wimm.) comb.
nov.

Cyanea argutidentata E. Wimm., Engler's Pflanzenreich IV, 276b(1): 75–76, fig. 21, 1943.

HOLOTYPE: Hawaii, "Wald unterhalb Koa Kanehaha-Kona, blühend im Juni (C. N. Forbes n. 263 H)" (BISH). This was a translation by Wimmer of the original data: Growing in the forest under koa, Kanehaha (=Kanahaha), Kona, June 26, 1911. J. F.

Rock has subsequently redetermined Wimmer's species as *Delissea undulata* Gaud., reaffirming his opinion of the Hawaiian plants expressed in his monograph of 1919. That grouped the diverse plants of Kauai, Niihau, Maui, and Hawaii as one species. The writer here shows that the holotype was from West Maui, a plant having flowers with three gibbous humps; that the Kauai record is dubious; that the Niihau one is a new species, *D. niibauensis*; and that the one from Hawaii having calyx lobes 1–2 mm. long, and usually smaller, shorter leaves is still a different one, *D. argutidentata*. This latter is very close to *D. fallax* Hbd. from the Hilo region on eastern Hawaii, which is known only from the type collection and shows calyx lobes "about 3 mm. long." When more collections are found to represent *D. fallax*, its placement should probably again be re-examined. Concerning the other segregates, the evidence is more abundant, and the conclusions more certain.

A close examination of Forbes's field notebooks reveals that his no. 263.H was an undetermined grass, and that no. 264.H is the correct number of this collection of Lobeliaceae. Forbes himself made the correction on one sheet (BISH), but the duplicate sent to Wimmer went under the number 263.H. Thus the holotypic collection of *D. argutidentata* should now read Kanehaha (=Kanahaha).

COMPOSITAE

Lipochaeta kawaihoensis sp. nov.
(§ *Lipochaeta*)

Fig. 9

NOM. VERN.: "ko'oko'olau."

DIAGNOSIS HOLOTYPI: Perennis suffruticosa erecta 3–8 dm. alta, corona pluri-ramifera, caulibus principalibus griseis deinde brunneis longitudinaliter sulcatis multi-ramosis in basi 2–7 mm. diametro, ramis lateralibus anguste pluri-angulosis adpresso-hispidulosis late divergentibus, petiolis 4–18 mm. longis gracili-

bus adpresso-hispidulis, laminis 1.2–4 cm. longis 7–28 mm. latis ovatis ad deltoideo-ovatis acutis vel obtusis firme crasse chartaceis et scabrissimis marginibus grosse crenatis vel etiam serratis supra obscure olivaceis in nervis adpresso-hispidis in intervallis adpresso-hispidulosis pilis cum basibus pustulatis infra pallide viridibus et adpresso-hispidulosis, capitulis terminalibus solitariis vel raro in ramulis parvis cum bracteis reductis et cymis elongatis 3-capitatis simulantibus, pedunculis 3–17 cm. longis nudis, involucris in flore 6 mm. altis 10–12 mm. diametro sed in fructu rotatis et subreflexis, phyllaris biseriatis viridibus crassis coriaceis 13-nervosis subacutis ellipticis vel lanceolatis extra et infra adpressi-hispidulosis, phyllaris exterioribus 5 et 4–8 mm. longis, interioribus 6–7 et simulantibus, receptaculo in flore lanceoloideo in fructu conico 4 mm. alto, paleis 5–6 mm. longis oblanceolatis scabris carinatis plurinervosis, floribus radiatis 6–9 luteis, laminis 7–9 mm. longis late ellipticis pluri-nervosis emarginatis et subtridentatis, tubo 1 mm. longo, setis pappi 3–5 inaequalibus 1–2 mm. longis linearibus vel oblanceo-linearibus crassis rigidis scaberulis eis majoribus canaliculatis, stylo 2 mm. longo filiformibus, stigmatibus 2 ligulatis 1.5–2 mm. longis, achaeneis juvenalibus 1.8–2 mm. longis 1.7–1.9 mm. latis trigonatis latere distali convexo late cuneiforme apice dense breve albo-hispiduli, achaeneis maturis 2.7–3.1 mm. longis 1.9–2.7 mm. latis trigonatis late cuneiformibus lateribus brunneis et nigro-maculatis forte tuberculatis apice subplanato luteo-hispiduloso, aristis 1.5–2 mm. longis subulatis adscendenti-hispidulosis subsistentibus, floribus disci ca. 80, corollis 4 mm. longis luteis, tubo 1.5 mm. longo tubuloso, limbo anguste infundibuliforme 2.5 mm. longo 5-lobato, lobis 0.8 mm. longis deltoideis divergentibus, filamentis 1 mm. longis filiformibus pallidis, tubo staminalis 1.8 mm. longo in apice 0.5 mm. diametro ad basim attenuato, saccis antherae nigris, apicis connectivi pallidis deltoideo-ovatis, stylo 3 mm. longo pallido basi 0.4–

0.5 mm. longo cylindrico subnigro firmo, stigmatibus 1 mm. longis ligulatis acutis, arista pappi unica ligulata subulata 2.1–2.3 mm. longa, achaeneis disci juvenalibus 1.8–2 mm. longis 0.7–0.9 mm. latis cuneiformibus compressis lateribus convexis glabris apice obliquo hispidulo, achaeneis disci maturis 2.5 mm. longis 1.7–2 mm. latis late cuneiformibus subluteis et pallide brunneo-maculatis in parte levibus in parte tuberculatis tetragonis basi obtusa vel truncata apice lato dense luteo-hispiduli marginibus tuberculatis, seta pappi plerumque una 1–2.3 mm. longa subulata hispidula curvata.

Perennial suffruticose, erect, 3–8 dm. tall; the crown bearing several branches; the main stems much branched, gray, becoming brown, longitudinally fissured, 2–7 mm. in diameter at base; the lateral branchlets sharply several-angled, appressed hispidulous; petioles 4–18 mm. long, slender, appressed hispidulous; blades 1.2–4 cm. long, 7–28 mm. wide, ovate to deltoid-ovate, acute or obtuse, thick, firm chartaceous and very scabrous, the margin coarsely crenate or even serrate, above dull olive green, appressed hispid on the veins, on the intervals closely appressed hispidulous from pustulate bases, below pale green and closely appressed hispidulous; heads terminal, usually solitary at tips of branches but rarely on small shoots with reduced bracts simulating an elongate 3-headed cyme; peduncles 3–17 cm. long, naked; heads heterogamous, radiate; involucre in anthesis 6 mm. tall, 10–12 mm. in diameter, but in fruit widespreading and rotate or somewhat reflexed; phyllaries in 2 rows, green, thick, coriaceous, with about 13 longitudinal nerves, subacute, broadly or narrowly elliptic or lanceolate, rough appressed hispidulous without and within, the outer ones mostly 5 in number, 4–8 mm. long, the inner ones 6–7, similar; receptacle in anthesis lanceoloid, in fruit conic, about 4 mm. tall and taller than broad; chaff 5–6 mm. long, oblanceolate, cartilaginous, rough scabrous, carinate, the back keeled, with numerous close longitudinal

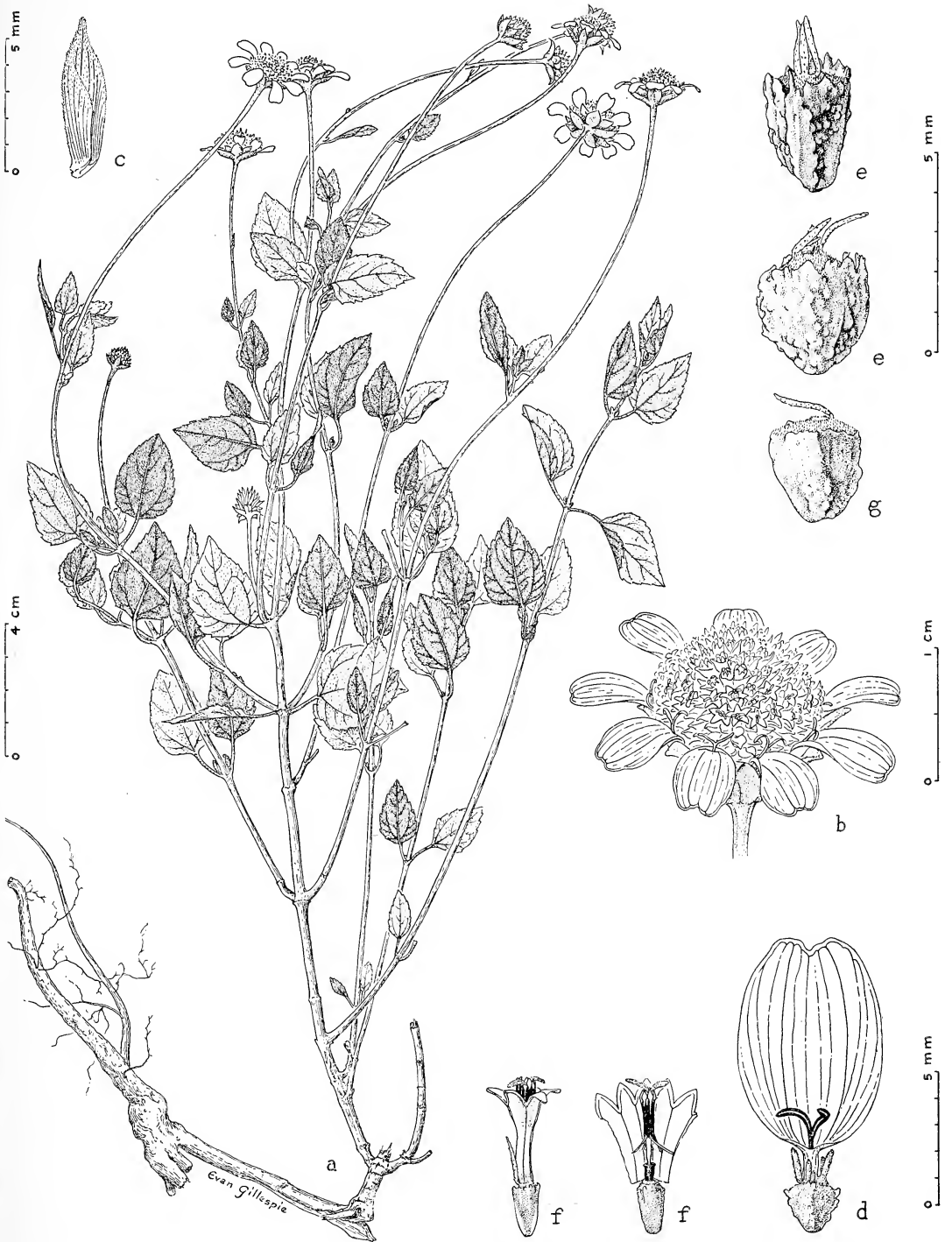


FIG. 9. *Lipochaeta kawaihoensis*, from holotype: *a*, habit $\times \frac{1}{2}$; *b*, head $\times 2$; *c*, chaff $\times 4$; *d*, ray flower $\times 4$; *e*, ray achene $\times 6$; *f*, disk flower $\times 4$; *g*, disk achene $\times 6$.

parallel veins; ray flowers marginal, 6–9, bright yellow, the ray 7–9 mm. long, broadly elliptic, with numerous longitudinal parallel nerves, at apex emarginate and more or less 3-toothed; corolla tube 1 mm. long; pappus awns unequal, 3–5, and 1–2 mm. long, linear or oblance-linear, thick, rigid, ascending scaberulous, the larger ones channelled on the inner side; style 2 mm. long, filiform, the base not distended; stigmas 2, ligulate, 1.5–2 mm. long; the young ray achene 1.8–2 mm. long, 1.7–1.9 mm. broad, trigonous, and the broad distal face convex, broad cuneiform, the apex densely short white hispidulous; when mature the ray achenes 2.7–3.1 mm. long, 1.9–2.7 mm. wide, almost as thick, trigonous, broadly cuneiform, the sides brown, mottled with black and strongly tuberculate, the broad apex flatish or sloping, yellowish hispidulous, awns 1.5–2 mm. long, subulate, ascending hispidulous, several of them persistent; disc flowers about 80; disc corollas 4 mm. long, yellow, the tube 1.5 mm. long, tubular, the limb narrow funnel-form, 2.5 mm. long, 5-lobed, the lobes 0.8 mm. long, deltoid, spreading; filaments 1 mm. long, filiform, pale; staminal tube 1.8 mm. long, 0.5 mm. in diameter at apex, narrowing below, the linear anther sacs black, the apical connective tips pale, deltoid-ovate; style 3 mm. long, pale, springing from a dark firm style base 0.4–0.5 mm. long, cylindrical, slightly tapering below, and with an expanded apical marginal rim; the 2 stigmas 1 mm. long, ligulate, acute; pappus of a single ligulate, subulate awn 2.1–2.3 mm. long, attached apically near the base of the corolla tube; the young disk achenes 1.8–2 mm. long, 0.7–0.9 mm. wide at apex, narrowly cuneiform and tapering downwards, compressed, the two sides convex, glabrous, the sloping apex densely hispidulous; disk achenes when mature 2.5 mm. long, 1.7–2 mm. wide, broadly cuneiform, yellowish, mottled with pale brown, partly smooth, partly low tuberculate, less thick than wide, but clearly tetragonal, the base obtuse or truncate, the apex broad,

gently sloping, closely yellowish hispidulous, the margin with low tubercles, the usually single awn apical, 1–2.3 mm. long, subulate, ascending hispidulous, sharply bent.

HOLOTYPE: Niihau, Kawaihoa Point, 300 ft. alt., in dry tuff, head of steep gully, erect, much branched shrubs, rays yellow, disk dark yellow, March 31, 1949, *H. St. John* 23,611 (BISH).

This plant has been carefully compared with the known species and varieties of *Lipochaeta*. It is outstanding in the genus by having the receptacle at first lanceoloid, then ultimately conic, instead of flat or gently convex. It is most similar to *L. lobata* var. *denticulata* of the island of Oahu, but this variety has the petioles 2–5 (-9) mm. long; inner and outer phyllaries oval, subequal; chaff obtuse; ligulate flowers 8–18; and the achenes 2.9–3.6 mm. long, verrucose, sharply angulate, narrowly obdeltoid, compressed. *L. kawaihoaensis* differs from it by having the petioles 4–18 mm. long; the inner phyllaries lanceolate, longer and narrower than the outer ones; chaff acute; ligulate florets 6–9; and the achenes 2–3.1 mm. long, 1.7–2.7 mm. wide, the sides tuberculate, the angles not winged or margined. There is a lesser similarity in appearance to *L. tenuis* var. *Sellingii* of Puu Hapapa, Oahu, which variety is different in having the habit decumbent or suberect; blades oblong-lanceolate, at base broadly cuneate, the margin sharply serrate; peduncles 2–5 cm. long; disk flowers with corolla lobes equaling the tube, the pappus of 4 bristles as long as the corolla tube, and the achenes obovate, triangular with the angles more or less winged. On the other hand, *L. kawaihoaensis* can be known by having the habit erect; blades ovate to deltoid-ovate, at base rounded, the margin coarsely crenate or even serrate; peduncle 3–17 cm. long; disk flowers with corolla lobes $\frac{1}{3}$ as long as the tube, pappus of a single ligulate-subulate awn slightly more than $\frac{1}{2}$ as long as the corolla tube; achenes broadly cuneiform, tuberculate, not winged.

The new species is named from its only known locality, the volcanic, mountainous point at the south end of Niihau Island; to its name is added the Latin suffix, *-ensis*, indicating place of origin.

Lipochaeta lobata DC., var. *incisior* var. nov.

Fig. 10

L. lobata sensu C. N. Forbes, not of DC.

L. lobata DC. var. *Aprevalliana* sensu Sherff as to Niihau specimen, not of (Drake) Sherff. NOM. VERN.: "nehe."

Foliis majoribus inciso-serratis lobatisque.

It has the larger blades incised serrate and lobed.

HOLOTYPE: Niihau, Kaaliwai, in thicket with *Euphorbia celastroides* and *Artemisia australis*, 750 ft. alt., shrub 1–1.5 m. tall; leaves scabrous, chartaceous; involucre green; rays

yellow, March 29, 1949, *H. St. John* 23,572 (BISH).

SPECIMENS EXAMINED: Niihau, Kaali, January 1912, *J. F. G. Stokes*. This is an immature specimen, only 34 cm. tall, and with the blades lance-ovate, merely incised serrate, but it is from the same locality, has blades similar to the smaller ones on the holotype, and is certainly of the same variety.

The most similar variety to this new one is *L. lobata* var. *denticulata* of Oahu, which has the blades subentire to crenate-dentate or serrate, but not lobed. The new varietal name is from the Latin, *incisor*, more deeply cut.

Lipochaeta lobata DC. var. *maunaloensis* Sherff

L. lobata sensu C. N. Forbes, not of DC. Niihau, south half of Island, January 1912, *J. F. G. Stokes*.

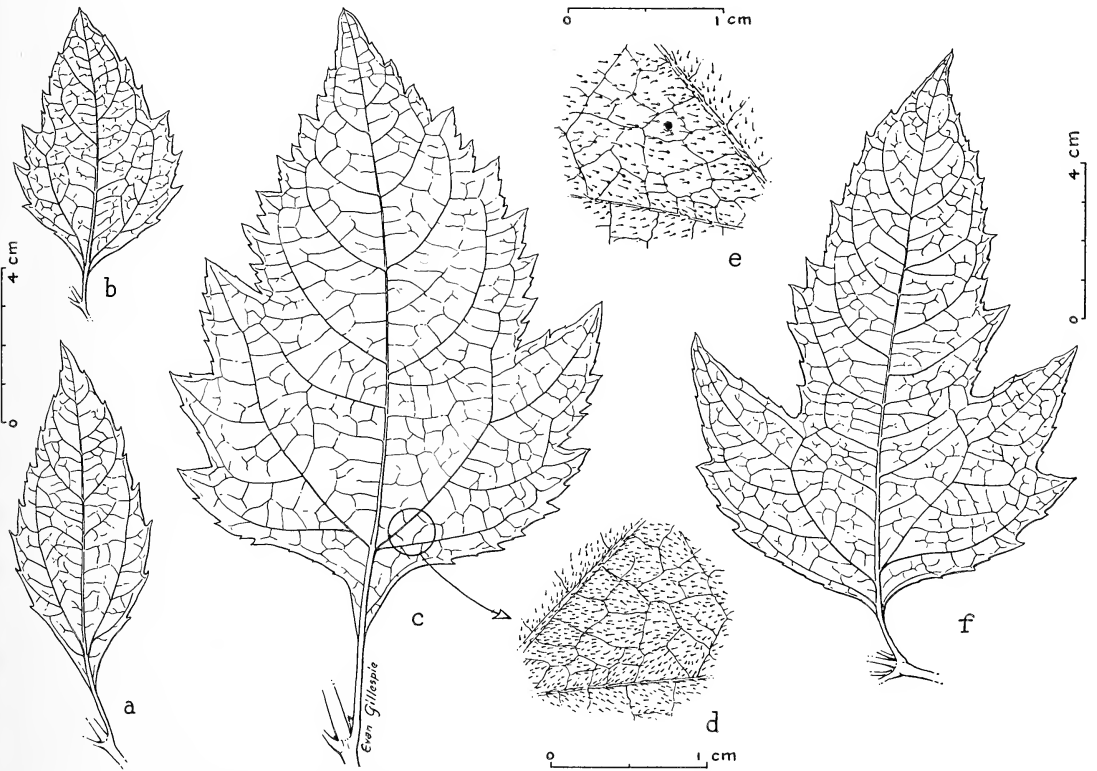


FIG. 10. *Lipochaeta lobata* var. *incisior*, from holotype: a, b, c, f, leaves $\times \frac{1}{2}$; d, lower leaf surface $\times 2$; e, upper surface $\times 2$.

This is a good flowering and fruiting specimen and it matches nicely the holotypic specimen from Mauna Loa, the dry end of Molo-kai. This Niihau specimen was not seen by Sherff.

Lipochaeta niihauensis, sp. nov.

(§ *Lipochaeta*)

Fig. 11

NOM. VERN.: "pa'apa'a'ina" (= crackle; probably in allusion to the stiff, brittle leaf blades).

DIAGNOSIS HOLOTYPI: Frutex 1 m. altus erectus ramosus, caulibus principalibus tertiis scabris, ramulis angulosis scabris et adscendenti-adpressi-hirsutulibus, petiolis 4–20 mm. longis oppositis minime connatis et perfoliatis in apice basi que dilatatis et adscendenti-albo-hispidulis, laminis 1.5–6.2 cm. longis 8–56 mm. latis crasse chartaceis sed rigidis et maxime hirsutulo-scabris et subadpresso-albo-hispidulis late ovatis in basi rotundatis vel subcordatis apice abrupte subacuti marginibus bidentato-serratis infra pallidioribus proxime basi triplinervatis, capitulis in cyma laxa 3-capitata vel ita cum ramulis axillaribus tardis tenuibus cymis tricapitatis ferrentibus, pedunculis 1.5–6.5 cm. longis nudis dense subadpresso-albo-hispidulis, capitulis in flore cum involucre 4–5 mm. alto 8–10 mm. diametro sed in fructu patelliforme, phyllaris bi- (vel tri-) seriatis subviridibus exterioribus 5 (-7) subacutis 3–3.5 mm. latis late ovatis in marginibus et extra adpressi-hirsutulibus firmis coriaceis 7-nervosis in basi carnosae, phyllaris interioribus paullo longioribus 2.5 mm. latis obovatis acutis, receptaculo in flore depresso-conico 1 mm. alto 2 mm. lato, paleis 3.5–5 mm. longo anguste cuneatis conduplicatis lateribus 0.8–1 mm. latis plurinervosis scariosis apicibus exsertis hispidulis, floribus radiatis marginalibus 8–14 in flore luteis, ligulis 8–9 mm. longis 3.8–4 mm. latis late ovalibus subtridentatis in latere distali valde bicostatis nervis gracilioribus 8, tubo 1.4 mm. longo aristis pappi plerumque

3 inaequalibus 0.6–0.9 mm. longis subulatis adscendenti-scaberulis, stylo 2.5 mm. longo, stigmatibus 0.7 mm. longis filiformibus, achaeneis radiatis juvenalibus 1.2–1.4 mm. longis trigonatis cuneiformibus in marginibus et apice hispiduli-ciliatis, achaeneis maturis 2.5–2.8 mm. longis 1.2–1.8 mm. latis valde trigonatis late cuneiformibus nigro-brunneis et griseo-maculatis ad apicem scabro-hispidulis ad basim ita diminuendis ad basim marginibus lacero-alatis, aristis 3 (-4) inaequalibus 0.6–1.2 mm. longis subulatis, floribus disci ca. 100, corollis in flore viridi-luteis 4 mm. longis tubo 1 mm. longo cylindrico, limbo anguste infundibuliforme 0.9 mm. diametro 4-lobato lobis 0.5–0.6 mm. longis deltoideis adscendentibus, filamentis 1 mm. longis ligulatis pallidis, tubo staminalis 1.4 mm. longo 0.5 mm. diametro, sacis antheris subnigris apice connectivi pallidi deltoideo-ovatis, stylo 3.5 mm. longo filiforme pallidi et basi 0.3 mm. longi cylindrici subnigri, stigmatibus 0.7–0.8 mm. longis ligulatis apice rhomboidei, aristis pappi binis 0.7–1.3 mm. longis subulatis barbellatis, achaeneis disci juvenalibus 1.3–1.9 mm. longis 0.6–0.8 mm. latis gracili-biconvexis cuneiformibus in marginibus et apice hispidulis, achaeneis maturis 2.8–3.2 mm. longis 1.1–1.7 mm. latis valde compressis et biconvexis medie vel anguste elliptico-obovatis basi obtusi apice truncati vel excavati brunneis et griseis maculatis ad apicem tuberculato-hispidulis marginibus cum alis membranaceis sive integris sive laceratis sive hispidulo-ciliato-laceratis, aristis binis 0.7–1.7 mm. longis aequalibus vel inaequalibus subulatis barbellatis in apice affixis.

DESCRIPTION OF ALL SPECIMENS: Shrub 1 m. tall, erect, with several branches; main stems terete, brown, scabrous from the remnants of pubescence; branchlets several-angled, roughened and ascending appressed hirsutulous; petioles 4–20 mm. long, opposite, connate and slightly perfoliate, dilated at base and apex, ascending white hispidulous; blades 1.5–9 cm. long, 8–77 mm. wide, thick chartaceous but stiff and very hirsutulous sca-

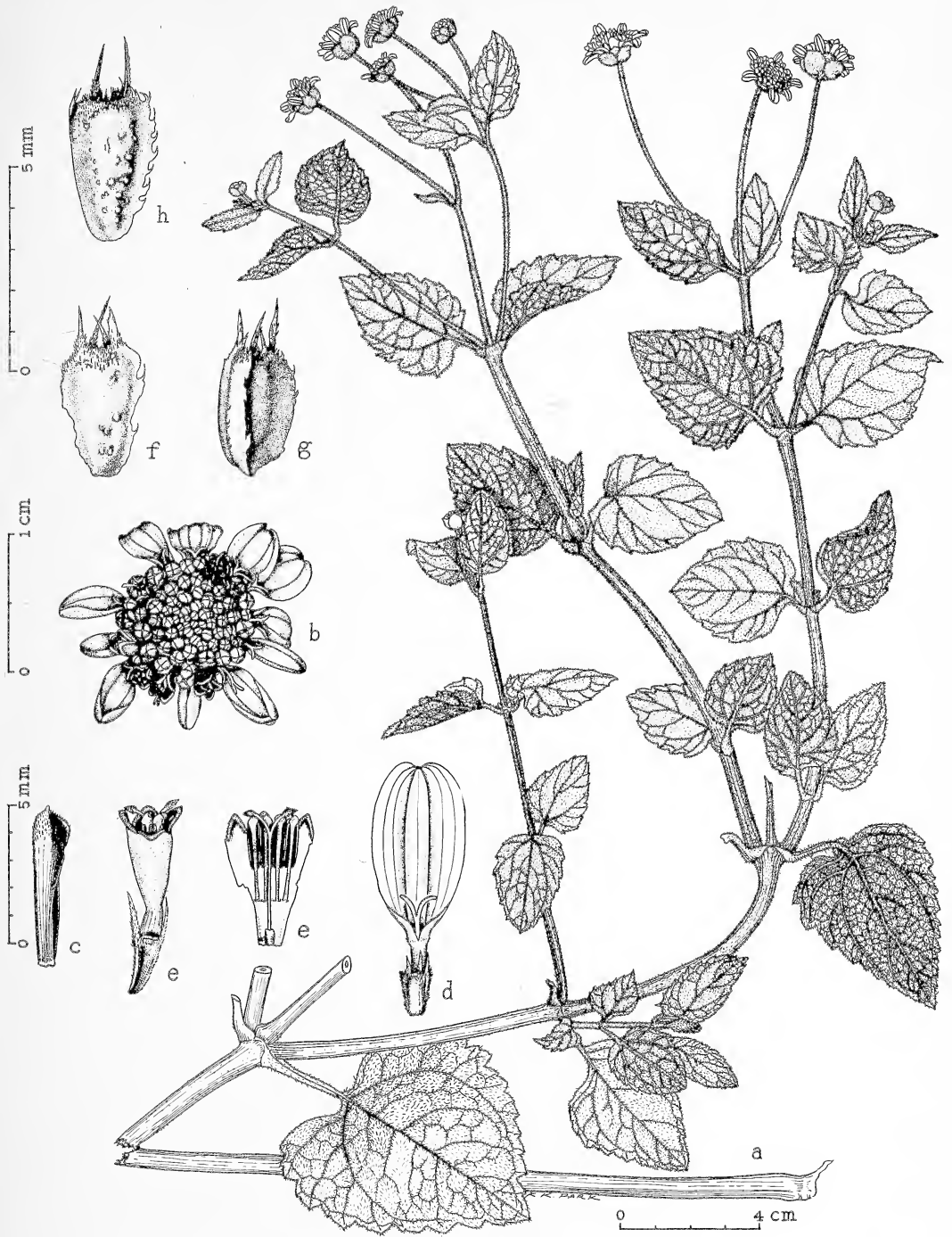


FIG. 11. *Lipochaeta niibauensis*, from holotype: *a*, habit $\times \frac{1}{2}$; *b*, head $\times 2$; *c*, chaff $\times 4$; *d*, ray flower $\times 4$; *e*, disk flower $\times 4$; *f*, ray achene, dorsal view, $\times 6$; *g*, ray achene, lateral view, $\times 6$; *h*, disk achene, dorsal view, $\times 6$.

brous, and white subappressed hispidulous, broadly ovate, the base rounded or subcordate, the apex abruptly subacute, the margin doubly dentate-serrate, below a little paler, triplinerved from just above the base; heads in a loose, mostly 3-headed terminal cyme, or with 3-headed cymes on weak, late, lateral branchlets, peduncles 1.5–6.5 cm. long, naked, closely subappressed white hispidulous; heads heterogamous, radiate; involucre in anthesis 4–5 mm. tall, 8–10 mm. in diameter, but in fruit more widely spreading, knee-pan-shaped; phyllaries in 2 (or 3) rows, greenish, the outer ones 3–3.5 mm. wide, 5 (-7) in number, broadly ovate, subacute, appressed hirsutulous on the outer surface and the margin, firm coriaceous except at the firm fleshy base, 7-nerved; inner phyllaries slightly longer, 2.5 mm. wide, obovate, acute; receptacle in anthesis low conical, 1 mm. tall, 2 mm. broad; chaff 3.5–5 mm. long, narrowly wedge-shaped, the apex rounded to an acute tip, folded along the midrib, the sides 0.8–1 mm. wide, many nerved, scarious, the exposed tips hispidulous; ray flowers marginal, 8–14, when fresh yellow, the ray 8–9 mm. long, 3.8–4 mm. wide, broadly oval, shallowly 3-toothed at apex, on the distal side with 2 strong salient ribs from which the sides are infolded, weaker longitudinal ribs 8; ray corolla tube 1.4 mm. long; pappus awns mostly 3, unequal, 0.6–0.9 mm. long, subulate, ascending scaberulous; styles 2.5 mm. long; stigmas 0.7 mm. long, filiform; the young ray achenes 1.2–1.4 mm. long, trigonous cuneiform, the margins and apex hispidulous ciliate; when mature the ray achenes 2.5–2.8 mm. long, 1.2–1.8 mm. wide and nearly as thick, sharply trigonous, broadly cuneiform, dark brown, mottled with gray, towards the apex rough hispidulous and less so towards the base, the angles lacerate winged, awns 0.6–1.2 mm. long, 3 (or 4), unequal, subulate; disk flowers about 100; disk corollas when fresh greenish yellow, 4 mm. long, the tube 1 mm. long, cylindrical, the limb very narrowly funnel-form, 0.9 mm. in diameter, 4-lobed, the lobes 0.5–0.6 mm.

long, deltoid, ascending; filaments 1 mm. long, ligulate, pale; staminal tube 1.4 mm. long, 0.5 mm. in diameter, tapering downwards, the anther sacs blackish, the apical connective tips pale, deltoid-ovate; style 3.5 mm. long, filiform, pale, springing from a dark, cylindrical style base 0.3 mm. long, with the upper rim expanded and lobed; the 2 stigmas 0.7–0.8 mm. long, ligulate with a narrowly rhombic tip; pappus of two subulate awns 0.7–1.3 mm. long, upward barbellate, attached above the lateral angles; the young disk achenes 1.3–1.9 mm. long, 0.6–0.8 mm. wide, thin biconvex, wedge-shaped, hispidulous on margins and apex; when mature the disk achenes 2.8–3.2 mm. long, 1.1–1.7 mm. wide, strongly compressed and biconvex, elliptic-obovate or narrowly so, the base obtuse, the apex truncate or excavate, the surface mottled brown and gray, the sides smooth towards the base, but upwards tuberculate hispidulous; each of the margins bearing a thin wing that is entire, lacerate, or hispidulous-ciliate lacerate; awns two 0.7–1.7 mm. long, equal or unequal, subulate, upwardly barbellate, attached apically.

HOLOTYPE: Niihau, Kii, among rocks on basalt knoll, 100 ft. alt., April 2, 1949, *H. St. John* 23,664 (BISH).

SPECIMENS EXAMINED: Niihau, Kii, between basalt boulders on rocky knoll, 75 ft. alt., April 2, 1949, *H. St. John* 23,671.

L. niibauensis is a member of the section *Lipochaeta* (*Microchaete*). Its closest relative is *L. subcordata* Gray var. *populifolia* Sherff of the island of Lanai, which variety is distinguished by having the stems 3–6 dm. tall; petioles 1–3 cm. long, slender; blades from narrowly ovate-cordate to lanceolate-cordate or narrowly deltoid, the principal ones broadly ovate, subcordate, the margins doubly sharply attenuate serrate; outer phyllaries about 4 mm. long; ray flowers 5–6, and 5–7 mm. long, their achenes 2–2.5 mm. long, 1.8–2 mm. wide, black, oblong-cuneate, trigonous, wingless, the apex truncate, the back with many high tubercles; disk corollas 3 mm. long,

narrowly funnellform, not contracted, pilosulous, their achenes 2–2.5 mm. long, 3-angled on the high convex back, giving a 4-angled appearance, the margins bluntly lobed or toothed, the sides high tubercled. *L. niibauensis* differs in having the stems 1 m. tall; petioles 4–20 cm. long, slightly dilated at base and connate; blades broadly ovate, the margins doubly dentate-serrate; outer phyllaries 5–6 mm. long; ray flowers 8–14, and the ray 8–9 mm. long, their achenes 2.5–2.8 mm. long, 1.2–1.8 mm. wide, dark brown mottled with gray, broad cuneiform, the angles lacerate winged, the apex crateriform, the back hispidulous; disk corollas 4 mm. long, cuneate-cylindric, contracted near the base, glabrous, their achenes 2.8–3.2 mm. long, thin biconvex wedge-shaped, the margins with a thin wing that is entire, lacerate, or hispidulous ciliate lacerate, the sides tuberculate hispidulous above but smooth towards the base.

The specific epithet is coined from the name of the island; and the Latin place ending, *-ensis*.

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Composition and Nutritive Value of Palolo (*Palola siciliensis* Grube)¹

CAREY D. MILLER and FLORENCE PEN²

PALOLO is the Polynesian name of an annelid worm, which rises to the surface of the sea from the coral reefs of a number of tropical islands in the Pacific Ocean. For generations the native people have been able to predict the day and approximate hour in October and in November, which is their spring, when this swarming will take place. Sometimes it is November and December, or even later, as the time of the risings, both dates and hours, differs for the various locations and the phases of the moon.

According to Dr. Olga Hartman (1958), the annelid is designated *Palola siciliensis* (Grube) 1840, (= *Palola viridis* Gray, 1847). (In the past, the names *Eunice viridis*, *Eunice siciliensis*, and *Palolo viridis* have also been used.)

PALOLO IN THE SOUTH PACIFIC

The areas in the South Pacific Ocean where the palolo has been observed and where the natives have long used it as food have been reported by a number of scientists. Burrows (1955: 154) lists the following from the evidence which he has collected: "Fiji; Western Samoa; American Samoa; Tonga; Rarotonga (Cook Group), but not in the northern atolls; New Hebrides, but not in the three southern islands; Solomons, in a number of places."

The famous navigator, Mr. Harold Gatty,³ who with Wiley Post flew around the world in 1931, and who collected the sample which we analyzed, was mainly interested in the "remarkable periodicity" of the rise. His in-

vestigations covered Samoa, the Fiji group, the New Hebrides, and the Solomons. In Fiji the worm is called "mbalolo," and in a letter dated January 21, 1954, Suva, Mr. Gatty wrote as follows:

From records over many years, there has been no deviation on the date of its two risings per year. If the last quarter of the moon is after the 15th of October, it will rise then and again on the last quarter of the moon in November, but if the last quarter of the moon is early in November, it will rise then and again on the last quarter of the moon in December. The rising is most exact on those days but only between the hours of four and eight a.m. The rising is usually continued on the next two succeeding mornings.

They (palolo) rise everywhere on and inside the reefs but are very few in numbers where they are in proximity to fresh or brackish water. The quantities that rise have to be seen to be believed. For instance, throughout the Fiji group there are actually many thousands of tons rising at the same instant. One can remain stationary either wading in shallow water, or anchored with a small boat in deeper water, and not fail to scoop up many pounds from any one spot.

In conversation with the senior author, Mr. Gatty stated in October, 1954, that the palolo rose not merely in thousands of tons, but, he estimated, in hundreds of thousands of tons.

COLLECTION OF PALOLO

Stair (1897: 142) describes collection of the palolo in November, 1843, near his residence on Upolu, Samoa, as follows:

"The worms are caught in small funnel shaped baskets, beautifully made, with handles about the centre. These baskets are skillfully glided over the surface of the ocean, and the worms emptied out as required into

¹ Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Technical Paper 413.

² Department of Foods and Nutrition, University of Hawaii Agricultural Experiment Station. Manuscript received February 4, 1958.

³ Mr. Gatty died in Fiji, August 30, 1957.

another receptacle. When taken on shore, the worms are tied up in leaves in small bundles and baked. Large quantities are eaten uncooked, but, either cooked or uncooked, they are universally esteemed a great luxury. Such is the strong desire to eat palolo shown by all classes, that, immediately the fishing parties reach the shore, messengers are dispatched in all directions, bearing large quantities to parts of the islands on which none are found."

Buck (1930: 440) found that the coconut fiber scoops and those made from the coconut leaflet midrib were no longer in use in Samoa in 1927, as thin gauze or scrim which could be easily obtained from the traders made better scoops.

Figure 1, from photographs taken by Mr. Gatty in November, 1953, shows the Fijians collecting the palolo, using various kinds of homemade scoops, mostly of cloth. Since at this location the palolo start to rise about 4 o'clock in the morning, Mr. Gatty took these pictures as soon as it was light. When the sun rises, the worms disappear rather rapidly.

Kramer (1903: 405) observed that the rise of the palolo was an occasion for special feasts with singing, dancing, and general rejoicing among the Samoans.

NATURE OF PALOLO

Figure 2 shows broken specimens of the palolo. In the original fresh state, Wood-

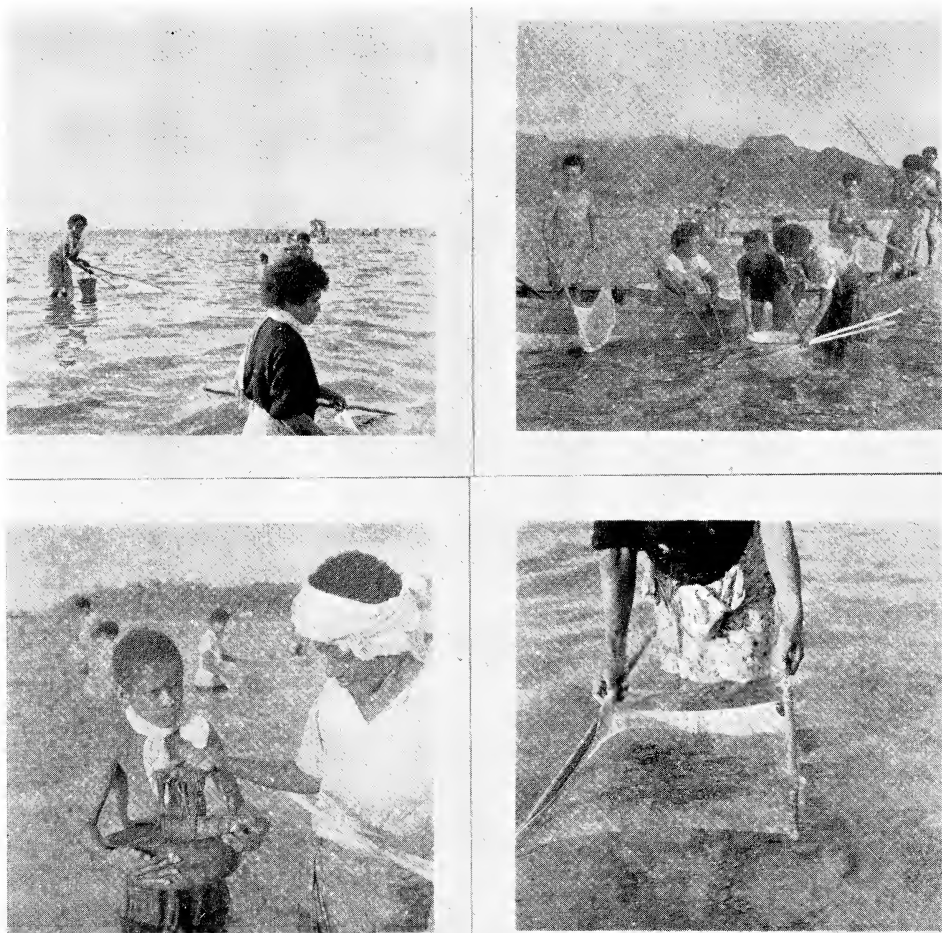


FIG. 1. Natives collecting palolo in Fiji.

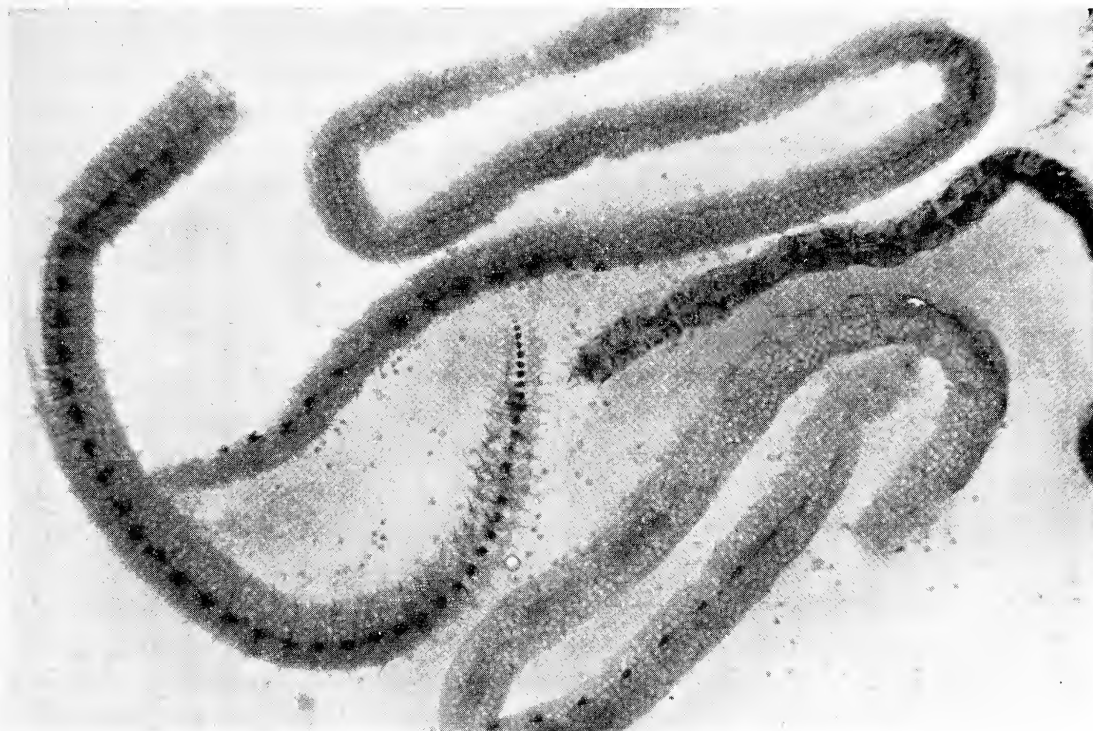


FIG. 2. Palolo showing eggs. About 5 × natural size.

worth (1907: 7) reports the longest one he measured was 30 centimeters (about 12 inches) in length, which is also "the average of the measurements given by seven authors." Our fresh-frozen specimens were 1 to 1½ millimeters in diameter. The females are filled with eggs, green in color, and the males with reddish-brown sperm. Since there are more females than males, the entire mass has a green color, resembling some of the edible sea weeds of the *Enteromorpha* species. In reality, the palolo which rises is the epitokal or long posterior end, i.e., the tail, of the worm. The head portion (atokal), which makes up about one fourth of the total length, stays in the coral rocks and generates a new body (Woodworth, 1907: 7).

Although marine biologists have been interested in the palolo for many years and the literature relating to taxonomy, morphology, and periodicity is extensive, the only chemical analyses we have found for *Eunice siciliensis* are those published by von Brand (1927: 688–

691) as follows: dry matter, 31.19 per cent; ash, 2.94 per cent; and fat, 2.97 per cent.

PROCEDURE

Sample Analyzed

The sample of palolo analyzed was obtained by Mr. Harold Gatty on November 30, 1953, in the Fiji Islands. Immediately after it was collected it was placed in a refrigerator on his launch and taken to Suva where it was quick-frozen a little less than 24 hours after it was gathered. The day that a Pan American plane was due from the Antipodes on its way to Honolulu, a thermos jug containing the frozen palolo was flown in one of Mr. Gatty's planes from Suva to Nandy. At Nandy, it was kept in a refrigerator until placed on the Pan American plane (via Canton to Honolulu) and in less than 20 hours it was in our own freezer.

Analytical Methods

The methods used for the determination of

the approximate composition, minerals, and vitamins of palolo were the same as those previously outlined for pandanus (Miller, Murai, and Pen, 1956: 9).

RESULTS AND DISCUSSION

The composition of palolo is given in Table 1 along with a familiar protein food, raw beef round, for purposes of comparison. Although primitive people with a limited food supply usually make good use of all foods available, the enthusiasm of the Samoans and Fijians for palolo seems justified, as the analyses prove it to be a food of high nutritive value.

Palolo has 15 per cent of protein compared with about 20 per cent in beef; and the fat content is about half that of beef. Palolo has three times more calcium, about twice as much phosphorus, and about the same quantity of iron as beef. Beef would furnish no vitamin A or carotene, but palolo is an excellent source, having a greater vitamin A value than whole eggs. The thiamine content of both foods is low. Palolo has almost four times as much riboflavin as beef, but beef has almost four times as much niacin as palolo. Sufficient material was not available and we were not prepared to make analyses for additional vitamins or for amino acids.

The palolo are eaten in the raw state just as they take them from the ocean; they are also eaten in the cooked state, and after cooking, they may be sun-dried to preserve them for future use. In Samoa the palolo are wrapped in leaves and cooked in the native oven of hot stones, often with coconut cream.

Mr. Gatty thought that palolo made the finest soup he had ever tasted and considered it warranted commercial exploitation as an Epicurean food. It is said to have a very delicious flavor, something like a cross between oyster and lobster, but superior to either.

Since palolo is a good protein food, rich in vitamin A, riboflavin, phosphorus, and iron, it seems unfortunate that it cannot be utilized to better advantage in the areas where it swarms. Because of the extremely short period when it can be gathered, the problem of reaping this nutritious harvest of the sea in any quantity will probably always remain a difficult one.

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TABLE 1
COMPOSITION OF PALOLO COMPARED WITH BEEF,
PER 100 GRAMS

	PALOLO (raw)	BEEF (raw round)
Water, per cent	76.2	69.0
Protein, gm.	15.1	19.5
Fat, gm.	4.9	11.0
Crude fiber, gm.	0.78	0
Ash, gm.	2.42	1.0
Calcium, mg.	37	11
Phosphorus, mg.	310	180
Iron, mg.	2.9	2.9
Vitamin A, I.U.	514	0
Carotene, mcg.	1,350	0
Thiamine, mg.	0.07	0.08
Riboflavin, mg.	0.59	0.17
Niacin, mg.	1.3	4.7
Ascorbic acid, mg.	1.6	0

Vegetative Anatomy of *Dubautia*, *Argyroxiphium*, and *Wilkesia* (Compositae)¹

SHERWIN CARLQUIST²

BECAUSE *Dubautia*, *Argyroxiphium*, and *Wilkesia* are endemic Hawaiian genera of uncertain position within the Compositae and are characterized by species markedly different in habit, a more thorough knowledge of anatomical structure in these genera and in putatively related genera is desirable. The purpose of this study is to explore the variation pattern of anatomical characters in vegetative organs of *Dubautia*, *Argyroxiphium*, and *Wilkesia*, and to suggest which of these appear to be important in indicating relationships among the genera and to other genera. The data may also be helpful in outlining natural groups within the genus *Dubautia*.

Information concerning secondary xylem of *Dubautia* is included in a separate study (Carlquist, 1958). The peculiar leaves of *Argyroxiphium*, and comparison of them with leaves of *Wilkesia*, form the subject of an earlier paper (Carlquist, 1957d). The present paper concerns the vegetative anatomy of the three genera in other respects. For the purposes of this study, the writer interprets *Dubautia* as including *Railliardia*, a treatment offered by Keck (1936: 24–28) and accepted by St. John (1950).

The dubious position of *Dubautia* can be appreciated by comparing the works of authors who have dealt with the genus. Although recent authors agree that *Dubautia* and *Railliardia*, if both genera are recognized, are closely related, earlier authors recognized both genera and relegated them to widely separated portions of the family. Bentham and Hooker (1873: 393), for example, place *Dubautia* near *Argyroxiphium* and *Wilkesia*, whereas they locate *Railliardia* (*loc. cit.*, p.

442) between *Railliardella*, a genus traditionally placed in Senecioneae, and the Juan Fernandez Senecioneae *Robinsonia* and *Rbetinodendron*. Although the systematic positions of *Argyroxiphium* and *Wilkesia* have been in doubt, they have been interpreted as belonging to the tarweeds (Heliantheae, subtribe Madinae) by such authors as Hoffmann (1890: 248). Hoffmann, however, places *Dubautia* and *Railliardia* in the subtribe immediately preceding Madinae, Galinsoginae. Skottsberg (1931: 56; 1956: 211) finds *Dubautia* and *Railliardia* possibly related to *Robinsonia* and *Rbetinodendron*, as well as to a New Guinea genus of Senecioneae, *Brachionostylum*. Keck (1936: 8) agrees, although he emphasizes the relation of *Dubautia* to *Argyroxiphium* and *Wilkesia*, which he excludes from Madinae and places in Galinsoginae; and he suggests that *Dubautia* (*sensu lato*), *Argyroxiphium*, and *Wilkesia* form a related endemic group. The fact that he relates *Dubautia* to elements of both Heliantheae and Senecioneae is not incongruent, in his opinion, because *Dubautia* may be regarded as a genus transitional between the tribes. *Dubautia*, therefore, would seem to be a critical genus in the delimitation of the tribes of Compositae. St. John (1950: 240) finds no genus with close affinities to *Dubautia*, and Sherff (1935) declines to comment. Because the Heliantheae mentioned above are American, demonstration of relationship between them and *Dubautia*, *Argyroxiphium*, and *Wilkesia* would be important by validating an example of Hawaiian-American phytogeographical affinity.

MATERIALS AND METHODS

The author's collections (listed below) from which portions were preserved in Carnoy's Fluid (3 parts absolute ethyl alcohol:

¹ Manuscript received November 20, 1957.

² Claremont Graduate School, Rancho Santa Ana Botanic Garden, Claremont, California.

1 part glacial acetic acid) provided good material for anatomical study. The others of the species, however, were studied from fragments of herbarium specimens treated according to techniques described earlier (Carlquist, 1957a: 207). The liquid-preserved material was prepared by means of techniques described in that paper. Preparations made from herbarium material, both as whole mounts and as sections, gave quite satisfactory information concerning vegetative anatomy. Every effort was made to secure mature leaves, to analyze structure of several portions of a leaf, and to secure stems both in primary condition, for a study of stem structure, and with some secondary growth, for study of mature pith types. Pith of the rosette species of *Argyroxiphium* (*A. sandwichense*) was taken from basal (epicotyl) portions of the rosette. Leaf anatomy was studied in all species except *D. coriacea* (Sherff) Keck, *D. demissifolia* (Sherff) Keck, and *D. kohalae* (Skotts.) St. John. These species would probably add little to the gamut of variation presented here. Stem anatomy was studied for the majority of the species of *Dubautia* and *Argyroxiphium*, as well as for *Wilkesia*. Subspecific variation was disregarded in this study, and analysis of the hybrids recognized by Sherff (1935) did not seem feasible at present.

Dubautia arborea (Gray) Keck, Rock 8344 (UC); *D. ciliolata* (DC.) Keck, var. *laxiflora* (DC.) Keck, Rock 10326 (UC); *D. Hillebrandii* (H. Mann) Keck, Hillebrand s.n. (GH, syntype); *D. Knudsenii* Hillebr., Carlquist H15 (UC); *D. laevigata* Gray, Heller 2616 (UC); *D. latifolia* (Gray) Keck, Heller 2887 (UC); *D. laxa* H. & A., Carlquist H12 (UC); *D. linearis* (Gaud.) Keck, Rock 8123 (UC); *D. lonchophylla* (Sherff) Keck, St. John 10303 (UC); *D. magnifolia* Sherff, Rock 9012 (BISH); *D. Menziesii* (Gray) Keck, Carlquist H17 (UC); *D. microcephala* Skotts., Carlquist H14 (UC); *D. molokaiensis* (Hillebr.) Keck, Forbes 86Mo (UC); *D. montana* (H. Mann) Keck, Rock 8594 (UC); *D. paleata* Gray, Forbes 914K (BISH); *D. plantaginea*

Gaud. var. *platyphylla* Hillebr., Carlquist H20a (UC); *D. platyphylla* (Gray) Keck, Forbes 1101M (UC); *D. raillardioides* Hillebr., Carlquist H16 (UC); *D. reticulata* (Sherff) Keck, Rock 8573 (UC); *D. Rockii* (Sherff) Keck, Rock 8601 (BISH); *D. scabra* (DC.) Keck, Carlquist H20 (UC); *D. Sherffiana* Fosb., St. John 23924 (BISH); *D. struthioloides* (Gray) Keck, Wilkes Exped. s. n. (GH, type); *D. ternifolia* (Sherff) Keck, Forbes 1175 (BISH); *D. thyrsiflora* (Sherff) Keck, Forbes 1203M (GH); *D. waialealae* Rock, Rock Oct. 1911 (GH, cotype). *Argyroxiphium Caliginii* Forbes, Carlquist H28 (UC); *A. Grayanum* (Hillebr.) Degener, Carlquist H27 (UC); *A. sandwichense* DC., Carlquist H19 (UC); *Wilkesia gymnoxiphium* Gray, Carlquist H10 (UC).

Gratitude is expressed to the curators of these herbaria for use of their materials. Data concerning the stem of *D. platyphylla* were obtained from a slide (prepared from a liquid-preserved collection by Degener, no. 19188) kindly given to the writer by Dr. John W. Hall. Thanks are due Dr. Harold St. John for his assistance during the author's field work in the Hawaiian Islands.

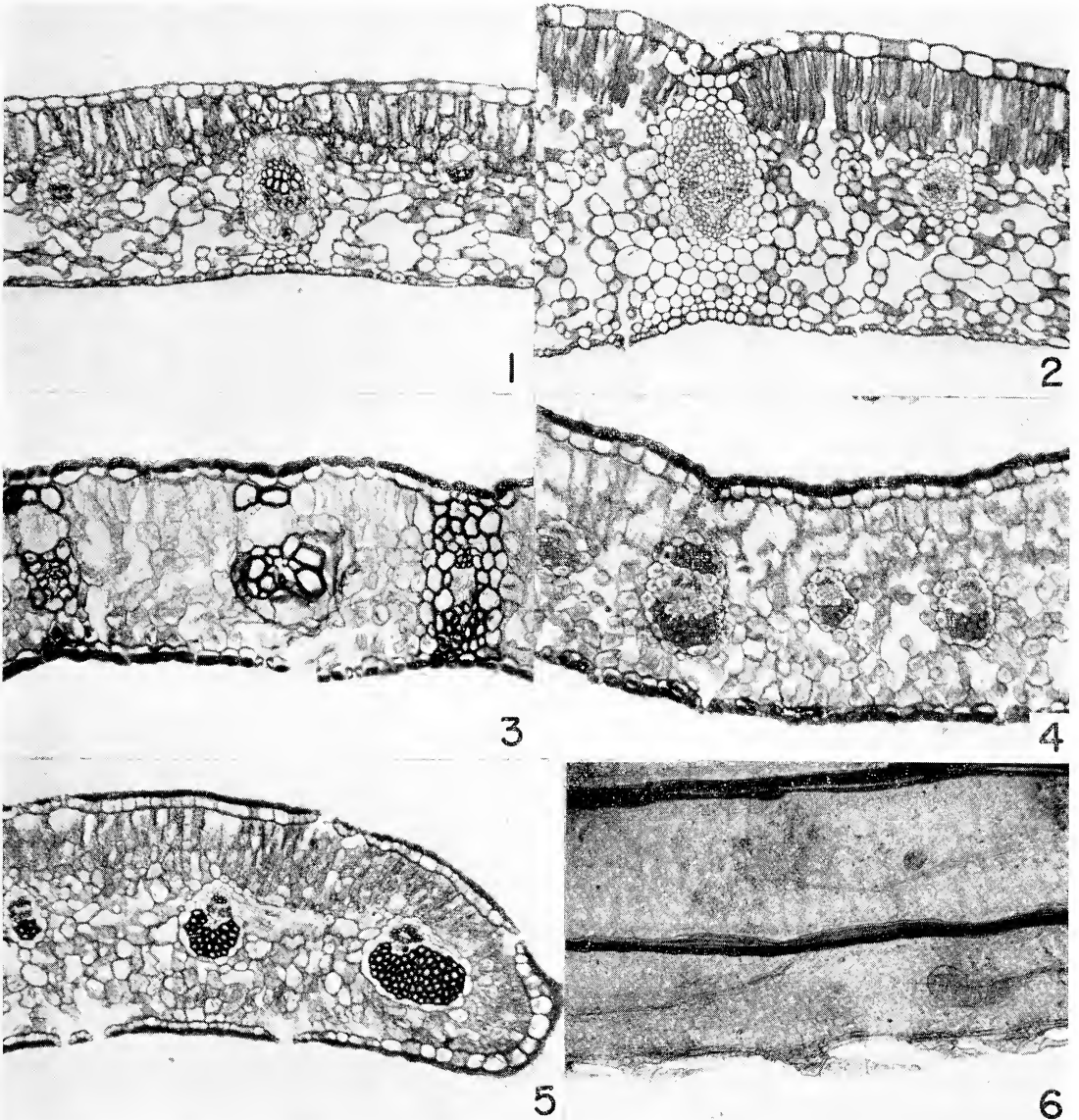
ANATOMY

Leaf Transections

Characters of leaf anatomy as seen in transections constitute the best indications of specific diversity in *Dubautia*. These characters include bifacial or isolateral organization, relative size of cells in upper and lower epidermis, thickness of cell walls in epidermis, width of palisade, frequency of bundle-sheath extensions, presence of fibers within the bundle sheath, presence of secretory canals in the bundle sheath, and occurrence of uniseriate nonglandular or biseriate glandular hairs. Cuticle is not included in description of epidermis cell wall thickness, because it was invariably a very thin layer. Numerous preparations showed separation of the cuticle from the epidermis (e.g., Fig. 3). The species of *Dubautia* are compared below by reference to "types" based on the species illustrated. No

taxonomic significance is necessarily implied by this arrangement. The groups below, however, do appear to be natural groups in some instances. For each group, the illustrated species is used as a basis for description, and the species most closely resembling it are listed beneath, with the features by which they differ mentioned in parentheses.

1. *D. Knudsenii* (Fig. 1). Leaf bifacial; cells of upper epidermis larger than those of lower epidermis, thin walled; 1 layer of palisade present; bundle-sheath extensions present on major veins only; fibrous bundle cap present only on major veins; secretory canals 4 near larger veins, 1 or 2 near smaller veins; trichomes absent at maturity.



FIGS. 1-6. Leaves of *Dubautia*. (1-5) Leaf transections. (1) *D. Knudsenii*, $\times 75$. (2) *D. raillardioides*, $\times 67$. (3) *D. latifolia*, $\times 95$. (4) *D. waialealae*, $\times 87$. (5) *D. Menziesii*, $\times 67$. (6) *D. lonchophylla*, portion of cleared leaf to show marginal trichomes, below, and secretory canals, which appear as darker lines (on account of resins) beside two larger veins, $\times 58$.

Like *D. Knudsenii*:

D. laxa (a few uniseriate hairs on lower surface).

D. molokaiensis (thicker outer walls on upper epidermis).

D. reticulata (thick-walled upper epidermis; uniseriate hairs frequent on both surfaces, especially in the grooves overlying veins on the upper surface).

2. *D. raillardioides* (Fig. 2). Leaf bifacial; cells of upper epidermis larger than those of lower epidermis; prominent grooves on upper surface above major veins; 2 palisade layers present; sheath extensions present on many larger veins; fibers common at both poles of larger veins; 4 secretory canals in outer portion of bundle sheath of larger veins, 1 or 2 near smaller veins; scattered uniseriate trichomes on lower surface and margins (upwardly appressed).

Like *D. raillardioides*:

D. magnifolia, *D. microcephala*, *D. plantaginea* (virtually identical with *D. raillardioides*).

D. paleata (sheath extensions on major veins only; fibers more common at phloem pole of veins; secretory canals absent; numerous uniseriate hairs on both surfaces).

D. ternifolia (fibers more common on phloem face of bundles).

D. scabra, *D. ciliolata*, *D. lonchophylla*, *D. linearis*, *D. Sberffiana*, *D. thyrsiflora* (upper epidermis very large celled; bundle-sheath extension on midvein only; fibers mostly on phloem face of bundle; usually 1 secretory canal above xylem pole of larger veins).

D. platyphylla (fibers at phloem face of bundles only; secretory canals absent; biseriate glandular hairs with large multicellular capitate heads and long stalks abundant on both surfaces; uniseriate hairs absent).

3. *D. latifolia* (Fig. 3). Leaf bifacial, thin; upper and lower epidermis cells of approximately the same size, very thick walled; a single layer of cells weakly defined as palisade; bundle-sheath extensions frequent, consisting of isodiametric to fiber-like sclereids, although no "bundle cap" fibers are present on the vascular bundles; 1 or 2 secretory canals present within the bundle sheath or sheath extension of many veins; hairs absent at maturity.

Like *D. latifolia*:

D. laevigata (sclerenchyma of bundle sheaths and sheath extensions consisting of thick-walled fibers; secretory canals absent).

4. *D. waialealae* (Fig. 4). Leaf bifacial; cells of upper and lower epidermis of about the same size, very thick walled; 1 or 2 layers somewhat differentiated as palisade; sheath extensions present only on midvein; prominent strands of thick-walled fibers on phloem face of veins, also on xylem pole of larger veins; secretory canals absent; large uniseriate trichomes abundant on upper surface and on margins.

5. *D. Menziesii* (Fig. 5). Leaf somewhat isolar (stomata frequent on upper surface; adaxial palisade cells short, nearly isodiametric; cells on abaxial face like adaxial palisade cells in shape, with more numerous chloroplasts than cells in the central portion of the leaf); leaf very thick; bundle-sheath extension only on midvein; large groups of fibers on phloem face of veins (a few fibers on xylem pole of larger veins); secretory canals infrequent, 1 or 2 in bundle sheath of larger veins near leaf base; thick-walled uniseriate trichomes scattered over both surfaces and margin of leaf.

Like *D. Menziesii*:

D. Hillebrandii (nearly identical with *D. Menziesii*).

D. arborea (fibers lacking near veins; biseriate glandular hairs present on both leaf surfaces).

D. Rockii (a single secretory canal adaxial to most veins).

D. montana (fiber strands near veins small).

D. struthioloides (more nearly isolateral than *D. Menziesii*).

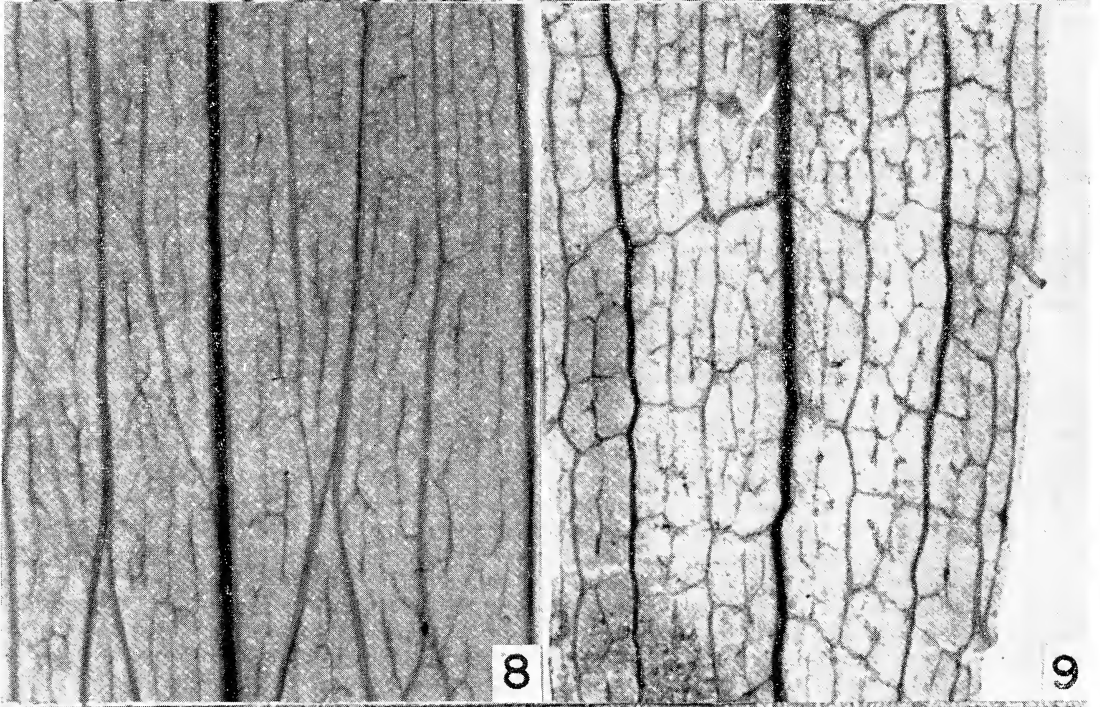
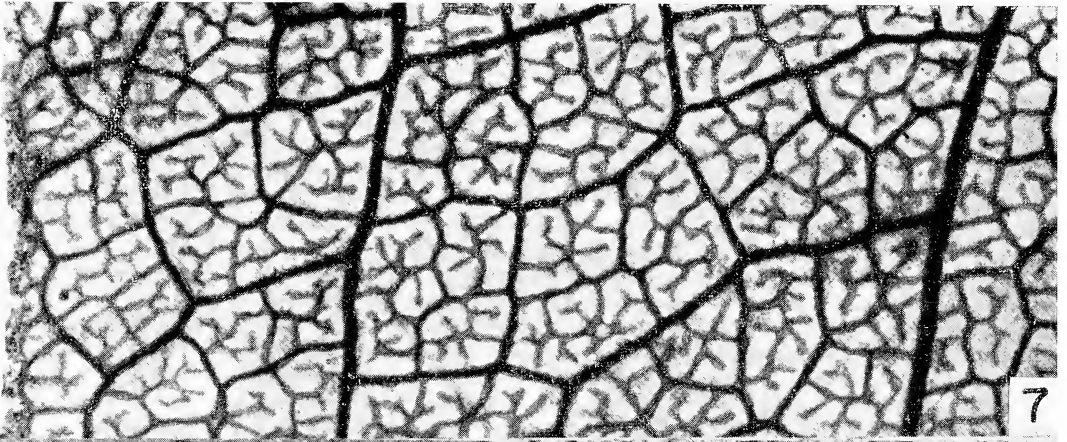
The different types of leaf structure detailed above reflect ecological conditions for *Dubautia* to a certain extent, as well as being indicative of taxonomic groupings. The thin, glabrous leaves of *D. Knudsenii*, with thin-walled epidermal cells, correspond to the moist forest areas on Kauai where that species grows. On the contrary, the tendency toward thick, isolateral leaves with thick-walled epidermal cells in *D. Menziesii* seems related to the dry, sunny alpine habitat of this plant. Most of the species indicated here as having similarity to *D. Menziesii* are also alpine types.

The highly specialized leaf anatomy of *Argyroxiphium* (Carlquist, 1957*d*) bears little superficial resemblance to that of even the isolateral-leaved species of *Dubautia*. The presence of fiber strands along veins, secretory canals (in *A. Caliginii*), and the presence of uniseriate hairs (much more abundant in *Argyroxiphium*) are similar features. The capitate biseriate glandular hairs on inflorescence bracts of *Argyroxiphium* and *Wilkesia* are very similar to those on leaves of *Dubautia platyphylla*. *Dubautia* shows little differentiation of leaves near inflorescences into inflorescence bracts, whereas in *Argyroxiphium* a marked difference, reflected in the anatomical structure, is seen between vegetative leaves and bracts of the inflorescence. The leaf of *Wilkesia*, which differs markedly from that of *Argyroxiphium* (Carlquist, 1957*d*), appears much like the leaf of *Dubautia laevigata* in transection. Although the genera *Dubautia* and *Wilkesia* lack the intercellular deposition of pectic compounds which is characteristic of *Argyroxiphium*, cell walls in leaves of *Dubautia* and *Wilkesia* are rich in pectic compounds. Treatment of leaves of the latter with hydrofluoric acid prior to sectioning proved

impracticable because the acid released such compounds from the wall and caused swelling and distortion of the leaves. The phenomenon described by the writer as "abaxial meristem" in *Argyroxiphium* is totally lacking in *Dubautia*, as it is in *Wilkesia*.

Leaf Venation

Figures 7–9 show the range of venation types which may be seen in the genus *Dubautia*. *Dubautia latifolia* (Fig. 7) is exceptional for the genus in its reticulate vein pattern with polygonal areoles containing numerous freely-terminating veins. Except for the major veins (two of which are shown, left and right of center, respectively), there is no tendency for orientation of veins longitudinally in the leaf. *D. latifolia* is apparently the only species which has this venation pattern. This distinctive feature is recognized by the segregation of *D. latifolia* as a separate section of the genus, "*Venoso-reticulatae*" (Sherff, 1935: 111), whereas the remainder of the *Railliardia* species are included by Sherff in the section "*Nervosae*." The most typical venation condition in *Dubautia* is illustrated by *D. linearis* (Fig. 9). In this species, the five main veins run the length of the leaf, as in *D. latifolia*. Marginal veins and those between the primary veins also have a distinctly longitudinal course. Areoles are more nearly rectangular, elongated with the long axis of the leaf. Vein endings are frequent. *Dubautia microcephala* (Fig. 8), *D. plantaginea*, and *D. raillardioides* show a modification of this pattern. In these species all of the major venation and much of the minor venation show a longitudinal orientation. Areoles are very elongate, and vein endings are more infrequent than in *D. linearis*. The predominant pattern of venation in the genus *Dubautia*, then, is like that of *D. linearis*, and is therefore a departure from typical reticulate dicotyledonous venation. One may question whether the reticulate venation of *D. latifolia* is a primitive condition or a "reversion." The advanced position of *D. latifolia* in characters



other than venation may suggest the latter interpretation. Probably the type of venation shown by *D. linearis* is basic for the genus because it is found in conjunction with other unspecialized characters in some of the putatively primitive species. The type of venation illustrated by *D. microcephala* seems clearly a specialized condition.

Comparison of leaf venation in *Dubautia* with that of *Argyroxiphium* and *Wilkesia* is pertinent in this regard. Paradermal sections of *Argyroxiphium* leaves reveal that the basic venation is similar to that of *D. linearis* if the additional vein series denoted by the writer as "upper" and "lower" sets of veins (Carlquist, 1957*d*) are disregarded. *Wilkesia* (Fig. 10), on the contrary, is markedly different from *Argyroxiphium* in its venation. This remarkably monocotyledonous venation pattern is characterized by longitudinal orientation of virtually all of the major and minor veins. Cross-connections between the longitudinally oriented veins are infrequent. Although this pattern appears to be anomalous in comparison with the types described above, it may well have been derived from a type like that of *Dubautia microcephala* by means of a more nearly exclusive production of longitudinally oriented veins. Venation similar to that of *Wilkesia* has been described for another member of Compositae in *Schlectendalia luzulaefolia*, a member of the tribe Mutisieae (Urban and Möbius, 1884).

Nodal Anatomy

The genus *Dubautia* is curious because of the variation in phyllotaxy and the presence of both petiolate and sessile clasping leaves within the genus. Both of these characters of leaf attachment are related to the vascular pattern of nodes. Although the author's material did not prove sufficient for placing each species in a category, the data below probably indicate the full range of types which occur in

the genus. The types indicated include all that have been reported previously for the family, except for multilacunar nodes with an alternate-leaved condition. This latter type does not occur in any of the alternate-leaved species, which are uniformly trilacunar. As some of the examples below show, transitions between the recognized types may occur in a single stem.

1. Trilacunar, alternate leaves. Examples: *D. Sberffiana*, *D. lonchophylla*.
2. Trilacunar, opposite (decussate) leaves. Examples: *D. Menziesii* (Fig. 12), *D. montana*, *D. latifolia*, *D. platyphylla*, *D. scabra*. The drawing of *D. Menziesii* shows, below, a trilacunar node with only the traces of the facing leaf indicated. Above is a node in which both leaves of the pair are supplied by 4 traces. This node, then, is transitional between trilacunar and multilacunar. The additional pair of traces, on the far side of the stem, fuse to a single trace a short distance below the node. Such fusion of adjacent laterals is not characteristic of trilacunar nodes in *Dubautia*.
3. Trilacunar, verticillate leaves. Examples: *D. ternifolia*, *D. waialealae*. The 3 traces of each leaf at a node continue downward into the vascular cylinder without fusion of adjacent laterals.
4. Multilacunar, opposite (or decussate) leaves. Examples: *D. laxa* (Fig. 14), *D. laevigata* (Fig. 13), *D. magnifolia*, *D. Knudsenii*. As comparison of Figures 13 and 14 shows, multilacunar nodes can differ in number of traces and in the fusion of traces below a node. In *D. laxa* (Fig. 14), each leaf is provided with 5 (or 6) traces, which continue downward into the vascular cylinder independently. The most lateral traces in each leaf base increase the number of veins in the leaf margin by branching toward the margin. In *D. laevigata* (Fig. 13), more numerous traces con-

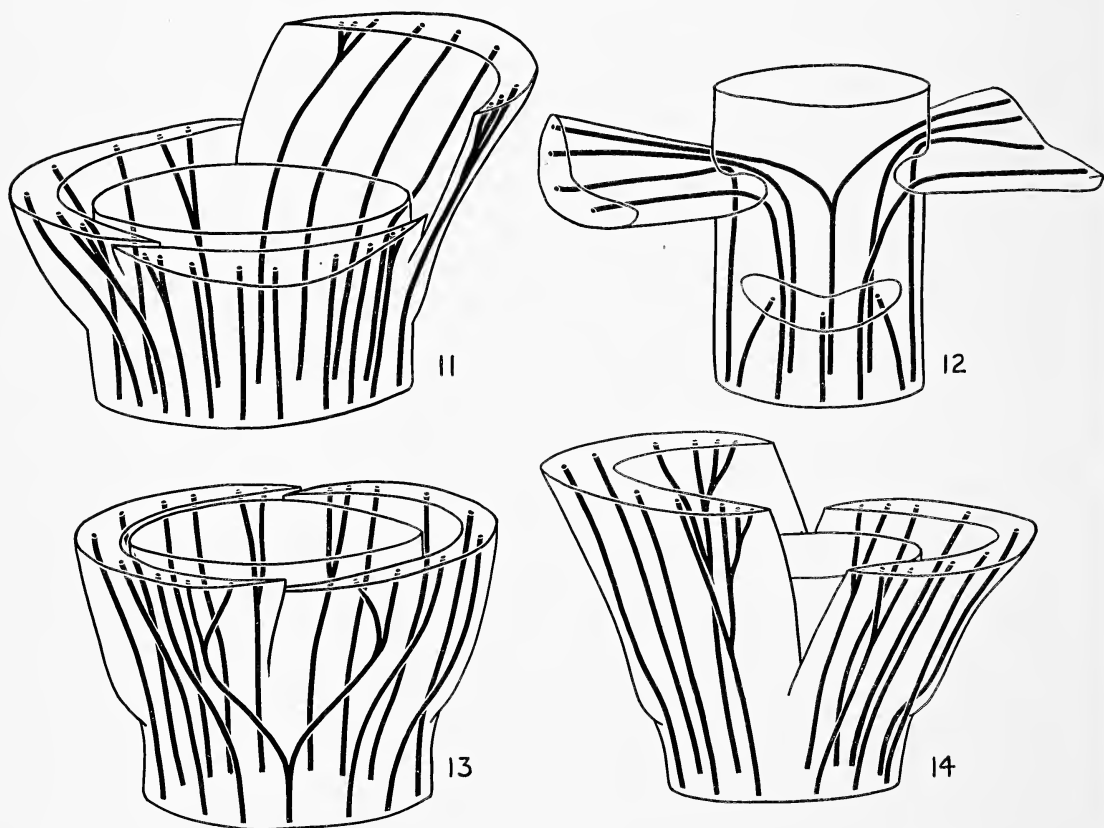
FIGS. 7-10. Portions of cleared leaves to show venation. (7) *D. latifolia*; margin at left; $\times 10.5$. (8) *D. microcephala*, $\times 13.5$. (9) *D. linearis*; margin at right; $\times 9.5$. (10) *Wilkesia gymnoxiphium*; margin below; $\times 9.5$.

tinue downward into the vascular cylinder. In addition, the most lateral pair shown on the near side of the stem unite. This union of adjacent laterals, mentioned above for *D. Menziesii*, is characteristic of some Heliantheae with opposite leaves, and has been reported by Carlquist (1957c) for *Fitchia* and *Oparanthus*.

5. Multilacunar, verticillate leaves. Example: *D. raillardioides* (Fig. 11). Five traces, related to 5 gaps, enter each leaf at a node, which usually consists of 3 leaves. As in *D. laxa* and *D. laevigata*, increase in number of veins at the leaf base is accomplished by branching of the laterals. The occurrence of a multilacunar condition at a verticillate node is of particular signifi-

cance because, according to Dr. I. W. Bailey (personal communication), this condition has never been reported in dicotyledons. The author (1957d) suggested that it may occur in *Argyroxiphium Grayanum*, a species which was demonstrated to have alternate leaves with multilacunar nodes, but in which rare individuals have verticillate leaves.

The great diversity of nodal types in *Dubautia* is of considerable interest. Despite this diversity, however, a marked contrast with *Wilkesia* occurs in regard to branching of veins in the leaf base. *Wilkesia* has verticils of numerous leaves, each of which is related to a trilacunar condition (Carlquist, 1957d, fig. 18). At the leaf base, the laterals are at the



FIGS. 11-14. Reconstructions of nodes of *Dubautia* (based on serial sections). (11) *D. raillardioides*, $\times 6$. (12) *D. Menziesii*, $\times 11.5$. (13) *D. laevigata*, $\times 5.6$. (14) *D. laxa*, $\times 6.5$. Darker lines represent veins; lighter lines represent the outlines of a nodal segment including leaf bases.

margins of the leaf and branches are given off toward the margin, whereas in *Argyroxiphium* the branches are given off toward the midveins. *Dubautia* resembles *Wilkesia* in this respect. In *Argyroxiphium* (Carlquist, 1957d, fig. 17), however, the alternate leaves are related to multilacunar nodes, and adjacent laterals of successive leaves in the spiral are united below the leaf base.

Dubautia, *Argyroxiphium*, and *Wilkesia*, then, are amply distinct from each other in nodal anatomy. The taxonomic interest of the different types within *Dubautia* seems evident; the phylogenetic relationship of the various types in the three genera, however, will be better understood when greater knowledge of nodal anatomy in Compositae at large is available.

Pith

The wide range of pith types in *Dubautia* is suggested by comparison of Figures 15–18 (see also Figs. 21, 22, right). As with patterns of leaf construction, these can be referred to a number of types; these should not be regarded as categories, however, although some reflect natural assemblages of species:

1. *D. plantaginea* (Fig. 15). Pith cells thin walled with small intercellular spaces; periphery (inner margins of bundles) sclerified; secretory canals present (opposite inner faces of larger bundles); no carbonized resin deposits present.

Like *D. plantaginea*:

D. microcephala, *D. raillardioides*, *D. lonchophylla* (virtually identical with *D. plantaginea*).

D. paleata (peripheral sclerenchyma very thick walled).

D. scabra (secretory canals infrequent).

D. magnifolia (periphery unsclerified).

D. ternifolia (patches of sclereids present throughout pith).

D. Knudsenii, *D. platyphylla*, *D. laxa*, *D. ciliolata* (secretory canals absent).

D. thyrsoflora (no secretory canals;

some cells in center of pith sclerified; carbonized resin deposits in intercellular spaces).

D. laevigata (no secretory canals; entire pith sclerified, more markedly so at periphery).

2. *D. linearis* (Fig. 16). Entire pith sclerified, not more so at periphery than at center; intercellular spaces small; no secretory canals; carbonized resin deposits not observed.

Like *D. linearis*:

D. Sberffiana, *D. reticulata* (carbonized resins in intercellular spaces).

3. *D. latifolia* (Fig. 17). Pith thin walled except at periphery, where it is prominently sclerified, and in the center, where nests of sclereids occur; the central sclereids are much narrower in diameter than other cells of the pith; intercellular spaces small; secretory canals absent; carbonized resin deposits in intercellular spaces of thin-walled area of pith. This pith type appears to be a marked specialization over the preceding types.

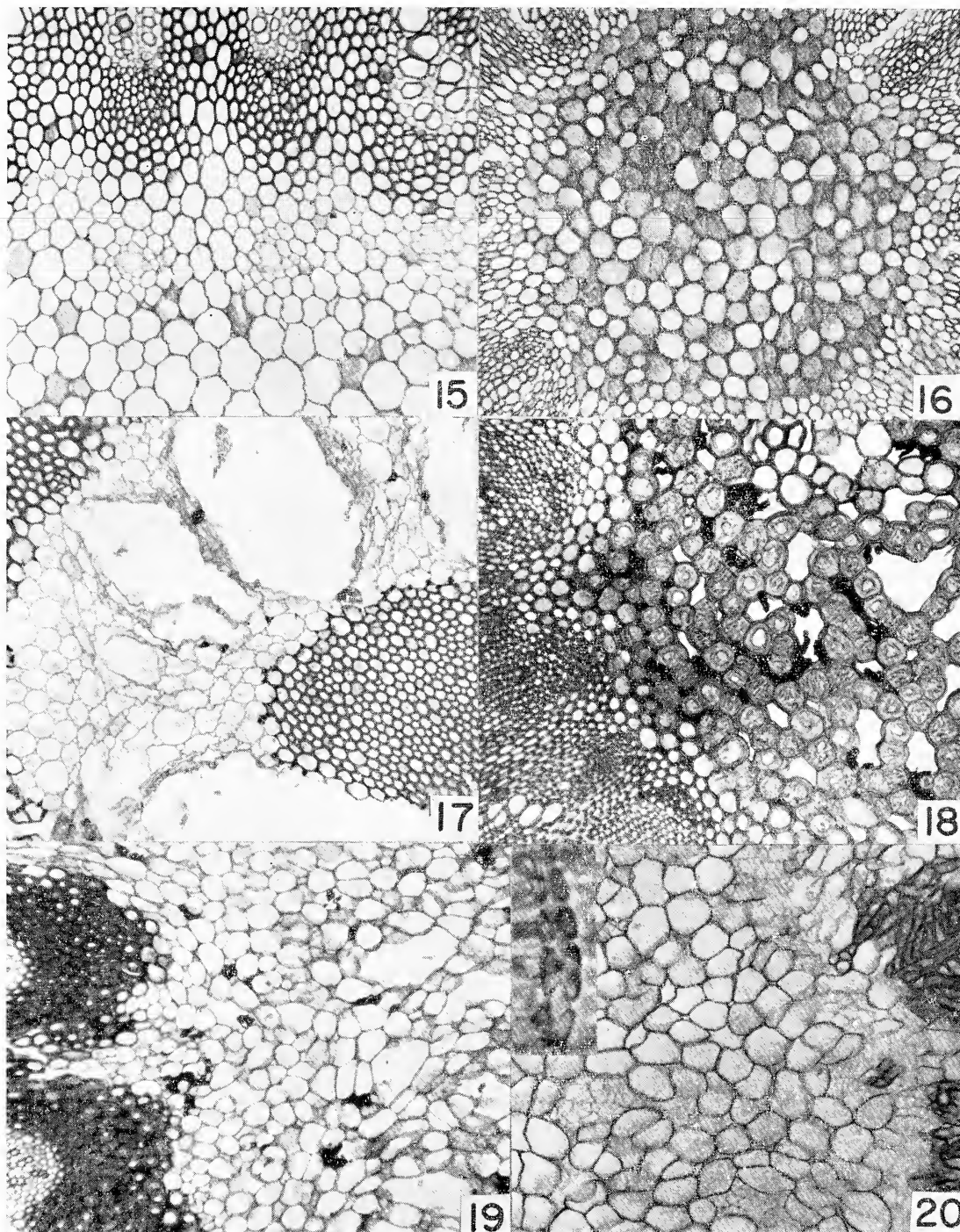
4. *D. Menziesii* (Fig. 18; Fig. 21, right). Pith highly lacunose, owing to large intercellular spaces; periphery consisting of small fiberlike sclereids adjacent to bundles; remainder of pith composed of large cells, both sclerified and unsclerified; no secretory canals; carbonized resins abundant in intercellular spaces. Figure 21 shows an early stage in the development of this pith, whereas pith from an old stem is shown in Figure 18. The progressive sclerification is evident, although some thin-walled cells remain in the pith shown in Figure 18.

Like *D. Menziesii*:

D. montana, *D. struthioloides*, *D. Hillebrandii* (virtually identical with *D. Menziesii*).

D. arborea (fewer sclereids).

This type of pith would seem to represent a specialization over the condition indicated for *D. plantaginea*. An intermediate



FIGS. 15-20. Transections of pith. (15) *D. plantaginea*, $\times 75$. (16) *D. linearis*, $\times 80$. (17) *D. latifolia*, $\times 84$. (18) *D. Menziesii*, $\times 78$. (19) *Argyroxiphium Caliginii*, $\times 72$. (20) *A. sandwichense*; packets of pith tracheids at right; groups of procambial cells below and left; $\times 90$; inset shows bordered pits between two pith tracheids, $\times 870$.

stage in specialization may be represented by *D. waialealae*.

5. *D. waialealae* (Fig. 22, right). Pith entirely thin walled, with large intercellular spaces; no secretory canals present; carbonized resin deposits in intercellular spaces.

The pith of *Argyroxiphium Caliginii* (Fig. 19) is highly lacunose, and carbonized resin deposits are present. The inner margins of vascular bundles are clothed with a conspicuous zone of very thick-walled fibers. The remainder of the pith, however, remains thin walled and unligified. An identical condition occurs in *A. Grayanum*. *Wilkesia* differs only in lacking carbonized resin deposits.

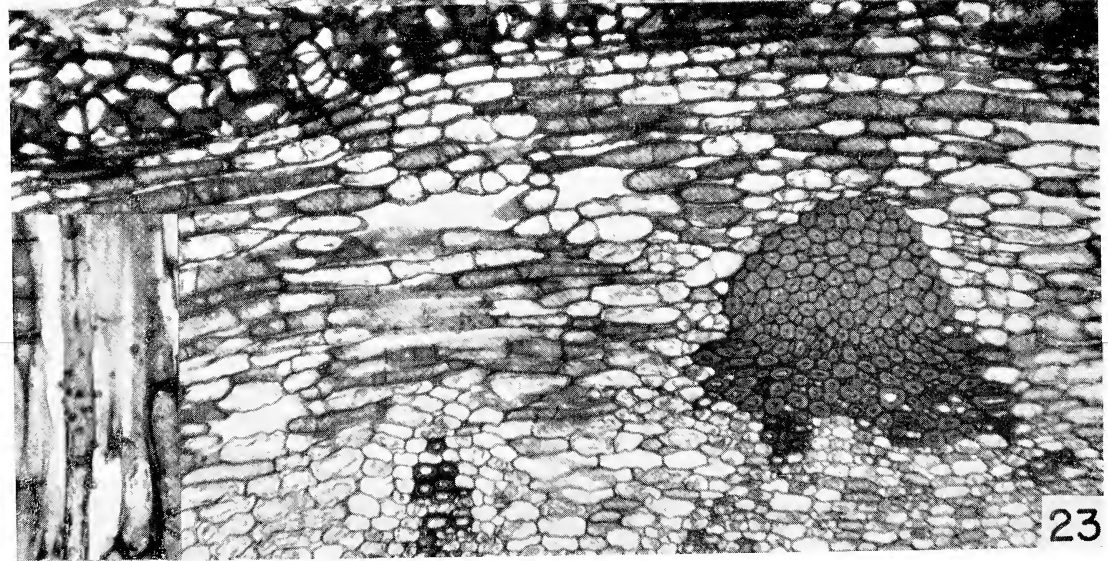
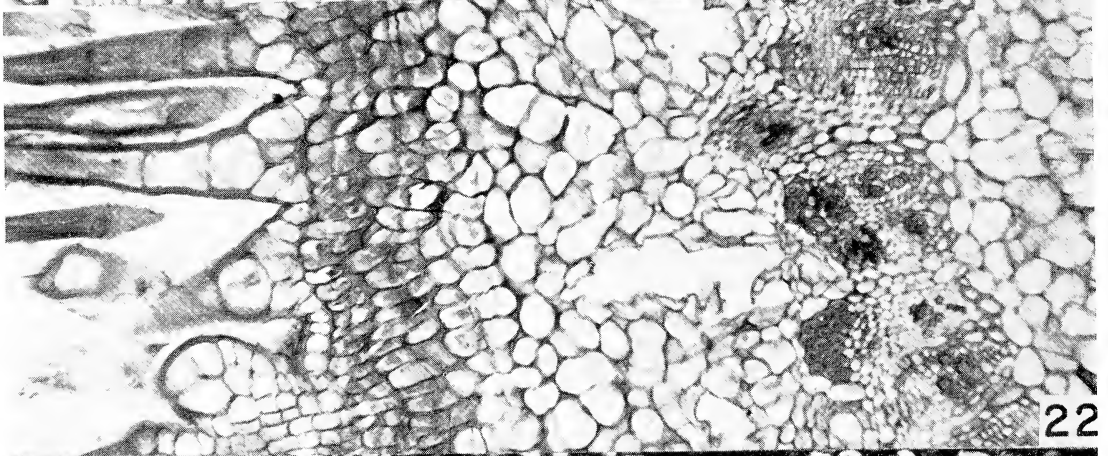
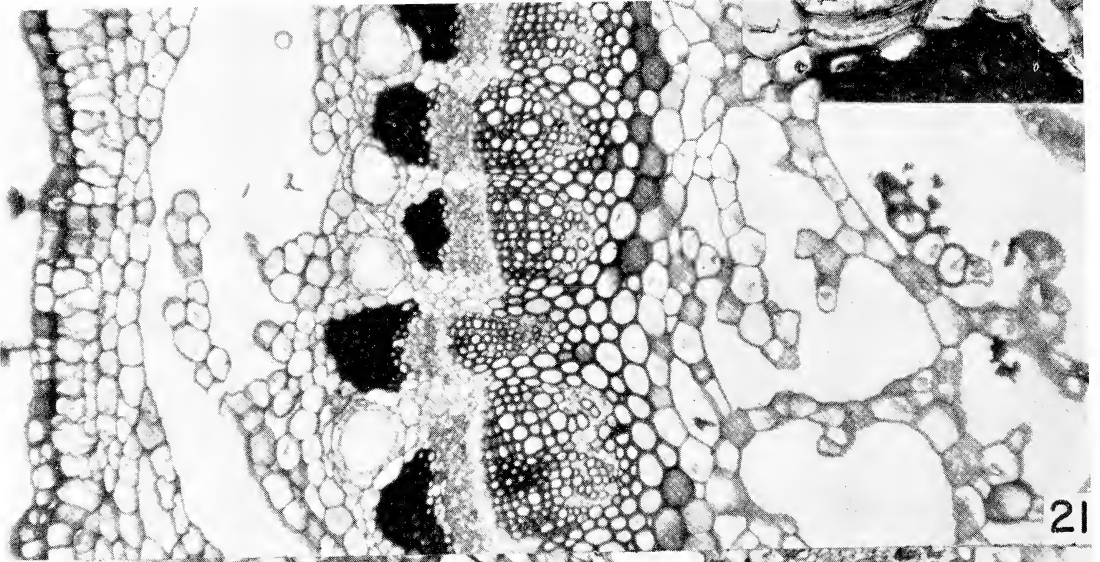
The pith of *Argyroxiphium sandwichense* (Fig. 20), however, shows a remarkable anomalous feature. Basically, pith in this species is identical with that of *A. Caliginii* in that it is lacunose and has fibrous caps on inner faces of the bundles. Into the large intercellular spaces of the cells of mature pith, however, new cells are proliferated by pre-existing pith cells. These new cells subdivide in various planes, often forming packets oriented in a particular direction. Most of these packets mature into sclerified cells (Fig. 20, right) although some of them (Fig. 20, left) apparently remain thin walled. Some of these sclerified cells, although somewhat elongate and fiberlike, have simple pits and should probably be termed sclereids. Others, as the inset in Figure 20 shows, have bordered pits and must therefore be termed tracheids. However, because Compositae do not have tracheids in the proper sense in their xylem, these tracheids are perhaps more nearly comparable to the "vascular tracheids" (i.e., degenerate vessels which lack perforation plates) which do occur in the secondary xylem of *A. sandwichense* (Carlquist, 1958). For the phenomenon described above, the term "pith tracheid" might be invented to accommodate their distinctive origin and mode of occurrence. The formation of these pith tracheids might be likened to the formation of tracheids in callus, such as those which occurred

in the experiments of Wetmore and Sorokin (1955). The formation of nests of sclereids and pith tracheids in *A. sandwichense* pith, however, is apparently not related to pre-existing vascular tissue, with which the pith tracheids are not in continuity. The formation of these nests is centripetal: the central portion of the pith was observed to contain only thin-walled cells, whereas such packets have matured into sclereids and tracheids near the periphery of the pith. A given nest may contain tracheids only, sclereids only, or a mixture of the two cell types. As in the experiments of Wetmore and Sorokin, no phloem could be detected in association with the pith tracheids.

Although the diversity of pith types in *Dubautia* is considerable, the pith of *Argyroxiphium* and *Wilkesia* does not match that of any given species of *Dubautia*. The presence of certain features, such as carbonized resins, is very similar, and pith of *Argyroxiphium* and *Wilkesia* can be considered to be within the range of the variation pattern of *Dubautia* pith.

Stem

The structure of the stem in respects other than nodal anatomy and pith anatomy is relatively uniform within *Dubautia*, *Argyroxiphium*, and *Wilkesia*, so that a small number of examples may be used, and variations may be described where they occur. In *Dubautia Menziesii* (Fig. 21), the vascular bundles develop prominent bundle caps of proto-phloem fibers. The layer of cells immediately exterior to the fibers is a well-marked endodermis (Fig. 21, inset) in which a Casparian strip may easily be demonstrated. The endodermis accompanies the bundle cap of a leaf trace in its departure from the vascular cylinder, although no endodermis occurs in leaf base or leaf. Although stem endodermis is uncommon in dicotyledons at large, it is frequent in Compositae, as the data of Metcalfe and Chalk (1950: 788) and Carlquist (1957c: 47) show. Numerous secretory canals are arranged adjacent to the vascular bundles.



Although the secretory canals appear at first glance to be arranged at random, examination of serial sections shows that they occur in pairs beside larger bundles which, farther up the stem, depart from the vascular cylinder as leaf traces. Cortical secretory canals, then, are initiated continuously with growth in length of the stem, because departure of secretory canals in association with leaf traces would result in their total absence in upper portions of a stem if new ones were not initiated. In *D. Menziesii*, cortical secretory canals continue into the leaf base for a short distance, although distal portions of the leaf lack them. In species which characteristically have such canals in the lamina, such as *D. Knudsenii* (Fig. 1), these canals continue from the stem into the leaf and either ramify or (particularly in the case of canals adaxial to veins) originate *de novo*. As the portion of a cleared leaf of *D. lonchophylla* in Figure 6 shows, these canals mainly parallel the larger longitudinally oriented veins. The cortex of *D. Menziesii* exterior to the secretory canals is highly lacunate. In the stem shown in Figure 21, cork formation is beginning. Periclinal divisions may be seen both in the epidermis and in the layer immediately beneath the epidermis. Cork formation, then is not restricted to a single layer of the stem. At extreme left in Figure 21, two degenerating biseriate glandular hairs may be seen.

The stem of *D. waialealae* (Fig. 22) illustrates several points of contrast. Only small lacunae are present in the cortex (gaps in that region in Fig. 22 probably resulted from the fact that a dried specimen was used for this preparation). Secretory canals are infrequent, although a small canal may be seen below the large bundle cap, lower right. Cork formation is not initiated in the epidermis, which is almost entirely involved in the formation of trichomes, but may be seen in the two or three

cell layers below the epidermis. As in *D. Menziesii*, therefore, cork formation is not limited to a single layer. The hairs which thickly clothe the stem of *D. waialealae* are nonglandular and uniseriate in their upper portions. The multicellular nature of the trichome base results from elongation of epidermal cells subtending the hair. The trichome proper, therefore, may be termed uniseriate.

The differences between *D. Menziesii* and *D. waialealae* mentioned above are not great, and represent the extremes of variation observed in the genus. The majority of the species have moderately lacunate cortex, intermediate between these two types. Although secretory canals were found to be scarce or lacking in the stems of *D. waialealae* and *D. platyphylla* examined, they are present to some extent in the remaining species.

In the aspects of stem structure mentioned above, *Argyroxiphium* and *Wilkesia* are referable to exactly the same pattern. In *Argyroxiphium*, carbonized resin deposits, like those of the pith, occur in intercellular spaces in the cortex, as well as between fibers in bundle caps. *Argyroxiphium Caliginii* is the only species of its genus in which secretory canals are present in the leaves (Carlquist, 1957*d*): secretory canals accompanying leaf traces continue into the leaves. In other species, they terminate below the level at which leaf traces enter leaf bases. In *Wilkesia*, which also lacks foliar secretory canals, many of the leaf traces are not accompanied by secretory canals, although canals are abundant around the vascular cylinder proper. Secretory canals in *Wilkesia*, for the most part, terminate below separation of leaf traces from the cylinder.

Abundant cork formation from subepidermal layers is characteristic of *Argyroxiphium Caliginii* and *A. Grayanum*, whereas little cork occurs in the rosette species *A. sand-*

FIGS. 21–23. Transections of stems of *Dubautia*. (21) *D. Menziesii*; epidermis at left; $\times 98$; inset shows endodermis with Casparian strip (line running through cells above fibers), $\times 350$. (22) *D. waialealae*, $\times 115$. (23) *D. platyphylla*; stem showing secondary growth; cork above, secondary phloem below; $\times 107$; inset shows an area of lacunate cortex, enlarged, in which pectic warts are present on cell walls, $\times 218$.

wickense and *A. virescens*. In *Wilkesia*, the layer beneath the epidermis is differentiated into a discrete hypodermis consisting of thick walled sclereids, and cork formation is initiated in a single layer immediately interior to the hypodermis.

The stems of both *Argyroxiphium* and *Wilkesia* lack endodermis demarcated by Casparian strips, although the formation of tangential sheets of cytoplasm in the layer of cells immediately exterior to bundle caps indicates that this layer of cells may be somewhat differentiated as an endodermis.

Biseriate glandular hairs with capitate multicellular heads are characteristically present on the stems of both *Argyroxiphium* and *Wilkesia*. These trichomes are of the same type as those illustrated by Carlquist (1957*d*) for inflorescence bracts of *Wilkesia* and *Argyroxiphium sandwichense*.

The similarities between stem structure of *Argyroxiphium* and *Wilkesia* and that of *Dubautia* are considerable, and are what one would expect if the three genera represent derivations from a common ancestry.

Secondary Growth

Aspects of secondary xylem structure in *Dubautia*, *Argyroxiphium*, and *Wilkesia* have been considered in an earlier paper (Carlquist, 1958). The stem of *D. platyphylla* (Fig. 23) demonstrates alterations in phloem and cortex structure as a result of secondary growth. Abundant cork development is evident, above. Formation of fibers in secondary phloem may be seen, below. The stem illustrated is young enough so that the cortex has not been ruptured, and characteristics of old cortical cells are shown. Cortical cells have experienced considerable tangential stretching. A particular feature of interest is the formation of pectic warts on the surfaces of cell walls which face intercellular spaces (Fig. 23, inset). These structures have been reported for cortical cells of Compositae only in *Wyethia ovata* (Carlquist, 1956). They do, however, occur on pith cells of *Argyro-*

xiphium sandwichense (Carlquist, 1957*d*).

Root

Roots of the genus *Dubautia* were not studied. In *Argyroxiphium* and *Wilkesia*, which the writer was able to grow from seed he collected in the Hawaiian Islands, anatomical studies were made. Adventitious roots of *A. Caliginii* were preserved in the field. Roots in these genera show typical dicot root structure. In *A. sandwichense*, roots varied from diarch to pentarch, depending on the diameter of the root. The primary root of the seedling, and all of the finer roots of a mature plant were found to be diarch. In the adventitious roots of *A. Caliginii*, which have a relatively larger diameter, five to seven xylem poles were observed. A variation of two to five xylem poles was observed in *Wilkesia*.

In roots of *A. sandwichense*, there are numerous small quadrangular "endodermal" secretory canals, of the type described by Tetley (1925) and Williams (1954). In the adventitious roots of *A. Caliginii*, a pair of somewhat larger secretory canals occurs exterior to each phloem strand. These secretory canals are similar to those figured by Carlquist (1957*c*: 116-119) for *Fitchia speciosa*. Small quadrangular secretory canals of the type found in *A. sandwichense* are characteristic of the roots of *Wilkesia*, although they may enlarge in size during secondary growth in the root.

In both *Argyroxiphium* and *Wilkesia* maturation of the central core of the root is characterized by fiber development more than vessel development. Conversion of some cortical parenchyma cells to sclereids was observed in roots of *Wilkesia* which showed secondary growth.

Secretory Canals: Summary

The details of secretory canal distribution in the vegetative parts of the plant have been detailed above. The fact that secretory canals are characteristic of all three genera is quite noteworthy, however. The mode of occurrence of these canals is highly reminiscent of the patterns in other Heliantheae, such as

Fitchia. The distribution of secretory canals in vegetative parts of *Dubautia*, *Argyroxiphium*, and *Wilkesia* follows very closely the diagram given by Carlquist (1957c: 58) for *F. speciosa*, differing only in those species which do not characteristically have secretory canals in pith, cortex, or leaves. The occurrence of secretory canals in inflorescence structures of *Dubautia*, *Argyroxiphium*, and *Wilkesia* will be considered in subsequent studies.

Trichomes: Summary

Although occurrence and types of trichomes have been mentioned above, the basic pattern underlying trichome occurrence needs to be stated. In the genera *Dubautia*, *Argyroxiphium*, and *Wilkesia*, two types of trichomes are present: uniseriate nonglandular and biserial glandular. Examination of shoot apices indicates that these two types may be formed initially, but are variously matured or degenerate upon maturation of organs of the plant. In *Dubautia raillardioides*, for example, both uniseriate hairs and biserial glandular trichomes with subdivided multicellular tips may be seen on young leaf primordia. On mature portions of the plant, both types of hairs are absent except for retention of uniseriate hairs in leaf axils. Thus, differences in indument of the mature plant are the result of elimination or retention of these two basic types. The leaves of *D. platyphylla* furnish an example of marked development of the biserial hairs with subdivided pits, whereas leaves and stem of *D. waialealae* demonstrate conspicuously the uniseriate nonglandular hairs with no evidence, in the mature plant, of the biserial type.

The precise nature and distribution of trichomes in Compositae is inadequately known. The occurrence of the capitate glandular hairs mentioned above, however, appears significant in connection with relations of the three genera to certain non-Hawaiian groups.

DISCUSSION

The importance of the data developed lies

in the application of anatomical characters to taxonomy of the genera discussed, description of relationships among the three genera, and in determination of the relationships of these seemingly isolated genera. Within the genus *Dubautia*, characters of vegetative anatomy seem to offer good criteria for taxonomic decisions, although inflorescence anatomy cannot be overlooked.

The results of the present study, and one reported separately (Carlquist, 1958) indicate that Keck (1936: 24) is justified in uniting the species of *Raillardia* with *Dubautia*. No anatomical character, or combination of such characters, seems to support the division of the species into the two genera as they have been traditionally delineated. For example, *D. waialealae* (invariably treated as a *Dubautia*) seems closer in node and leaf anatomy to *D. Menziesii* (included under *Raillardia* by authors recognizing that genus) than to *Dubautia plantaginea* (type species of the genus) or its close relatives (*D. microcephala*, *D. raillardioides*).

Rather, the writer believes that a picture of species groups emerges, although these cannot yet be defined with sufficient precision to permit division of the genus into subgenera on the basis of the characters described here. Attention may be called, however, to certain alliances which seem quite certain:

- (1) *D. Menziesii*, *D. arborea*, *D. Hillebrandii*, *D. montana*, and *D. struthioloides* agree in leaf, pith, and wood anatomy.
- (2) The species with narrow strap-shaped leaves and wide leaf bases, *D. plantaginea*, *D. microcephala*, *D. raillardioides*, *D. paleata*, *D. magnifolia*, and *D. ternifolia*, seem close in leaf anatomy, presence of secretory canals in pith, and, to a certain extent, in nodal anatomy. *D. Knudsenii* appears close to this assemblage on the basis of its foliar secretory canals and its pith structure.
- (3) A grouping of species including *D. ciliolata*, *D. lonchophylla*, *D. scabra*, *D. Sherffiana*, and *D. thyrsoflora* seems justifiable on the basis of near identity in leaf structure,

particularly in regard to the single secretory canal on the xylem face of veins.

Dubautia waialealae and *D. latifolia* show peculiarities of anatomy not closely matched by other species, and are probably rather isolated from whatever species each of them may most closely resemble. Each of these two species should probably form a "group" by itself. Inclusion of species other than those mentioned does not seem to be justified on the basis of present anatomical information.

The material for *Argyroxiphium* supports the interspecific relationships in that genus suggested earlier by the writer (1957*d*).

The suggestion of Keck (1936: 10) that *Dubautia*, *Argyroxiphium*, and *Wilkesia* must be considered a group within themselves could be defended on the basis of vegetative anatomy. The presence and distribution of trichome types, the patterns and nature of secretory canals, the lacunate character of the cortex, and the presence of carbonized resins in intercellular spaces are notable in this regard. In fact, the three genera could not be separated on the basis of some anatomical characters. Other structural features offer excellent criteria, however, and *Dubautia*, *Argyroxiphium*, and *Wilkesia* are amply distinct in respect to leaf and node anatomy.

Because there is little published information on anatomy of genera which are putatively related to these three genera, no comment can be made in this regard at present. The writer hopes to demonstrate, however, that characters described here are worthy of consideration in comparing these genera with such taxa as the American genera of *Madinae*, *Railliardella*, and certain *Senecioneae*.

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NOTES

A Note on Walford's Transformation

ROBERT H. RIFFENBURGH¹

WALFORD² determines the asymptotic maximum of growth of an organism (or population) in the following manner. If size measure at successive ages N is plotted along an abscissa and size measure at successive ages $N+1$ along an ordinate, the points of intersection will form a linear function, say L_1 , with slope less than unity. The line $N=N+1$, say L_2 , will be the line of no growth; i.e. if size at age $N+1$ is the same as size at age N , no growth has occurred. The intersection of these

two lines represents the desired asymptotic maximum for growth.

But L_1 is a line whose parameters are estimated from random variables and therefore which is itself a random variable. Often the slope of L_1 is so similar to that of L_2 that the random fluctuation of L_1 makes the desired point of intersection uncertain.

In general, if $N+k$, k a positive integer, is plotted against N , the same asymptotic maximum will occur, but L_1 will have slope sufficiently deviant from that of L_2 to permit confidence in the asymptotic maximum. k is chosen as the smallest integer assuring sufficient deviation.

¹University of Hawaii and Pacific Oceanic Fishery Investigations. Manuscript received August 7, 1958.

²WALFORD, LIONEL A. A new graphic method of describing the growth of animals. *Biological Bulletin* 90(2): 141-147.

News Note

THE TENTH PACIFIC SCIENCE CONGRESS

The Pacific Science Congresses are held under the auspices of the Pacific Science Association. The Association was founded in 1920 by the holding of the First Pan-Pacific Scientific Conference in Honolulu, Hawaii.

A number of institutions and organizations, from 1900 on, planned and worked towards the systematic exploration of the Pacific, but the direct action resulting in this first Pacific science congress came from the Committee on Pacific Investigations of the U.S. National Research Council and its predecessor under the National Academy of Sciences, the Committee on Pacific Exploration.

The work of the Committee between 1916 and 1919 brought out the complexity of the problem, and a plan for a conference at which representative scientists from Australia, New Zealand, Java, China, Japan, Canada, continental U.S. and Hawaii, and the Philippines might be present.

The committee accepted the proposal that the conference might meet in Honolulu in 1920 under the auspices of the Pan-Pacific Union—a Hawaii organization devoted to developing friendly relations among the different nationalities of the Pacific. The program of the conference was arranged through

the Committee on Pacific Exploration of the National Research Council, and local arrangements were made by a committee appointed by the Governor of Hawaii and acting as a committee of the Pan-Pacific Union. The chairman of the congress was Professor Herbert E. Gregory, Director of Bishop Museum in Honolulu and Silliman Professor of Geology at Yale; the vice-chairman and secretary was Dr. Arthur L. Dean, President of the University of Hawaii.

The purpose of the congress was "to outline the scientific problems of the Pacific Ocean region and suggest methods for their solution. The conference undertook to take stock of our present knowledge of the Pacific area, its geography and geology, its plants and animals and the races of men which inhabit it, and proceeding from this comprehensive view to formulate the programs for future research."

In addition to defining the purpose of the congresses, and the scope of the program, the first congress set other important precedents. First, the congresses are nongovernmental, meaning that the scientists meet and discuss

their problems as individuals and not as the representatives of their governments. Second, field trips are as much a part of the scientific program as the technical sessions. The first congress spent a week on the island of Hawaii, concentrating on the volcano Kilauea, which was obligingly active. The field trips are planned and led by the local scientists and are their opportunity to discuss in the field their particular problems.

Since that first congress in Honolulu, eight further Pacific Science Congresses have been held—Australia (1923), Japan (1926), Netherlands Indies (1929), Canada (1933), California, U.S.A. (1939), New Zealand (1949), Philippines (1953), and Thailand (1957). The Tenth Congress, returning to Hawaii, is planned for the last week of August and the first week of September, 1961.

Dr. Laurence H. Snyder will be president of the Tenth Pacific Science Congress. Dr. Snyder, who has accepted, is president of the University of Hawaii and a distinguished scholar in human genetics. He is immediate past president of the American Association for the Advancement of Science.

utively 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.

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——— 1920b. Cerotrioza (Psyllidae, Homoptera). *Proc. Hawaii. Ent. Soc.* 4(2): 374-375.

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PACIFIC SCIENCE

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



IN THIS ISSUE: Kenyon and Rice — *Life History of the Hawaiian Monk Seal* • Solem — *Marine Mollusca of New Hebrides* • Sund — *A Key to the Chaetognatha of the Tropical Eastern Pacific Ocean* • Wells — *Notes on Indo-Pacific Scleractinian Corals* • Sherman and Ikawa — *Occurrence of Gibbsite Amygdules in Haiku Bauxite* • Swanholm, St. John, and Scheuer — *Survey for Alkaloids in Hawaiian Plants* • News Note



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Life History of the Hawaiian Monk Seal

KARL W. KENYON and DALE W. RICE¹

THE HAWAIIAN MONK SEAL, *Monachus schauinslandi* Matschie, 1905, has long remained one of the rarest and least known of marine mammals. Few zoologists have been able to reach the remote mid-Pacific coral atolls on which it breeds, and their visits have been brief. While engaged in zoological studies in the Leeward Chain of the Hawaiian Islands, we were able to observe these seals from aircraft throughout their principal range, and to make detailed studies of those inhabiting Midway Atoll. We also landed on Green Island in Kure Atoll. Our field study covers the period from November 17, 1956, to October 11, 1957.

We gratefully acknowledge the help of the following: J. W. Aldrich, P. L. Breese, V. E. Brock, E. H. Bryan, M. B. Chitwood, C. F. Clagg, E. Y. Dawson, R. Dodge, P. A. Dumont, L. A. Faye, Y. J. Golvan, J. E. Graves, E. Y. Hosaka, P. L. Illg, E. C. Jones, C. R. Joyce, J. E. King, J. A. Neff, G. H. Pournelle, W. Pointon, R. A. Rausch, F. Richardson, C. S. Robbins, V. B. Scheffer, D. W. Strasburg, S. W. Tinker, A. L. Tester, K. Waldron, K. A. Wong, and D. H. Woodside. The help of Naval personnel stationed at Midway was invaluable, particularly that given by Capt. E. T. Hughes, Comdr. J. L. Hooper, Lt. Comdr. D. E. Moritz, Lt. Comdr. J. F. Reilly, Lt. D. H. Picht, Ens. R. T. Takahashi, and Chief J. H. Green.

HISTORY

Sealing expeditions during the middle of the 19th century reduced the Hawaiian monk

seal population to near extinction. Undoubtedly guano diggers, bird hunters, and whalers further depleted the remnant during the late 1800's and early 1900's. In 1824 a sealing expedition by the brig "Aiona" was thought to have taken the last monk seal; but after a "sealing and exploring voyage" to the Leeward Islands between April 26 and August 7, 1859, Capt. N. C. Brooks of the bark "Gambia" returned to Honolulu having . . . "on board 240 bbls., seal oil, 1,500 skins. . . ."² During six weeks on Laysan in 1911, Dill and Bryan (1912) and their party watched for seals but saw none. They were told by Max Schlemmer that during the 15 years he had lived on Laysan, seven seals had been killed. One of these was the specimen given to Schauinsland in 1896, upon which Matschie (1905) based the description of the species. During subsequent years, the few expeditions visiting the Leeward Chain reported increasing numbers of seals (Bailey, 1952). For a more complete historical treatment, see King (1956).

² *The Polynesian*, August 13, 1859. We question this report for the following reasons: (1) In view of present populations, if in 1824 the seals were nearly wiped out, it seems doubtful that 1,500 could have been taken on a 103-day voyage in 1859. The reported take of seals indicates an average of about 15 seals per day. During this period, more than 2,200 miles were covered and explorations made in uncharted waters. (2) Seals are characteristically scattered along many miles of beach. These beaches are difficult of access from the sea. Skinning seals, scraping and curing skins, collecting and rendering the blubber of many widely separated individuals would have been a tremendous undertaking. Therefore, we made a careful search for the journals and log books of Capt. Brooks. His daughter, Miss Dorothy Brooks, told us that these were lost in the San Francisco fire of 1906. (3) In spite of the fact that *The Polynesian* gives an otherwise detailed report of the "Gambia's" voyage and explorations, including accounts of various wildlife species, it mentions seals only in the lead paragraph, as quoted above.

¹ Biologists, U. S. Department of the Interior, Fish and Wildlife Service, Sand Point Naval Air Station, Seattle 15, Washington. Manuscript received March 3, 1958.

Seven monk seals have been captured on French Frigate Shoals, with the assistance of the U. S. Coast Guard, and one at Pearl and Hermes Reef. These were held in captivity in the Honolulu Zoo, the Waikiki Aquarium, and the San Diego Zoo. One seal is still living in the Waikiki Aquarium after more than two and a half years in captivity, and another in the San Diego Zoo. Others have been kept for relatively short periods (Table 1).

TAXONOMY

Monk seals are the only phocids of tropical and subtropical waters. The genus *Monachus* is represented by three relict populations with a widely disjunct distribution. Their probable origins and relationships have been discussed by King (1956). It appears that the Mediterranean monk seal, *M. monachus*, is specifically distinct from the Caribbean monk seal, *M. tropicalis*, and the Hawaiian monk seal, *M.*

schauinslandi. The differences between the latter two are slight and have not been verified by comparison of adequate series of specimens of known sex and age. From the few specimens we have examined, certain distinguishing characteristics ascribed to *M. schauinslandi*—especially the shape of the palate and the shape of the zygomatic branch of the squamosal—do not appear to be constant. The form of the anterior border of the nasals and the shape of the infraorbital foramen are the most obvious distinguishing features. The morphological differences between the Caribbean and the Hawaiian monk seals are less than one would expect in two groups of animals so widely separated. Further study may indicate that *M. schauinslandi* should be regarded as a race of *M. tropicalis*.

Monachus is currently recognized as the only genus of the subfamily Monachinae (Simpson, 1945). The close relationship be-

TABLE 1
RECORD OF MONK SEALS HELD IN CAPTIVITY¹

DATE CAPTURED	DATE DIED	SEX	APPROX. AGE ²	WEIGHT, LBS.	LENGTH, CM. ³	WHERE HELD	REMARKS
May 12, 1951	August, 1951	♂	juv	110 ⁴	143	S. D. Zoo	Cause of death undetermined
May 12, 1951		♂	ad	300 ²	...	Honolulu Zoo	Refused foods; liberated near Kaneohe Bay, November, 1951
April, 1955	July, 1956	♀	juv	90 ²	...	Waikiki Aq.	Died of ulcers
October, 1955	October, 1957	♂	subad	200 ⁶	...	Waikiki Aq.	Postmortem: large gastric ulcer
August, 1955		♀	subad	230 ⁶	...	Waikiki Aq.	Alive in November, 1957
September 12, 1956	October 22, 1956	♂	juv	96	131	S. D. Zoo	Cause of death undetermined
September 22, 1956	November 9, 1956	♀	subad	160 ²	168 ⁵	S. D. Zoo	Acute pneumonia, vegetative endocarditis and peritonitis
July 21, 1957		♂	subad	119 ⁷	...	S. D. Zoo	Alive in January, 1958

¹ All taken at French Frigate Shoals, Territory of Hawaii, except male taken October, 1955, which was captured at Pearl and Hermes Reef.

² Estimated at capture.

³ Measured at death.

⁴ Eviscerated—estimated total weight 125 lbs.

⁵ Estimated at death.

⁶ Estimated July, 1957.

⁷ Weighed at capture. Estimated weight 180 lbs., December 31, 1957.

tween *Monachus* and the Antarctic phocids of the subfamily Lobodontinae has been pointed out by King (1956). Biological similarities, such as voice and certain aspects of behavior, are shared by the monk seal and Weddell seal (*Leptonychotes weddelli*), while the monk seal shares with elephant seals (*Mirounga*) a unique method of molt. It is evident that the Monachinae are even more closely related to the Lobodontinae and Cystophorinae than previously recorded biological data had indicated, and that the three subfamilies are more closely related to each other than any one of them is to the northern "hair seals" (subfamily Phocinae). Trouessart (1897) placed the Antarctic phocids and the monk seals together in the subfamily Monachinae, an arrangement with which V. B. Scheffer agrees (*in lit.*).

DISTRIBUTION

The breeding range of *Monachus schauinslandi* is confined to the islands and atolls of the Leeward Chain, which extends for 1,200 miles northwestward of the main Hawaiian Islands. The Leeward Chain consists of two geologically distinct portions (Bryan, 1942).

In the eastern half are four high volcanic islands: Nihoa Island, Necker Island, La Perouse Pinnacle, and Gardner Pinnacles. These rise precipitously from deep water. The only extensive area of shallow water is French Frigate Shoals, a crescent-shaped atoll containing a dozen sand islets, which half surrounds La Perouse Pinnacle. Paty (1857) gave the following account of a visit to Nihoa on April 27, 1857, ". . . on the sand beach ten or twelve hair seals were found; they didn't take much notice of us until His Majesty [King Kamehameha IV] had shot several, when they became more scared." None were seen at Nihoa between August 7–17, 1940, although looked for (Vanderbilt and de Schauensee, 1941), and Frank Richardson (*in lit.*) who visited the island in late 1953 and again in early 1954 found none. A small breeding colony occupies French Frigate Shoals. They

are not reported from Necker or Gardner.

The western half of the Leeward Chain consists of six low coral atolls. From Maro Reef, where only a few rocks are awash at low tide, two monk seals were reported in 1951 (Bailey, 1952). Lt. Comdr. D. E. Moritz flew over Maro Reef twice in October, 1957, and reported seeing no seals. Virtually all Hawaiian monk seals breed on the outermost five atolls: Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll.

Wandering seals are occasionally seen among the main Hawaiian Islands. At Hilo Bay, Hawaii, one was killed and eaten by the natives in 1900 (Henshaw, in Dill and Bryan, 1912). Here, perhaps, is an explanation of the restricted breeding range in the Leeward Chain, which had no aboriginal human population. Recent reports from waters of the main islands are shown in Table 2.

ENVIRONMENT

Climate

The fairly uniform subtropical maritime climate at Midway Atoll is typical of the western half of the Leeward Chain. Temperatures near freezing are unknown. Reef corals and their associated fauna grow fairly well but are near the northern limit of their range. They do not occur north of Kure Atoll. Two seasons are well marked. Winter, from early December through March, is characterized by low temperatures, frequent rains, and winds which sometimes reach velocities of 90 miles per hour. These gales cause heavy swells which break violently over the protecting reef and result in rough water in the lagoon. Summer, from April through November, is warm, very humid, and sunny, with occasional showers. The northeast trade winds blow quite steadily but mildly, and the surface of the lagoon and ocean is calm. Mean daily maximum and minimum air temperatures, and mean water temperatures, are presented in Table 3.

During the period March 23 to June 15, 1957, surface water temperatures in Midway

TABLE 2
REPORTS OF MONK SEALS FROM THE MAIN ISLANDS OF HAWAII

DATE	PLACE	OBSERVER	WHERE REPORTED	REMARKS
November 11, 1928	Oahu, windward shore (N.E.)	Thomas M. Blackman	<i>Honolulu Star-Bulletin</i>	". . . in the vicinity several days."
October 26, 1931	Oahu, north side	J. P. Kaleo	<i>Honolulu Star-Bulletin</i>	"Seal frequently seen 3 years ago. . . ."
May 12, 1948	Kauai, east side	Philip Palama	<i>Honolulu Advertiser</i>	"Seal climbed out of water onto rocks. . . ."
October, 1951	Oahu, entrance to Kewalo Basin	Robert Dodge	Letter, December 24, 1957	Seal bit at fishing line about 25 feet from shore
March 30, 1955	Oahu, ½ mile off Waikiki Beach	Gordon Freund	Letter, December 24, 1957	Followed seal below surface while skin diving with aqualung
Early July, 1956	Hawaii, Kaehole Point, Kona Coast	Eddie Y. Hosaka	Letter, August 23, 1957	Seen at 0600, swimming slowly, close to shore
July or August, 1956	Lehua (off Niihau)	Lindsey A. Faye	Letter, August 9, 1957	Large adult hauled out on rocks; photographed

Lagoon were recorded by the Midway Aerology Unit for Kenneth Waldron of Pacific Oceanic Fishery Investigations (POFI). The extremes were 66.7°F. (March 30 to April 5 mean and April 20–26 mean) and 76.8°F. (June 8–15 mean). Since these data differ little from those given in Table 3, they are not included here.

Climatic Adaptation

It is noteworthy that monk seals apparently show few adaptations to a warm climate. We were able to measure the deep body temperature of one 380-pound adult male (BDM 490). This seal had been resting for at least ½ hour prior to death on February 2, 1957, and did not move after it was shot. We immediately inserted a thermometer into a slit in the thoracic cavity. The heart was still beating and the thermometer was bathed in the blood gushing from the severed aorta. The rectal temperature was also taken by inserting the thermometer 5 inches into the rectum. Several readings in both locations were taken alternately. The thoracic temperature was 35.5°C., the rectal 31.1°C. The difference suggests that a rectal temperature taken with a 6-inch thermometer may not be a re-

liable indicator of body temperature. The deep body (thoracic) temperature of this individual was lower than those reported for other species of pinnipeds. The deep body temperature of a captive harbor seal (*Phoca vitulina*) approximated 38°C. (Scholander, Irving, and Grinnell, 1942). Adult northern fur seals (*Callorhinus ursinus*) at rest had a mean deep body temperature of 37.7°C. (Bartholomew and Wilke, 1956). The average thoracic temperature of nonmolting southern elephant seals (*Mirounga leonina*) was 36.5°C. (Laws, 1956a). The rectal temperature of our monk seal was markedly lower than that of sleeping adult northern elephant seals (*Mirounga angustirostris*) which averaged 36°C. during the day and 34°C. at night (Bartholomew, 1954).

The blubber layer on Hawaiian monk seals is light orange in color and about as thick as on arctic and antarctic seals. Our specimen had a heavy layer of blubber over the entire body. Over the mid-belly, it was 42–45 mm. thick. Pregnant females are especially fat but lose weight rapidly during the nursing period. The pup is extremely fat just prior to weaning.

Compared with northern phocids, the pelage of the adults is shorter, the individual

TABLE 3
MEAN AIR AND SURFACE WATER TEMPERATURES
(°F.) AT MIDWAY ATOLL

MONTH	AIR ¹			SURFACE WATER ²
	Mean high	Mean low	Mean	
January.....	70	62	66	68.4
February.....	69	62	66	66.8
March.....	70	63	66	66.4
April.....	72	64	68	66.9
May.....	75	68	72	69.5
June.....	80	72	76	73.6
July.....	82	74	78	76.4
August.....	82	75	78	77.5
September.....	82	75	78	78.1
October.....	79	73	76	75.8
November.....	76	69	73	73.2
December.....	73	66	69	69.7
ANNUAL MEAN....	76	69	72	71.8

¹ Data from Aerology Unit, U. S. Naval Station, Midway Island, 1941-57. Highest on record, 92°F.; lowest, 54°F.

² Data from Atlas of Climatic Charts of the Oceans, U. S. Weather Bureau, 1938, for the quadrat 175°-180°W., 25°-30°N.

hairs being only about 2-9 mm. long. The pelage of adult phocids can have little effect as a temperature regulator. However, in the young of cold-water seals which have not yet developed a blubber layer, the woolly natal pelage undoubtedly functions as an insulator. At birth, monk seals have a single-layered black pelage consisting of straight silky hairs 6-10 mm. long. In this respect, they differ markedly from the young of arctic phocine seals and antarctic lobodontine seals, which possess a woolly coat about 15-25 mm. long. Pups of the southern elephant seal have a single-layered woolly pelage about 23 mm. long (Laws, 1954). The lack of pelage with marked insulating properties in young monk seals may be a climatic adaptation. In this connection, it is interesting to note that, in young harbor seals, the white woolly fur is retained for several weeks after birth in the northern Bering Sea but is lost in a prenatal molt in southern parts of the species' range (Scheffer and Slipp, 1944).

In addition to black pelage, the newborn monk seal has nearly black skin. It has been suggested that black pigment is a protective

shield against harmful insolation. Prior to weaning, the monk seal pup spends much time in intense sunlight on the white coral sand beaches.

Habitat Requirements

Certain features are characteristic of monk seal breeding sites, as follows.

FEEDING AREAS: Seals occur regularly only on islands and atolls having extensive areas of shoal water. At Midway and elsewhere, we frequently saw seals swimming inside the reef but did not see them outside the lagoon, in deep water. That they do range in deep water, however, is evidenced by records far from the breeding grounds and by the fact that remote islands, such as Laysan, have been repopulated after local extermination took place during the 19th and early 20th centuries. Another indication that monk seals may spend considerable time at sea is the observation that certain individuals, when we saw them for the first time, exhibited a heavy growth of green algae in the hair on various parts of the body. The green tinge was lost after a number of days spent on Midway beaches. Food analysis indicates that they feed primarily on bottom fishes, kinds which they could obtain only in comparatively shallow water. In the lagoons, a rich bottom fauna is found on coral reefs and bordering sand areas.

HAULING GROUNDS: Monk seals generally haul out on sandy beaches and sandspits. They are absent from high rocky islets, which lack beaches, in the eastern half of the Leeward Chain. Though they prefer sand to rocks, they are occasionally seen on low, shelving reef rocks which slope into the water on Eastern Island and on reef rocks surrounding atoll lagoons. The southwest side of Laysan Island is bordered by a fairly high ledge of coral rock; we have never seen a seal hauled out along this stretch of shore, although they haul out on the low beaches bordering it. The shade of *Scaevola frutescens*, above the beachline is attractive to seals.

PUPPING AREAS: All of the newborn pups we saw at Midway and on other atolls were on permanent islands or islets above high tide, or on sandspits only a few yards from permanent dry land. We did not see them on isolated, temporary sandspits which could be covered by high tides or washed away by storms, although these are regularly used as hauling grounds by adults.

ABUNDANCE

Two methods were used to estimate the size of the Hawaiian monk seal population: aerial surveys and ground counts.

We conducted aerial surveys of all the atolls on which seals are known to breed, with the exception of French Frigate Shoals. Counts for the latter atoll were made by Paul L. Breese, director of the Honolulu Zoo, and by POFI biologists. Our aerial counts were made from Navy UF-1 Grumman Albatross amphibians flying at a speed of about 120 knots and altitudes between 100 to 500 feet. In most cases, each of us made an independent count using a mechanical hand-tally. Usually we made at least two successive counts during each flight. The counts were sometimes checked against photographs taken simultaneously with a Fairchild F-56 camera. During any one flight, the differences between successive counts by the same observer, between different observers, and between the observers and the aerial photographs, were insignificant. Few of the seals on land were missed. Occasionally, a seal resting under the edge of a *Scaevola* thicket was difficult to see. Large green turtles (*Chelonia mydas*) basking on the beaches were momentarily confused with seals but caused little difficulty in making counts.

Ground counts were made on Midway and Kure atolls by walking entirely around the beaches of the larger islands and by landing on all of the sandspits and small islets.

The number of seals on land varies with the time of day and the season (Table 7 and Fig. 7). The best time for counting seems to

be in afternoon during winter, when the most seals are on land. However, we had no way of knowing what fraction of the population was absent. Some individuals certainly were absent, as indicated by algae in the hair, mentioned elsewhere.

The population figures, by atolls, are presented in Table 4. The total prior to the pupping season is based on the highest counts of all seals during the winter of 1956-57, or else the highest counts of seals of age one year and older made during the spring of 1957. The total number of pups is based on the highest single count of pups, or on combined counts when it was evident, from age or location of pups, that different pups were counted. The total after the birth of the pups is the sum of the largest count of adults plus the total count of pups, and thus does not necessarily represent a single count. Because of the distances involved, we do not believe that the same seals were seen twice in widely separated atolls. Following is a brief description of the six atolls on which monk seals breed, and a listing of the dates on which we made counts of the seals.

Kure Atoll

The reef encloses a circular lagoon 6 miles across. Inside the southeast reef is Green Island, 1 mile long by $\frac{1}{2}$ mile wide, largely covered with a dense growth of *Scaevola*. Several variable sandspits extend to the westward of the island for about 2 miles. Flights were made over Kure on December 9 (1100-1130), December 21 (0900-0930), February 12 (1430-1520), and May 14 (1355-1435). A ground count was made on June 5.

Midway Atoll

The lagoon at Midway is about 6 miles in diameter. Inside the southern part of the reef are two large islands. Sand Island, 2 miles long and 1 mile wide, is the site of a U. S. Naval Station. Eastern Island, $1\frac{1}{4}$ miles long by $\frac{3}{4}$ mile wide, is uninhabited except for a single Navy unit. Between the two islands are sev-

TABLE 4
HAWAIIAN MONK SEAL POPULATION IN SPRING, 1957

ATOLL	ADULTS AND SUBADULTS, WINTER, 1956 SPRING, 1957	DATE OF COUNT	PUPS BORN, SPRING, 1957	DATE OF COUNT, 1957	TOTAL POPULATION, SPRING, 1957
Kure Atoll.....	105	June 5, 1957	23	June 5	128
Midway Atoll.....	67	January 14, 1957	4	April 2	71
Pearl and Hermes Reef.....	257	December 17, 1956	33	April 15 May 14	290
Lisianski Island.....	241	April 15, 1957	15	April 15	256
Laysan Island.....	214	April 15, 1957	19	January 7 April 15	233
French Frigate Shoals ¹	35	July 20, 1957	?	June 26 ² July 20	35
Total.....	919		94		1013

¹ Count by Paul Breese, Honolulu Zoo. A count of 30 sea's was recorded in the scientists' log, April 24–May 12, 1957, cruise No. 39, M/V "Hugh M. Smith," POFI, U. S. Department of Interior, Fish and Wildlife Service.

² Partial count by David H. Woodside, Division of Fish and Game, Territory of Hawaii.

eral small islets and sandspits. On the east side of the lagoon, the reef-rock is about 5 feet above low tide level, exposing a 5-mile strip up to 15 yards in width, see map (Fig. 1). Aerial counts were made on December 9 (1415–1430), December 21 (1000–1130), January 7 (1345–1400), January 24 (1330–1400), February 12 (1600–1800), and May 14 (1630–1645). Complete ground counts were made on December 20, January 14, March 5, 14, 27, and May 2.

Pearl and Hermes Reef

This atoll is roughly diamond shaped, 20 by 12 miles. There are three small islands (Kittery, Seal, and Grass) in the southwestern part of the lagoon. Seven to 12 fluctuating sandspits stretch eastward just inside the reef toward Southeast Island, the largest island in the atoll, which is about ½ mile long. In the northeast corner of the lagoon is North Island, with several sandbars immediately to the south. All the larger islets, except Kittery, are covered with low herbaceous vegetation. We made flights over Pearl and Hermes on December 9 (1245–1325), December 17 (1000–1100), January 7 (1300–1315), January 24 (1515–1545), April 15 (1550–1625), and May 14 (1520–1610).

Lisianski Island

This island is a coral "pancake," an atoll in which the lagoon has dried up entirely, leaving a depression in the interior of the island. The island is 1¼ miles long by ¾ mile wide. Reef formations surround the island, extending several miles to the southeast as Neva Shoal. We flew over Lisianski on January 7 (0930–0945) and April 15 (1250–1310).

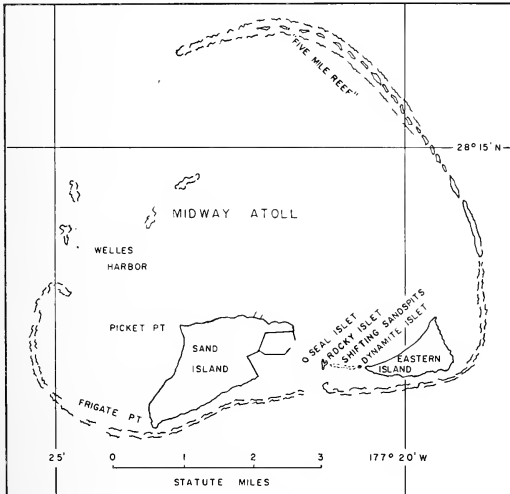


FIG. 1. Map of Midway Atoll.

Laysan Island

Laysan is a raised atoll in which the lagoon has no connection with the sea. The dimensions of the island are 1 by 2 miles, of the lagoon, $\frac{1}{3}$ by 1 mile. It is surrounded by submerged coral reefs. We made aerial counts on January 7 (1100–1130) and April 15 (1405–1430). David Woodside camped on Laysan from June 25 to July 3.

French Frigate Shoals

This crescent-shaped atoll is 20 miles long by 6 miles wide. It contains about 12 permanent islets and several sandspits which occasionally shift position. The largest islet is occupied by a U. S. Coast Guard unit. Seal counts here were made by Paul Breese and by POFI scientists in 1956 and 1957.

From near extinction in the 19th century, the monk seal has increased slowly in numbers. In 1923, Alexander Wetmore visited all the islands and atolls in the Leeward Chain and estimated the total population at about 400 (Allen, 1942). Galtsoff counted 68 seals at Pearl and Hermes Reef in 1930 (Galtsoff, 1933). In 1951, the total population was placed at about 477, based on estimates made by Robert L. Sheehan on Kure, and Vernon E. Brock on all the other atolls (Bailey, 1952). In 1954, Johnson A. Neff and Philip A. DuMont made an aerial count of 334 seals on all the atolls except French Frigate Shoals. Biologists of POFI have made counts of seals during various cruises to all the Leeward Islands, except Kure, from 1950 to 1957. The total of their highest counts for each location is 589 seals. The 1957 total of 1,013 (Table 4) does not mean that there has been a recent and rapid population increase but that more intensive observations were made.

POPULATION FACTORS

Sex Ratio

The lack of obvious secondary sex characters makes it difficult to ascertain the sex of monk seals in the field. If a seal is not lying

with the ventral surface exposed, it can usually be made to roll over on its side by poking it sharply with a stick. Thus, under field conditions, it is practicable to identify sex of only a small number of seals. Males are recognizable by the penile opening (Fig. 2). With practice, this cannot be confused with the less conspicuous umbilical scar on females. The females are recognizable by two pairs of teats.

JUVENILE SEX RATIO: Five pups were born in Midway Atoll in spring, 1957. Four were males; one prematurely-born pup found dead on the beach was a female. At Kure Atoll, we sexed 17 pups, of which 10 were males and 7 were females. At Laysan Island, on June 26 and 28, 1957, David Woodside tagged and sexed 23 young seals. Most of these were pups but a few were possibly yearlings. There were 8 males and 15 females. The foregoing counts total 22 males and 23 females.

SUBADULT SEX RATIO: Young seals of the yearling class and older examined at Midway and Kure atolls totaled 35, of which 21 were males and 14 females.

ADULT SEX RATIO: At Midway, seals were sexed whenever possible as groups (see Table 5) and individually. Total observations included 38 males and 31 females (single observations are not shown in Table 5). Unfortunately none of the above was marked and it is impossible to say how many were seen more than once. The largest single day's observation included 9 males and 3 females. In

TABLE 5
SEX RATIO OF ADULT HAWAIIAN MONK SEALS
ON MIDWAY ATOLL¹

DATE, 1957	MALES	FEMALES
January 14.....	5	5
February 2.....	5	2
March 5.....	9	3
March 14.....	4	2
May 2.....	6	3
Total observations ¹	29	15

¹ On each of 5 occasions when 6 to 12 seals were examined.



FIG. 2. Adult male monk seal, showing penile opening. When annoyed with a stick, a seal will usually roll on its side or back making definite recognition of sex possible. The distinct color difference along the side is not characteristic but is here the result primarily of the animal having rested on its belly. Midway Atoll, February 2, 1957 (KWK 53-3-9).

addition, 6 adults were tagged, 2 males, 3 females, and 1 unidentified.

On Green Island in Kure Atoll, we observed 11 adult males, 11 females with pups, 15 additional females without pups, and 16 adults of unknown sex. The observed sex ratio was strongly biased, of course, because of the large unsexed element and because animals with pups were obviously females. On the sandspits west of Green Island, Comdr. J. F. Reilly counted 8 females and 10 males. The total for Kure was 21 males and 34 females.

Among 154 seals of all age classes, in which sex was determined, were 75 males and 79 females.

Sex ratio data on adult and subadult seals must be interpreted with caution because of the possibility of differences in hauling-out habits of the two sexes.

Age at Sexual Maturity

Monk seal pups and presumed yearlings were first marked with metal tags in 1957. Therefore, no positive data on growth rates and age at which reproduction takes place will be available for several years. According to Bertram (1940), the Weddell seal normally bears her first pup late in her third year and some crabeater seals (*Lobodon carcinophagus*) give birth at the age of 2 years. According to Laws (1956a), the southern elephant seal usu-

ally produces her first pup when 3 years of age. Because of the several characteristics which monk seals share with the animals mentioned above and in view of the rapid growth rate observed in captive monk seals, it seems possible that the monk seal might participate in reproductive activity in the third year of life. All seals which we observed exhibiting sexual behavior, and all females which bore pups, were fully grown animals.

Reproductive Rate

The reproductive rate (number of pups born per 100 animals older than pups) of the Hawaiian monk seal seems to be unusually low when compared with that of other mammals. The total count of pups and the total count of older seals at each atoll are presented in Table 4. From these data, certain reproductive rates have been calculated for the following localities:

	PER CENT
Kure Atoll.....	21.9
Midway Atoll.....	7.5
Pearl and Hermes Reef.....	12.8
Lisianski Island.....	6.2
Laysan Island.....	8.9

The count at Lisianski was made quite early in the pupping season, that at Laysan was not complete, and when the last count was made at Pearl and Hermes Reef, probably only about 60 per cent of the pups had been born. Therefore, the actual reproductive rate at these localities was undoubtedly higher than the figures indicate. The June 5 ground count at Kure Atoll is the most reliable and important figure. Considering that the total population numbered 67, remarkably few pups (5 including one prematurely born) were seen at Midway in 1957. Furthermore, there were only 6 yearling seals, indicating a small pup crop in 1956 as well. Blasting operations in the ship channel and other human disturbances may have depressed the birth rate.

It is apparent that annually a large proportion of adult female monk seals fail to pro-

duce a pup. The walrus (*Odobenus rosmarus*) is the only pinniped known (with fair certainty) to breed in alternate years, a trait correlated with a lactation period exceeding 1 year (Brooks, 1954). Do missed pregnancies occur more frequently in monk seals than in other pinnipeds? The bearded seal (*Erignathus barbatus*) frequently misses a season between successive pregnancies (Chapsky and Kovalev, 1938). About 16 per cent of sexually mature female Weddell seals, and perhaps 20 per cent of sexually mature female crabeater seals, fail to become pregnant each year (Bertram, 1940). In a collection of 14 leopard seals (*Hydrurga leptonyx*), 21 per cent had missed pregnancy (Brown, 1957). Missed pregnancies occurred in 8 out of 66 sexually mature female southern elephant seals (Laws, 1956*b*). Several large samples of apparently mature female northern fur seals from the Pribilof Islands have been studied. Preliminary findings indicated that about 32 per cent fail to reproduce annually (Taylor, Fujinaga, and Wilke, 1955). Representing a sample of the commercial kill, 12,762 female fur seals, aged 4 years and older, were examined in 1956 and 1957. Of these, 46 per cent had missed pregnancy in the season studied (C. E. Abegglen and A. Y. Roppel, *in lit.*).

Age Groups

Pup and yearling monk seals are recognizable in the field by size. Between yearlings and adults, no distinct size classes were recognizable. Animals of intermediate size are lumped together as subadults.

Age group composition estimates at Kure Atoll and at Midway Atoll are presented in Table 6. It was not feasible to classify age groups other than pups during aerial counts. The following figures, therefore, are based on ground counts. The pup counts are the most accurate, as pups stay on land or in shallow water near shore where they are easily observed. Our observations indicate that subadults, and yearlings especially, do not haul out as frequently as do adults. Therefore, the

TABLE 6
ESTIMATED AGE GROUP COMPOSITION OF TWO
POPULATIONS OF HAWAIIAN MONK SEAL

AGE GROUP	KURE ATOLL		MIDWAY ATOLL		TOTAL	
	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent
Adults	79	62	53	75	132	66
Subadults (2+? years)	19	15	8	11	27	14
Yearlings	7	5	6	8	13	6
Pups	23	18	4	6	27	14
Total	128	100	71	100	199	100

counts of yearlings and subadults may be proportionately low. An unknown number of animals were doubtless at sea at both atolls.

Mortality

Little evidence of mortality among monk seals came to our attention. We found only

one dead adult, on December 6, 1956. As no baculum could be found, it was probably a female. The occipital region of the skull was fractured. The only other dead seal we saw was a prematurely born female pup mentioned elsewhere.

On January 14, 1957, an adult with an infected penis was observed. Northern fur seals occasionally die as a result of similar infections.

Scars of various sizes are present on the bodies of all monk seals except nursing pups. Most are visible as dark lines through the hair, they range in length from about an inch to 2 feet. Most of these are probably made by contact with sharp coral. On December 20, a seal was observed with a large, open, fresh wound on its side. Of 67 seals seen at close range on January 14, 2 had large areas of bare, dark-brown scar tissue on their sides (Fig. 3). It is surprising that an animal could survive such a wound. One adult was seen with half of the outer digit of the right hind flipper



FIG. 3. A large scar (partially hidden by the foreflipper), possibly inflicted by a shark, marks the side of this resting monk seal. Midway Atoll, January 14, 1957 (KWK 57-3-17).

missing. Large sharks which could inflict wounds of this nature are often seen in and around Midway Atoll. While the junior author was skin diving in Welles Harbor, Midway, watching the underwater swimming behavior of a seal, a school of 8 or 10 white-tipped sharks (*Triænodon obesus*) was in the immediate vicinity. One of the sharks, about 4 feet long, and the seal swam within 4 feet of each other. Neither, however, showed the slightest alarm or concern.

During late May and June of 1956, Fish and Wildlife Service biologists of POFI made the following observations: "On Southeast Island [Pearl and Hermes Reef], a pair of adult seals was seen well up from the beach. The smaller of the pair was seriously wounded on the lower abdomen and right side. . . . On Whale Island [French Frigate Shoals], a young adult was found dead on the beach, apparently as a result of shark attacks. Most of the flesh was gone from the right side of the head and neck and the sides showed slashes typical of shark bites. At this island, a school of 20 to 25 three- to four-foot sharks was seen continuously milling about the shallow reef in the lee of the island." (E. C. Jones, FWS, *in lit.*)

We have not heard of killer whales (*Orcinus orca*) in waters around Midway.

The monk seal is able to increase and maintain its numbers in the Leeward Islands in spite of a low reproductive rate. The fact that 6 yearlings were marked at Midway and only 4 pups were born (plus 1 stillborn) there in 1957 may indicate that survival in the first year is unusually high. Nearly one-fifth of the fur seal pups born on the Pribilof Islands in recent years die before leaving the breeding grounds and an additional 50 per cent (approximately) die of natural causes before reaching their third birthday (Kenyon, Schaffer, and Chapman, 1954). It might be concluded that monk seals are fairly long lived and that mortality from disease and predation is relatively low.

MOVEMENTS

Marking

In order to follow the movements of individual seals, and to furnish a reservoir of animals of known source and age for future study, we tagged as many as possible (57). The tags were National Band and Tag Company size No. 19 monel metal cattle-ear tags. On one side was stamped a number preceded by "MS-"; the other side was stamped with "NOTIFY/F & W SERVICE/WASHINGTON 25 D.C." The tags were clinched on the web of the animal's hind flipper with special pliers designed for the purpose.

Pups, even weaned ones weighing up to 160 pounds, were easily tagged as they can be captured readily and held by hand. The yearlings were netted and firmly tied. In order to place tags on adults, the animals were quietly approached from the rear while they slept. The tag was then attached with a quick firm motion of the pliers. The seals always awoke with a violent thrashing motion that sent the pliers flying, but the tags usually clinched properly.

To facilitate recognition of individual seals at Midway, we attached to their tags strips of colored polyethylene plastic. We placed red strips on pups, yellow on yearlings, and blue on older animals. Each plastic strip was distinctively shaped (long, medium, or short; truncate, diagonal, pointed, or notched). Some of these were lost after about 1 month. These decorated tags were readily observed on sleeping seals. With binoculars, they aided identification by number on seals that were crawling towards or splashing into the water. It is often possible to approach a sleeping seal and read its tag number.

An attempt to mark seals by spraying them with quick-drying "Krylon" enamel was unsuccessful. The application of the paint awakened the seals and they crawled away into the water, the sand and water wiping off what little paint had got on to them before it dried. Fast drying paint (of the type used to mark highways) applied generously with a swab

should be successful for temporary markings (as it was found to be on the Alaska fur seal).

In Midway Atoll, we tagged 16 seals, including all of the pups (4), all of the yearlings (6), 3 subadults, and 3 adults. These represented about 23 per cent of the total Midway population. At Kure Atoll, we tagged 1 yearling and 15 pups, or 65 per cent of the pups born during the 1957 season. At Laysan Island, David Woodside tagged 25 seals, the majority being pups, possibly a few yearlings, 1 adult female and 1 subadult female. For the convenience of future workers, the series are listed: Midway, MS-1 to MS-16; Kure, MS-17 to MS-32; Laysan, MS-51 to MS-75.

Home Range

SIZE: With the exception of mothers with nursing pups, it is apparent that each seal ranges widely in Midway Atoll. Of the 16 seals tagged at Midway, 10 were subsequently seen a total of 22 times, exclusive of repeat

observations on nursing pups (Table 7). The observations of tagged animals reveal that individual seals do not habitually haul out at the same place. Rather, there are a number of favored hauling grounds which most of the seals use at one time or another. These regularly-used hauling grounds are several small permanent islets (Seal Island, Rocky Island, and Dynamite Island) plus one to three shifting sandspits which lie between Sand Island and Eastern Island. The south and east shores of Eastern Island are also frequented by seals. On Sand Island, with its many human inhabitants, seals occasionally haul out on Picket Point and Frigate Point. Particularly during the summer, a number of seals were seen hauled out on the flat rocks of "Five-mile Reef." The entire seal population in Midway Atoll seems to share a common home range which includes most of the lagoon, or at least its southern and eastern halves.

TABLE 7
MOVEMENTS OF TAGGED HAWAIIAN MONK SEALS IN MIDWAY ATOLL, 1957
(Repeats of unweaned pups excluded)

TAG NO.	AGE	SEX	TAGGED		OBSERVED		DISTANCE MOVED SINCE PREVIOUS OBSERVATION
			Date	Locality	Date	Locality	
MS-1.....	yr1	♀	March 5	Seal I.	March 14 March 18	Seal I. Sand I.	50 yards 0.5 mile
MS-2.....	ad	♂	March 5	Seal I.	April 5	Eastern I.	1.25 miles
MS-4.....	yr1	♀	March 5	Dynamite I.	March 27	Seal I.	0.6 mile
MS-5.....	yr1	♀	March 5	Dynamite I.	March 14	Rocky I.	300 yards
MS-7.....	ad	♀	March 5	Rocky I.	May 2 June 4	Rocky I. Eastern I.	10 yards 1.3 miles
MS-8.....	yr1	♂	March 22	Eastern I.	March 24	Eastern I.	50 yards
MS-9.....	pup	♂	March 27	Dynamite I.	May 27 May 31 June 4 October 11	Eastern I. Eastern I. Eastern I. Dynamite I.	1.0 mile 100 yards 100 yards 1.0 mile
MS-10.....	pup	♂	March 27	Dynamite I.	May 13 May 27 May 31 June 3 August 26	Eastern I. Eastern I. Eastern I. Eastern I. Eastern I.	0.5 mile 0.25 mile 100 yards 100 yards 1.0 mile
MS-12.....	pup	♂	April 2	Eastern I.	May 13 May 18 May 29	Eastern I. Eastern I. Eastern I.	1.0 mile 1.0 mile 100 yards
MS-14.....	ad	♂	May 2	East Sandspit	May 4 May 8	Eastern I. Eastern I.	0.5 mile 0.25 mile

TRAILS: The shade of *Scaevola* shrubs is attractive to seals (see Fig. 4). In order to reach the thickets, the seals must often crawl up the sloping sand beach, then up an embankment of solidly packed coral rubble a foot or two high. Certain favorite routes are habitually used and grooves, or trails, are worn in the sand and hard steep banks. These are visible from the air and during aerial counting help to locate seals lying partially hidden beyond the beach line (Fig. 5). On Rocky Island, the only small islet in Midway Atoll with vegetation, a number of seals use the same trails and resting places. Whether certain trails and resting places along less frequented beaches are used by certain individuals or by a number of seals was not ascertained.

WALLOWES: While resting on coral sand beaches, monk seals roll and root to form depressions about 6 inches deep. When digging such a depression, the nostrils are closed and the muzzle is pushed into the sand as the seal forces itself forward with its foreflippers (Fig. 6). In this way, the head becomes par-

tially buried and a ridge of sand is pushed up, rising to eye level or above. During such rooting and rolling, the eyes often become caked with sand and mucus. The eyes of one seal, seen sleeping, were so caked with sand that the lids could be only partially closed. This animal and others, seen sleeping with lesser amounts of sand sticking to the cornea, appear oblivious of any discomfort. When seen from the air, sand wallows are quite evident on beaches frequented by monk seals.

Daily Cycle of Activity

Very few seals may be seen on land early in the morning. Generally, as the day advances, an increasing number of seals haul out. About noon, or throughout the afternoon, the number on land reaches a maximum. Just before sunset, there is a drop in number on land. This is partially illustrated by the number of seals observed on the regular boat runs between Sand and Eastern islands. Table 8 presents the average number observed during 57 trips. We were unable to make comparable counts at sunset or shortly thereafter when seals were leaving the hauling grounds.

For this and other reasons (see food habits), it may be presumed that monk seals are nocturnal, or at least crepuscular, feeders. Nevertheless, swimming and feeding seals may be seen in the water all during the day.

Seasonal Movements

At Midway we have noticed a marked seasonal variation in the number of seals hauled out on the islets and sandspits between Sand and Eastern islands. In November and early December few seals hauled out. In late December, coincident with the beginning of the winter storm period, they increased markedly. About March, when calm summer weather began to prevail, the number dropped and by June very few were seen. Figure 7 shows the seasonal variation in six aerial counts, in six ground counts made when we landed on all of the islets and sandspits, and in the highest



FIG. 4. Large adult female. Monk seals often retreat to the shade of *Scaevola* shrubs above the beach line. Kure Atoll, June 5, 1957 (KWK 57-16-34).



FIG. 5. Trails and wallows as seen from the air aid in locating seals partially hidden among sand dunes and *Scaevola* clumps. Characteristically, seals are grouped near points of sand as shown here. Laysan Island, January 7, 1957 (KWK 57-1-17).

counts made on 49 days during the regular boat runs to and from Eastern Island.

The number of seals counted on land depended on the total area observed. The largest counts were made from aircraft, intermediate counts from land, and the smallest counts from the boat. The relative number of seals counted by the three methods indicated that the sample area observed from the boat was a reliable index of the abundance of seals on land in Midway Atoll. The monthly mean of boat counts is shown by a solid line in Figure 7 to indicate the general trend of seasonal abundance on land.

We suggest two possible explanations for the variation: (1) the seals spend more time

in the water during summer because of high air temperatures, and (2) the seals move out onto the unprotected reef during the calm summer season. We have some evidence to support the latter hypothesis. In five flights over "Five-mile Reef," from December 9 to February 12, we observed no seals hauled out on the reef. On March 27 we visited the reef in a small boat and counted 11 seals. On May 13 we cruised outside the reef in a tugboat and saw 13 seals lying on the exposed reef rock. Probably each of the above factors is partly responsible for the disappearance in summer of seals from their winter hauling grounds.

The yearling seals present an interesting



FIG. 6. Monk seals, while lying on beaches, push their noses into the sand to form shallow wallows. Such behavior may help the animals to keep cool and afford some protection from flies. Midway Atoll, February 2, 1957 (KWK 57-19-7).

problem. We saw the first yearlings¹ on December 20. After that, we saw yearlings regularly throughout the winter. In the spring, we tagged six of them, apparently the entire year-class at Midway. One yearling was observed on March 27, after which none were found. When first seen on land, all yearlings had noticeably more algae on their hair than adults. This suggests that yearlings spend more time in the water during the summer. A similar situation seems to exist among the Weddell and crabeater seals (Bertram, 1940) and elephant seals (Bartholomew, 1952).

There is no evidence that monk seals migrate regularly. Of their wanderings at sea, we know very little.

FOOD HABITS

In the Wild

The regurgitated stomach contents from a seal resting on a Midway beach were collected, as was the stomach of BDM 490. The stomach contents were identified by Donald W. Strasburg and other Fish and Wildlife Service biologists at POFI headquarters in

¹Animals born in the spring of 1956.

Honolulu (see Table 9). Previously no food items from Hawaiian monk seals had been identified. However, Munro (1942) stated that the stomach of a seal he killed contained half-digested fish.

The limited available material indicates that eels, which are numerous in atolls, and cephalopods comprise the major food taken by monk seals and that their food consists primarily of bottom inhabiting forms. It was not possible to determine whether the cephalopod remains (beaks and eye lenses) came from squid or octopus. Since the squid is largely pelagic and the octopus is a bottom form, the latter is more probable.

It might be deduced that the monk seal is primarily a night feeder. Conger eels remain buried in the sand during daylight. At night moray eels emerge from crevices in reefs to hunt for food and Strasburg saw conger eels with their heads and parts of their bodies protruding from the sand at night. Cephalopods are also nocturnal feeders. It was observed that, in general, few monk seals were on beaches in early morning hours; but that during the day, their numbers there increased (Table 8). While camped on Laysan Island in late June, 1957, David H. Woodside (*in lit.*) observed, "I noted a few seals feeding in shallow water at night . . . Their actions were very slow and deliberate as if they were after something stationary."

FECES: Fecal deposits are often seen on the beaches where the seals haul out. In general, the fecal matter is quite liquid but occasionally it is in lumps of claylike consistency. The color ranges from brilliant orange and other

TABLE 8
HOURLY VARIATION IN THE NUMBER OF SEALS
HAULED OUT AT MIDWAY

NUMBER OF COUNTS	TIME OF COUNTS	MEAN NUMBER OF SEALS ON LAND
26	0800	14
13	1200	25
18	1730	29

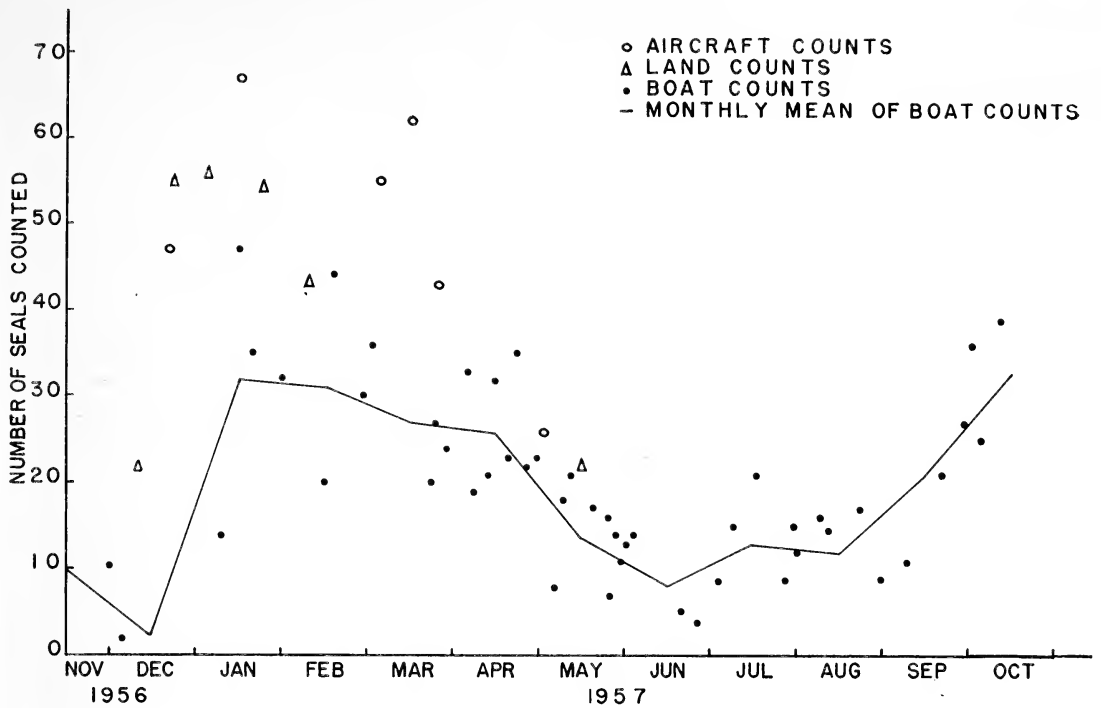


FIG. 7. Counts of seals. Midway Atoll, November, 1956–October, 1957.

yellow to whitish gray, brown, and purplish black. No hard parts of food items were observed in feces.

In Captivity

Two monk seals held captive in the Waikiki Aquarium showed a preference for eels. However, because other fish were less expensive and easier to obtain, the animals were usually fed smelt (*Osmerus mordax*) and California horse mackerel (*Trachurus symmetricus*) from California. The female ate both smelt and mackerel while the male preferred mackerel. Together, the two seals consumed about 25 pounds of fish per day, roughly one-seventeenth of the body weight. When living fish were placed in their pool, the seals showed a preference for them. All-purpose vitamin B capsules were placed in fish and fed to the animals daily (S. W. Tinker and K. A. Wong, *in lit.*). A captive Mediterranean monk seal was said to prefer eels over other

fish and consumed about 14 pounds of fish daily (King, 1956).

BEHAVIOR

Locomotion

While swimming slowly in shallow water near shore, forward motion is attained primarily with the foreflippers. However, when more speed is desired, the hind flippers and posterior part of the body undulate laterally as in other phocids. The foreflippers were seen to be in strong rapid motion through a vertical plane perpendicular to the body axis while seals were swimming rapidly in clear water over a white coral sand bottom. It appeared to us that the foreflippers were being used to increase speed as well as to steer.

While skin diving, the junior author has observed four seals swimming under water at close range. Two of these were kept under observation for a considerable time. Although the lateral undulations of the body trunk and

TABLE 9
FOOD OF TWO HAWAIIAN MONK SEALS

FOOD SPECIES	STOMACH CONTENTS BDM 490 VOLUME 100 CC.		SPEWING VOLUME 440 CC.	
	Num- ber items	Per cent vol- ume	Num- ber items	Per cent vol- ume
Conger eel (<i>Ariosoma bowersi</i>)	2	2	9	60
Moray eel (<i>Gymnothorax</i> sp.)	—	—	4	35
(<i>Echidna</i> sp.)	5?	3	—	—
Flatfish (<i>Bothus mancus</i>)	—	—	2	1
(<i>Bothus pantberinus</i>)	—	—	1	1
Scorpenid (<i>Scorpaenopsis gibbosa?</i>)	—	—	1	1
Larval fish (<i>Surgeon fish?</i>)	—	—	1	1
Squid or octopus (<i>Cephalopod</i>)	3	95	2	1

the vertically held hind flippers obviously furnished the chief means of propulsion, the foreflippers were in almost continuous motion. For only a few seconds, one seal was observed to hold the foreflippers motionless, when it trailed them back and down at an angle of about 45° from the body.

Regular and energetic use of the foreflippers for swimming appears to be unusual among phocids.

Progression by dorsoventral undulatory movements of monk seals on land is in every respect similar to other phocids (Fig. 18).

Vocalization

Sounds produced by monk seals fall into two categories: "bubbling" sounds and "bellowing" sounds.

BUBBLING SOUNDS: When a sleeping seal is awakened, it usually utters a rapid series of soft bubbling sounds which originate deep in the throat: "bgg-bgg-bgg-bgg-bgg." The sound is audible under usual circumstances to a distance of about 50 feet. It is similar to

the sound made as water flows from an inverted jug. To some observers, it sounds like a rapid series of belches. This sound appears to denote mild alarm. If the seal is not annoyed but approached closely, the mouth is kept closed while the sound is made. If the seal is touched, it opens its mouth in threat attitude while continuing to utter this sound. Weddell seals apparently make a similar sound (Bertram, 1940).

BELLOWING SOUNDS: When one seal is threatening another, when a mother is defending her pup, or when a seal's route to the water is blocked, several basically similar sounds are uttered, perhaps best described as a grunting bawl. Sometimes a blast of air is expelled simultaneously, forming a snort or snorting bellow. A mother defending her young from an intruder utters a louder version, best described as a bellow—"mrrraugh." The sound is very similar to that made by female northern sea lions (*Eumetopias jubata*). In general, the pup may be said to bleat—"mwaa-mwaa-mwaa." Except for its lesser strength and volume, and higher pitch, the sound resembles the bellow of the adult. When the mother is displaying affection toward her pup, she utters a hoarse throaty growl or moan, a modification of the bellow, to which the pup responds by bleating. When disturbed, the pup utters a diminutive version of the grunting bawl, an explosive "aaah" or "gaah."

Escape Reactions

The fearless nature of Hawaiian monk seals is similar to that of other marine mammals which have evolved and remained in remote oceanic areas. Terrestrial predators are unknown. Human populations have invaded only in recent times, and permanent settlements exist only on two of the six atolls where the seals breed. In some respects, the behavior of the monk seals is similar to that of the fur seals (*Callorhinus* and *Arctocephalus*) and certain antarctic phocids which breed in isolated regions. It is quite unlike that of the

northern phocids and sea lions (*Eumetopias* and *Zalophus*) which, in areas disturbed by man, quickly learn to avoid him.

Although adult monk seals resting singly on a beach can be easily approached, a large group usually takes to the water. Seals that awaken bump others as they begin to move and the result is a general alarm ending in a stampede. Yearlings, however, are not easily aroused and even after adults around them have made a hurried departure, these young animals may be left sleeping or languidly eyeing the intruder. Adults, if not disturbed, may quickly become accustomed to human presence. For six hours, four seals basked near us while we were working on a dead specimen. When we first arrived, these animals displayed mild alarm; before we departed, they ignored us even when we walked within 3 or 4 feet of them. Although seals are often poked at with sticks by people walking Midway's beaches and are sometimes annoyed by dogs, they remain surprisingly unwary. However, it may be significant that seals are found less frequently on the beaches most used by people. Seals only occasionally now haul out on the beaches of Sand Island where a large human population has been present for several years. They are regularly found on Eastern Island, and two pups were born there in 1957. Only about a dozen men occupy this island. We found that anyone who found a seal on a beach invariably drove it into the water. However, the Navy protects the seals from actual physical violence. By far the greatest number of seals haul out on the small islets and sandspits between Sand and Eastern islands.

Threat Display

Although a mother with a pup will charge with open mouth and bellow at human approach, the aggressive behavior is primarily a threat display rather than an attack. We failed to hold our ground in the face of such charges until a bite was possible. Generally, we have found it difficult to induce a charging

seal to grasp a stick held near its mouth. In one instance, however, our field notes in a manila folder were snatched from our hands, shaken violently and tossed aside by a mother seal defending her pup. This defense behavior is in marked contrast to that of northern fur seals. When a stick is presented to one of these animals under similar circumstances, it is invariably seized with the teeth. A man who failed to escape in the face of such a charge was severely bitten (Kenyon, 1957).

The threat display is also exhibited underwater. On July 20, 1957, while skin diving just inside the southwest reef at Midway, Richard T. Takahashi and the junior author cornered an adult female seal in a small deep hole about 10 by 15 feet, surrounded by high coral formations on three sides. After milling about in the hole for a minute or two, the seal started past us towards deeper water. We swam over to block her escape; we were at a depth of about 5 feet. When we got within 6 feet of the seal, on a course convergent with hers, she turned and came directly towards us with her mouth open in typical threat display. Her head was raised slightly above the axis of her body. When she was a yard from us, she swerved and made a break for the deeper water. She made no audible sounds underwater.

Play

On several occasions, adult seals pulled themselves on to sandbars covered by less than a foot of water. Here they would roll from one side to the other, waving their flippers in the air, apparently in play.

A two-month-old pup, after we awakened it at the water's edge on Eastern Island, romped and rolled in the shallow water near the beach; then as we walked along the shore, it followed along beside us for about a quarter of a mile. Frequently it raised its head to watch us, then returned to its frolicking. After about 10–15 minutes, it returned to the place of its birth on Dynamite Island, hauled out and went to sleep.

Nonreproductive Social Behavior

Monk seals appear to have no fixed social organization. Although aggregations of 2-3 to as many as 36 were seen hauled out on Midway beaches, the animals paid little attention to each other. Lone animals are frequently seen. At the end of the trails leading up into the *Scaevola* scrub, we seldom found more than one seal. When hauled out on sandspits or small islands in lagoons, it appears that the aggregations result more from a desire to rest on a favorable spot than from a gregarious tendency. Hostility between individuals was not observed except during sexual behavior.

Several times, however, it was noted that the presence of one seal appeared to stimulate another to haul out near it. For example, we visited the western point of Eastern Island frequently and no seals were seen there. Shortly after two mothers chose this point on which to bear their pups, we observed two other seals haul out to sleep in their general vicinity.

The Hawaiian monk seals are not thigmotactic as are northern elephant seals (*Mirounga angustirostris*) (Bartholomew, 1952) and most otariids. If a sleeping seal is touched, however lightly, it immediately awakens with a start. If the cause of its disturbance is another seal, it simply rolls or crawls a short distance and goes back to sleep. Monk seals were never observed lying in contact with one another.

When seen in the water during the nonreproductive period, seals were generally alone. When two or more individuals were seen together, it appeared to be because of their proximity to a favorite sandspit. When groups were startled into the water, each seal went its own way and the group quickly dispersed. Only once, on November 29, 1956, did we observe adults, not sexually excited, swimming in close company. On this occasion, three seals were swimming about 40 yards offshore. One soon left and the other two rolled leisurely on their backs and frequently raised their heads to look at us.

Reproductive Behavior

Field observation of sexual behavior in the monk seal is hampered by lack of obvious sexual dimorphism. Adult males are darker than most females. Females usually appear larger and fatter than males. In many of the observations which we interpreted as sexual behavior, the sex of the animals was not verified by observation of the external genitalia. Copulation was not observed; undoubtedly, as in most phocids, it takes place in the water. Seals which appeared to be pairs engaged in sexual behavior were observed on numerous occasions from March 5 to July 8.

Several times we observed seals (apparently males) approach females with pups. In every case, the female displayed threat behavior and the approacher was repulsed. Solitary males swimming near beaches occupied by females with pups showed considerable interest while still some distance away. On April 14, a male hauled out directly in front of a mother and pup, his head raised and appearing alert. He was quickly repulsed, whereupon he swam to another female and pup about 100 yards down the beach. Although one of us was standing only a few feet away, he hauled out. Without raising her head, the female snorted and the male backed into the water, leaving the vicinity.

The sense of smell may aid males searching for females. On April 17, we observed a male about 100 yards offshore suddenly stop, raise his head and gaze at a female directly up wind from him. Holding his head high above the water, he then swam rapidly and directly toward her, hauling out in front of her. The female reared, snorted, and threatened, to which the male responded in a similar way. Although open-mouthed sparring continued for several seconds at close quarters, the animals did not bite each other. The male then backed hurriedly into the water, glancing several times at the female as he swam away.

On April 2, when a female on the beach without a pup was approached by a male as

described above, he was threatened but not driven away. Before approaching the female, the male uttered several rolling bellows, sometimes ending in a snort. Repeatedly, the male nosed the abdominal region of the female, which caused her to threaten, and the male repeated the rolling bellow. He then lay with his head near her abdomen and his body at right angles to hers.

Pairs of animals in the position described above, were frequently seen lying dormant for long periods on the beaches. Occasionally, the male would sniff and nip at the female's genital and abdominal region. If, as frequently happened, this caused the female to attempt escape, the male attempted to stop her by following closely and gently biting at her abdominal region. An occasional hard nip precipitated bluffing bouts. If the female entered the water the male pursued her. The male sometimes chased the female quite rapidly, swimming high in the water with head raised and leaving a conspicuous wake. During such a chase, the male might utter coughing snorts repeatedly. In the water, the female sometimes put on a display wherein she beat the water with her flippers. On one occasion, a female lay on her side in very shallow water waving her hind flippers in the air and beating up a spray. She later beat the water with a foreflipper. The male, in the meantime, was beside her, facing her, uttering coughing snorts. On another occasion, a male was seen in the water beside a female; she rolled on her side and thrashed the water with a foreflipper. This was followed by both animals rearing up, facing each other and bluffing with open-mouthed threat displays. Finally, the female turned and swam away, the male following, both swimming with head and shoulders high in the water. On June 5, a female drove a courting male from her vicinity (Fig. 8).

No marked hostility between males was observed during the breeding season. Males which are with females seem to pay little attention to other seals as long as they do not approach closely. On March 27 we landed on



FIG. 8*a*. A courting male frolicked about a reluctant female.

a small sandspit where 17 seals, including a courting pair, were hauled out. All of the seals entered the water, the pair remaining together. While they were in the water, a third seal attempted to follow the female, but the male threatened him with raised head and open jaws, uttering coughing snorts. When we left the sandspit, the pair immediately hauled out, the male appearing to guide the female onto the sand as he remained close to her. The third seal attempted to haul out at the same place but was again repulsed and moved to another area. This animal made no hostile display.

On two occasions when we approached pairs of seals, whose sex was positively identified, the male took to the water; but when we prevented the female from leaving, the male hauled out again, giving threat display

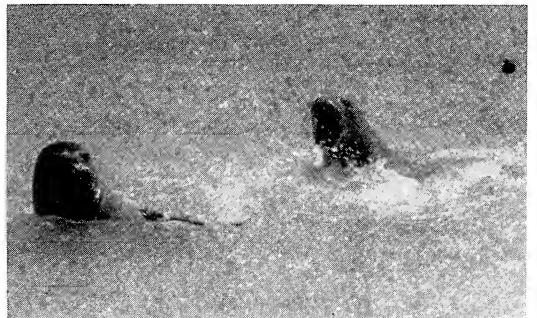


FIG. 8*b*. The female threatened the male, bellowing and charging with open mouth. The male quickly left the vicinity. Kure Atoll, June 5, 1957 (KWK 57-18-2 and 3).

toward us. Such behavior contrasted strongly with that of males not exhibiting sexual behavior.

Captive Animals

Mr. Spencer Tinker (*in lit.*) contributed observations on three monk seals, each of which he has kept in captivity at the Waikiki Aquarium for more than a year. Two seals, a male and female, were subadult and no breeding activity was observed.

The seals were playful and showed considerable tameness but would not allow themselves to be touched. While cleaning the pool, attendants were occasionally "nipped in the pants and on the leg" by the seals as they played nearby. The animals often played "for hours in mock battles and gentle wrestling." They also played with objects such as bits of rope, rubber balls, and pieces of wood which spectators dropped into their pool.

Their response to the presence of other animals in the pool varied considerably. They got along well with harbor seals (*Phoca vitulina*). The two species never fought. However, at feeding time, the harbor seals hung back and gave way to the monk seals. Sea turtles (*Chelonia mydas*) in the pool were persistently annoyed by the monk seals which would grasp the turtles' hind flippers in their teeth. The turtles were removed when their hind flippers became shredded by the seals' teeth. A hawks-bill turtle (*Eretmochelys imbricata*), however, would pinch the seals on the belly and the seals, in general, avoided it. During an encounter, this turtle was bitten by a seal and blinded. A 5-foot bottom-living species of shark was relentlessly pursued by the seals. Eventually, the shark was exhausted and a seal dragged it backwards through the water by the tail. When a small pilot whale (*Globicephala*) was placed in the pool, the seals were terrified, but in a few days "they were around it, smelling and rubbing it with their noses." In general, the seals appeared more nocturnal than diurnal. They spent most of the night in the water and would rest for

many hours on an island in the pool during the day.

BIRTH AND DEVELOPMENT OF YOUNG

Pupping Season

Pups are born from about the first of the year until at least the end of June. Most are apparently born from mid-March through May.

In 1957, the first pup was seen from the air on a Laysan Island beach on January 7. The earliest authentic birth date we can find for Midway Atoll is March 22, 1956. At 0900 on that date, J. E. Graves (*in lit.*) of Honolulu saw a newly born pup on the west tip of Eastern Island. "The pup was still wet and the fetal membranes were attached. It had probably been born less than an hour." Bailey (1952) recorded a newly born pup on Pearl and Hermes Reef in late December, 1912, and that on March 15, 1913, 20 females with pups were seen at Pearl and Hermes Reef.

During the spring of 1957, five pups were born at Midway. The first, a premature 9-pound female, was found dead February 27 on the beach at Eastern Island. Birth dates at Midway in 1957:

February 20 (est.)	1 female
March 24	2 males
April 2	2 males

On June 5, 1957, 19 pups were examined on the beaches of Green Island, Kure Atoll. One had been born the morning of our arrival. The weights of the others were estimated and their approximate birth dates, all in 1957, calculated by reference to known growth and molt rates:

	NUMBER BORN
April 10-20	1
April 21-30	7
May 1-10	3
May 11-20	3
May 21-30	2
May 31-June 5	3

Only one large female that could have been pregnant was seen. This indicates to us that the pupping season was virtually complete at Kure by June 5. The possibility exists that other pregnant females were at sea.

It is interesting to note that the pupping seasons of other monk seals differ from that of the Hawaiian seal. The Mediterranean species is said to pup during September and October (King, 1956) and the Caribbean species in early December (Ward, 1887).

Birth

The four pups born alive at Midway were born either at night or early in the morning. New pups were found in the morning where none had been seen the night before. On Kure, a newly born pup was found on the beach at 0900.

At birth, the monk seal pup is thin, but not as thin as the elephant seal pup (Bartholomew, 1952). The fetal membranes had been detached from three pups seen a few hours after birth. The still bloody, damp tissues lay on the coral sand nearby. We found no clue as to how the umbilical cord was parted so soon after birth. Young fur seals may trail the

placenta from the umbilicus for several days after birth. A captive sea lion broke the umbilicus from her pup by jerking the placenta with her teeth (Slijper, 1956). The newly born monk seal is wide-eyed (eye color, blue-black) and apparently is able to see quite well. It is toothless (see dentition) and has a well-developed single coat of soft black hair (see pelage). Like other pinnipeds, it moves about with surprising agility soon after it is born.

Nursing and Weaning

The mother monk seal nurses her pup from four abdominal nipples, which are extruded only when the pup is nursing. The bearded seal (*Erignathus barbatus*) (Mohr, 1952) and the monk seal are apparently the only phocids having four functional teats.

During the nursing period, the mother remains constantly near her pup. She rolls on her side to permit the pup to nurse (Fig. 9). During the first 30 to 40 days of its life, the pup normally nurses at frequent intervals (several times at 4 to 5 minutes) and gains weight rapidly (see growth). When not nursing or swimming, the pup sleeps beside its mother. When sleeping, the pup sprawls flat

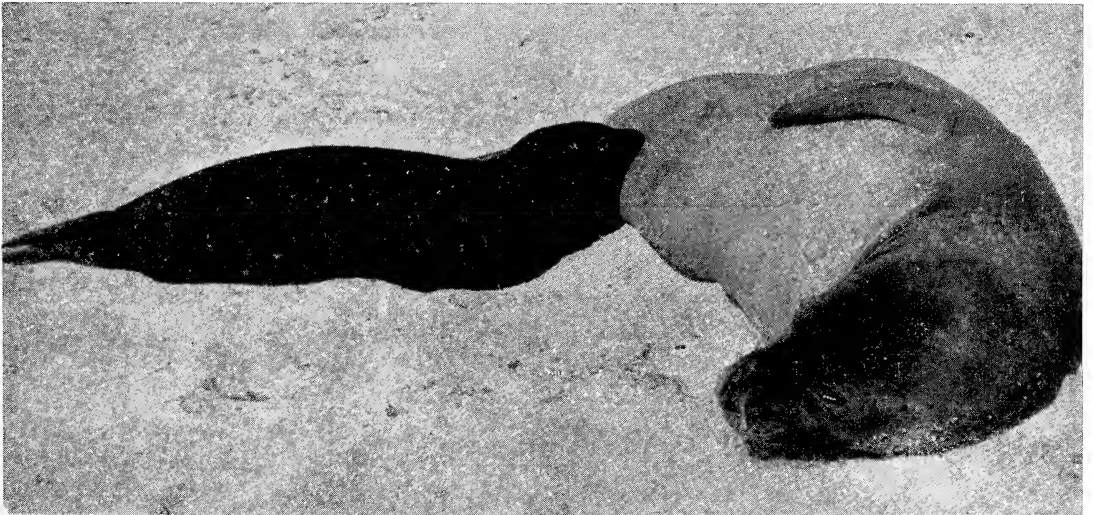


FIG. 9. A 12-day-old male monk seal pup nurses from one of its mother's four abdominal nipples. Nursing seals usually ignore human observers unless approached more closely than 8–10 feet. Midway Atoll, April 14, 1957 (KWK 57-16-9).

on its belly or rolls over and lies on its back (Fig. 10). The latter position seems to be a favorite one.

When the mother seal comes ashore to give birth, she is usually enormously fat (Fig. 11). As the nursing period approaches its end, the mother becomes quite gaunt. When she bends her body, huge wrinkles appear. While mothers were swimming with their pups we watched closely but saw no indication that they were attempting to find food. We found no indications that the mothers left their pups at night to feed. Near the beach camp of David Woodside on Laysan Island in late June, 1957, a nursing mother remained ashore with her pup during the night. We conclude from these observations that the mother fasts during the entire nursing period.

The maximum observed nursing period was 37 days. We would judge that the average pup is weaned in about 5 weeks at a weight of about 133 pounds (see growth).

The mother of pup MS-12, less fat than other mothers when her pup was born, nursed it for only 20 days and deserted it when it weighed only 82 pounds, somewhat more than half the more usual or apparently normal weaning weight. Pup MS-12 survived for

at least 27 days after being deserted, but whether it ultimately survived, we do not know, since it disappeared from its usual hauling-out places.

Since the pup's instinct to follow its mother is strong, we presume that the mother, after her supply of milk has been exhausted, slips away and deserts her pup while it is sleeping. This was the case when the mother deserted MS-12. Mother and pup were seen sleeping on the beach at 0300. By noon when we visited the area, we found the sleeping pup alone and the mother was not subsequently seen.

After it is deserted by its mother, the pup remains near the location of its birth. Pup MS-10 was frequently observed as it played in the water or slept near its birth site until it was 50 days old, when it was found sleeping about a half-mile away. After this it was occasionally seen at various places along the shore of Eastern Island over a mile from its birth place.

Swimming

The pup is able to swim at birth. When pup MS-12 was taken from its mother for tagging

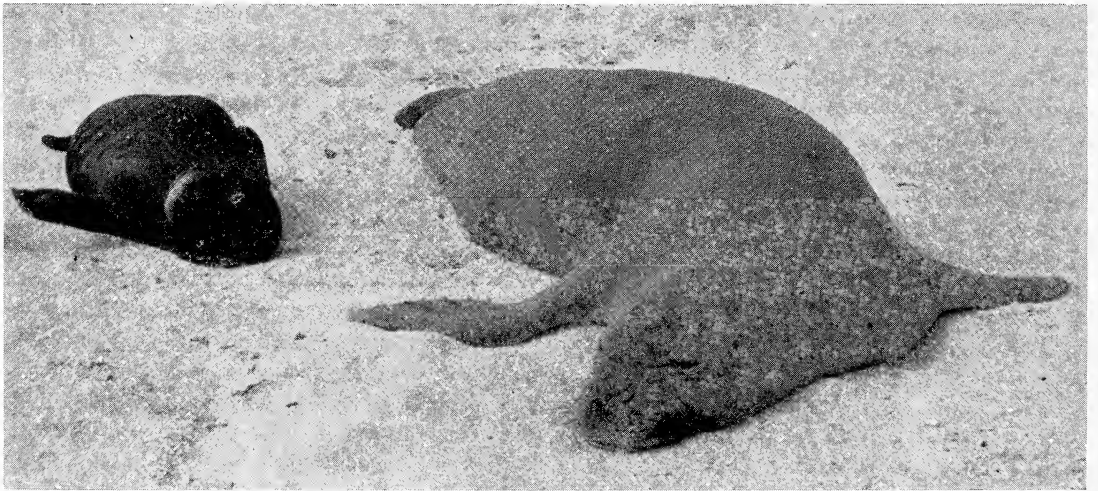


FIG. 10. A monk seal pup, satiated after a nursing period, sleeps on its back. After approximately 3 weeks of supplying milk for her pup, the mother here shows considerable loss of weight. Light hair, an indication of the postnatal molt, is visible on the pup's muzzle. Midway Atoll, April 22, 1957 (KWK 57-16-3).



FIG. 11. The mother monk seal characteristically attempts to keep her newly born pup under her muzzle or behind her when closely approached. The extreme obesity of the female at parturition is illustrated. Kure Atoll, June 5, 1957 (KWK 57-18-30).

and weighing on the day of its birth, it was moved down the beach parallel to the water for about 50 yards. By the time we had finished with it, its bellowing mother had joined it. She immediately led the pup to the water and both swam slowly along the beach until opposite the place of birth. Here the mother hauled out and led the pup to the spot from which we had removed it. The pup swam weakly, head high, and mainly with its front flippers.

Mother and pup usually remain on the beach for the first few days. The first time we saw a mother in the water (under undisturbed conditions) with her pup was the fourth day after birth. From this time, she spends short periods during the day swimming along the shore, closely followed by her pup, after which the two return to the general area where the pup was born. The mother spends much time on the beach where she lies facing the water while her pup frolics a yard or two

away in the shallows. As weaning approaches, mother and pup spend more time in the water and may go 100–200 yards from the beach.

Recognition of Pups by Mothers

When mother and pup are disturbed by humans, or when they are crawling along the beach, they keep in contact by a continuous series of calls, the mother bellowing and the pup bleating. When a pup is out of sight of its mother, she locates it by its bleating and crawls in the direction of the sound.

On May 4, when pups MS-12 and MS-13 were 33 days old and after MS-12 had been deserted by its mother, both pups were taken to a common location for weighing. As usual, the mother of MS-13 followed. After weighing MS-12, we released it on the beach, and then carried MS-13 behind a dune out of sight of its mother, so that she would not interfere with the weighing. When the mother of MS-13 noticed her pup was gone, she looked about and immediately noticed pup MS-12, which was bleating. She crawled rapidly to it, sniffed it several times, then turned away and continued her search for her own pup, indicating that a mother recognizes her pup by smell.

A few minutes later pup MS-12 approached MS-13's mother and tried to nurse. She did not at first object. However, when her own pup was returned, she became confused and very excited. She lunged at and bit both pups. A brief interval of bleating, bellowing turmoil followed. The mother bit both pups several more times and grasping them in her teeth she attempted to toss them both away from her. Pup MS-12 soon became discouraged and hastened to leave. Pup MS-13 continued to approach his mother's face, but still confused, she bit at him and he angrily bit back at her. The mother then proceeded toward the water, her pup following. Exhausted by the exertion, she soon stopped, and when her pup approached bleating, she nuzzled and accepted it. Within five minutes, she was

nursing her pup and MS-12 was not seen to approach her again.

Care and Defense of Young

The mother monk seal shows considerable affection toward her young. The pup often rubs and nuzzles its mother's head and neck, and the mother sniffs and nuzzles her pup in an affectionate way. When a bleating, frightened pup is allowed to return to its mother, she usually places her head and neck over it protectively (Fig. 11), and the bleats of the pup are answered by deep moaning sounds from the mother. This behavior is in marked contrast to that of the Alaska fur seal mother which, other than to nurse it, shows little regard for her pup. Rarely, and only within a few hours after birth, a mother fur seal will remain near her pup or attempt to drag it with her when she is frightened and other animals are departing.

From the time her pup is born until she deserts it, the mother monk seal normally remains aggressive toward humans and other seals, except toward other nursing females with whom she is loosely associated. In order to tag and to obtain weights and measurements of pups, it was necessary for one of us to divert the mother while the other made off with the pup.

On the day that pup MS-13 was born, it was taken from its mother for tagging and weighing. While one of us diverted the mother, the other dragged the pup behind a sand dune. The mother, occupied with her tormentor, failed to miss her pup until it was beyond her range of vision. When she missed it she first dashed toward the water, looking frantically about. Seeing no sign of her pup there, she turned rapidly about in several circles, constantly peering behind her and bellowing. Soon she heard the bleating of her pup and proceeded in the direction of the sound. This mother remained unusually aggressive in protecting her pup until shortly before deserting it at the end of the nearly 6-week nursing period.

On one occasion, we were weighing pup MS-12 recently deserted by its mother. Pup MS-13 and his mother were more than 100 yards away in the lagoon. Hearing the bleating of MS-12, the mother of MS-13 swam rapidly toward us, head raised and bellowing, her pup following closely behind. She continued her charge onto the beach for 10 feet or more, to within about 2 yards of us.

On another occasion, when MS-12 and his mother were swimming near the shore, we went to the water's edge to photograph the two. With head held high and mouth open in threat display, the mother charged to the beach, left the water, and pursued us up the beach for a distance of 20 feet (Fig. 12). She quickly returned to the water, but repeated the performance when we again went to the water's edge. Re-entering the water, she was about 50 yards from shore and did not see us as we approached the water's edge a third time. Therefore, we yelled loudly at her and

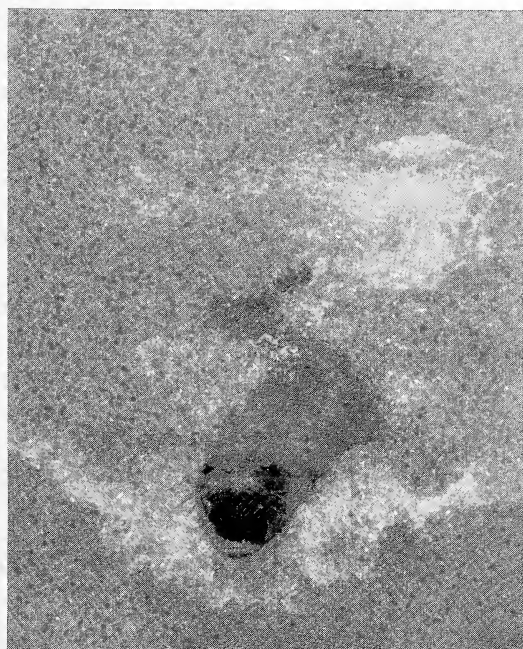


FIG. 12a. A mother monk seal, her pup dimly visible beneath the surface behind her, displays threat behavior when charging human observers on the beach. Midway Atoll, May 4, 1957 (KWK 57-17-29).

once again she charged to shore as before. We found that this behavior was quite dependable and facilitated the capture of her pup for weighing, since the pup always followed close to its mother. The same behavior was noted among mother seals at Kure, with the exception of one female which bellowed and opened her mouth in threat display at a distance of about 50 yards offshore, but refused to charge onto the beach.

One exceptionally aggressive mother began a charge on the beach while her newly born pup was in front of her. If we had not changed the direction of her charge by moving to one side, she would have crushed her pup. Although she crushed it only slightly under her chest, it appeared for a few moments to be dazed by having its breath expelled under her weight.

At Pearl and Hermes Reef in late May, 1956, "Tom Frazier, a fisherman, was attacked by an adult seal while spear fishing in about six feet of water near a beach where several new pups and adults were observed. The seal swam rapidly and directly at Frazier with its mouth open and turned away only after being poked repeatedly with a fish spear." (E. C. Jones, FWS, *in lit.*)

The mother of MS-13 would charge at us anywhere along a nearly half-mile stretch of beach, at a considerable distance from the place her pup was born. The display of hostility should probably be interpreted as behavior in defense of her pup rather than defense of a territory.

PHYSICAL CHARACTERS AND GROWTH

Dentition

The tiny milk teeth are apparently resorbed before birth, as in other phocids. When the skull of a 9-pound prematurely born pup (BDM 491) was cleaned, only one of these small teeth could be found.

At birth, the gums of the monk seal pup are almost smooth. Slight irregularities on the surface indicate the position of unerupted teeth, especially the postcanines. At age 27

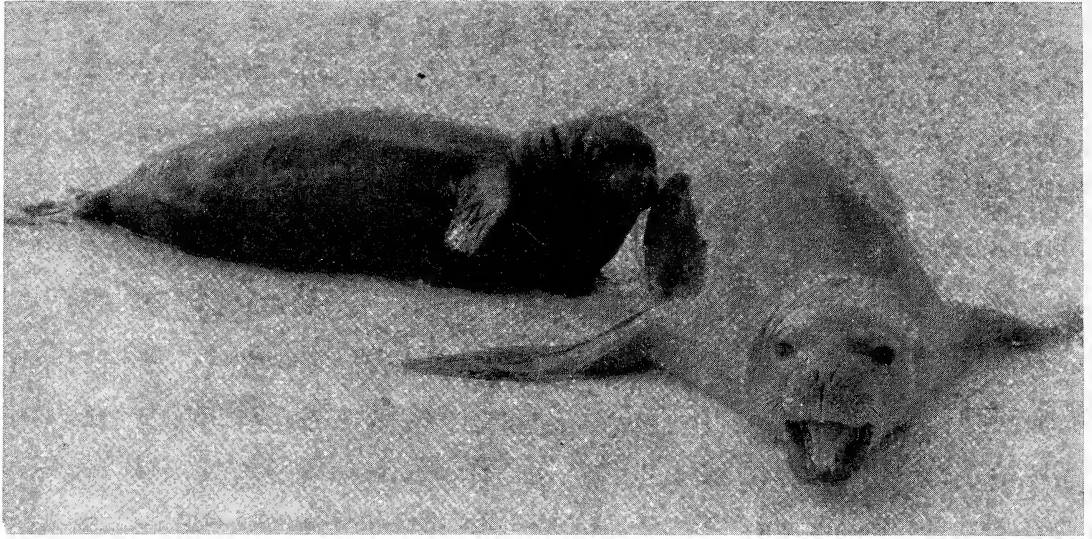


FIG. 12*b*. Charging from the water and accompanied closely by her pup, a mother monk seal leaves the water to threaten the photographer. Midway Atoll, May 4, 1957 (KWK 57-17-25).

days all permanent lower teeth were erupted. In the upper jaw, the canines and incisors had erupted but only the posterior (fifth) post-canines showed. By the age of 46 days, all teeth were approximately 3 to 5 mm. above the gums.

The adult dentition is (I 2/2, C 1/1, PC 5/5) $\times 2 = 32$.

Pelage and Molt

NATAL PELAGE: On February 27, an aborted 9-pound fetus was found. It was covered with soft black hair, 3 to 6 mm. long, which was slightly and variably curled, giving the surface an irregular ridged appearance. The first three digits of the right front flipper were tipped with white, and there was a small white patch on the belly.

At birth the pup is covered with soft coal-black hair 4 to 8 mm. long, appearing almost velvety, except that the direction of growth can be felt by rubbing with the hand. Rarely a flipper is white tipped at birth but this feature disappears with the first molt.

POSTNATAL MOLT: Four male pups (MS-9, 10, 12, and 13) were observed at frequent but

irregular intervals of several days or weeks from birth to the age of more than 2 months.

The rate of molt varied somewhat among individuals. The size of the mother, at the time the pup is born, influences the growth of the pup, and thus indirectly the rate of molt. The pup of a female of maximum size reached a large size before weaning and completed its molt more quickly than a pup that was weaned earlier and at a smaller size by a thinner mother.

The natal hairs fall out individually, not attached to pieces of cuticle as in older animals. The new hair grows in first on the face, chest, neck, and sides. The last areas to lose the natal coat on several pups were the lower back, sides of the abdomen, mid-ventral posterior, abdominal area, and hind flippers.

At age 20 days, a whitish tinge is evident on the muzzle. Light hairs, hidden beneath the black coat, protrude above the surface of the skin, particularly on the neck and chest. At this stage, the black body hair may be pulled out without difficulty. At age 30 days, the black hair is falling rapidly. When we handled the pups, our hands became coated with hair.

The black coat begins to appear "moth-eaten" and has faded from jet black to a dark chocolate brown. At age 39 days, MS-9 had patches of faded natal hair clinging to the lower back, sides, and abdomen, nearly meeting along the mid-ventral line, between the anal and penile openings. At this time, MS-10, the same age as MS-9 but larger, had completed its molt.

By the time the black pup coat is entirely lost, the first postnatal pelage has completely grown in.

ADULT AND SUBADULT PELAGE: After the postnatal molt, the ventral areas are silvery white, darkening to light silvery gray on the sides and dorsally to dark slate gray faintly tinged with a silvery sheen. When wet, the

back appears dark sooty brown (Fig. 13).

When the new pelage is fresh, immediately after molting, no yellowish tinge is evident. However, after about a month the light belly may, for unknown reasons, take on a slight yellowish tinge. Before the end of its first year, the pup becomes quite yellowish.

Yearlings and 2-year-olds of both sexes are lighter than older animals.

The color of all adult monk seals observed in fresh pelage was unmarked silvery white or light silvery gray ventrally and dark silvery tinged brown or slate gray dorsally. As the hair ages, the silvery tinge is lost, the ventral surface takes on a decidedly yellowish color and dorsally the hair becomes dull brown, darker in some individuals than in others.



FIG. 13. Male monk seal pup aged 39 days and recently weaned. The black natal coat has been completely lost. The pelage is marked by water splashes. Note extreme obesity. Midway Atoll, May 2, 1957 (KWK 57-17-17).

This is the usual pelage color of winter and early spring.

Adult males are generally darker than females. Some appear almost blackish on their backs and sides. However, a very large dark female was seen, and a nearly adult male was as light as any female seen.

The length of hair on an adult male (BDM 490) ranged from 2 mm. on the flippers to 9 mm. on the belly. The individual hairs are quite stiff and when dry stand fairly erect.

ADULT MOLT: In the subtropical climate of the Leeward Chain, the air temperatures are mild and comparatively uniform (see climate) and seasonally the hours of daylight vary less than at higher latitudes. As might be expected under such conditions, the molting of various individuals is spread over a long period.

The first molting adult, a large female, was seen on May 13. Her molt was complete except for a few irregular ragged patches of loose skin and hair on the lower back. A subadult male, partially molted, was seen on May 23. Among a group of 66 seals seen on June 5, 8 adults and 2 subadults were in the process of molting. Thirteen adults were closely observed on the same day. Of these, 2 had completed their molt and 3 had not begun to molt. Among 8 subadults, 7 had not yet molted and in 1 the molt was one-third complete. Molting subadults were observed on July 29, August 15, and November 18, 1957; molting adults as late as September 10 and 20, and October 1 and 11.

In general, adults appear to molt earlier than subadults. However, no adult females, either in fresh pelage or in the process of molt, were seen with nursing pups. Because of the extent of the pupping season, it is probable that some adult females do not begin their molt until midsummer or later.

A subadult male captured in October, 1955, and held in the Waikiki Aquarium molted in the fall of 1955 and again in April of 1957, and a female in October of 1957 (S. W. Tinker and K. A. Wong, *in lit.*).

The molt begins around the face and neck, proceeding posteriorly along the belly and sides, so that the central dorsal region and hind flippers are last to molt.

Molts subsequent to the first postnatal molt, except for their progression from anterior to posterior and from ventral to dorsal, are quite different from the first molt. The process of molting for the elephant seal is described by Laws (1956). It is said to be "unique, not only among the pinnipeds but among the mammals," and has been called "reptile-like." We were, therefore, interested to observe that Laws' description of the molt in the elephant seal applies remarkably well to that of the adult and subadult Hawaiian monk seal.

When the faded brown and straw-colored hair sloughs off during the spring and summer, it comes off in sheets and patches (Fig. 14) still imbedded in the outer layer of the epidermis (Fig. 15). One patch of shed skin and hair picked up from the beach beside a sleeping adult female, measured roughly 170×100 mm. The hair roots protruded 1 mm. from the lower side, and the old hair 8–10 mm. from the top. When this animal was examined from a distance of about 2 feet, it appeared that where the hair and adhering epidermis had been freshly lost, little or no new hair yet protruded from the blackish, rough skin. However, on the chest and shoulders, the slightly protruding new growth gave the surface a faint silvery sheen.

No animal was seen to roll or scratch to aid the loss of loose patches of skin and hair. Molting seals seemed to behave as usual, both in and out of the water, except for one adult male on October 1 which was reluctant to enter the water and charged the observer with threat display. The captive animal mentioned above fasted during the several weeks of molting. However, the female captured in August, 1955, "ate a fish or two a day but without any spirit" while molting (S. W. Tinker and K. A. Wong, *in lit.*).

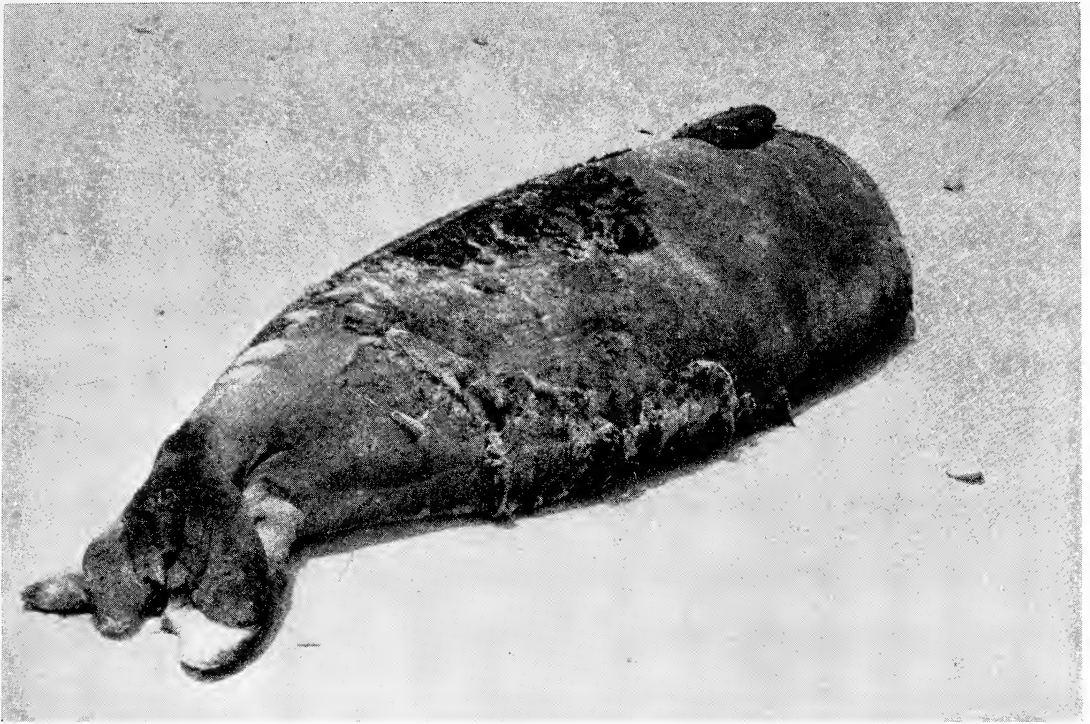


FIG. 14. Molting adult female, ventral view. Sloughing of hair and epidermis during the molt begins around the head and neck, progressing posteriorly and ventrally. The lower back and hind flippers are last to complete the molt. Green Island, Kure Atoll, June 5, 1957 (KWK 57-22-3).

Growth and Body Size

PUPS AND YEARLINGS: Seal pups and yearlings were weighed on 100-pound capacity Chatillon spring scales (Fig. 16). When an animal exceeded the capacity of the scale, two were used in combination. A steel tape was used to measure living pups and yearlings. Because they squirmed energetically, the length measurements (straight line, tip of nose to tip of tail) are not exact. However, the error probably does not exceed $\pm 1-2$ cm. and the mean values are, therefore, useful. Measurements other than standard length were virtually impossible to obtain with our technique from living yearlings.

At birth, the pup weighs about 35 to 38 pounds and its length is roughly 95 to 100 cm. (Table 10). At the age of 17 days, the weight of pup MS-13 had doubled; at age 28 days, its weight had tripled; and when last

weighed during the nursing period, at the age of 37 days, its birth weight had nearly quadrupled (Fig. 17). At Midway, the mean weight of three normal pups at the time of weaning was 133 pounds (Fig. 12). At Kure, the largest nursing pup observed had an estimated weight of 150 pounds; the estimated weights of recently weaned pups ranged from 95 to 160 pounds. The length and girth of only one normal pup at the time of weaning was recorded. This pup (MS-13) weighed 142 pounds, its length was 122.5 cm. and its girth was 108.3 cm. Its "degree of fatness" was, therefore, 88.4 (*cf.* Laws, 1953; Sivertsen, 1941; Smirnov, 1924).

After the pup is weaned, it steadily loses weight. Since it has grown relatively little in length during the nursing period, it is exceedingly fat when weaned (Fig. 13) and apparently takes no interest in food. (The apparent increase in weight shown for MS-10

TABLE 10
WEIGHTS AND LENGTHS OF LIVING
HAWAIIAN MONK SEALS

DATE, 1957	SEX	AGE	WEIGHT (lbs.)	LENGTH ¹ (cm.)
April 2.....	♂	1 day	36	97.5
April 2.....	♂	1 day	38	95.0
March 27....	♂	4 days	44	102.5
March 27....	♂	4 days	46	100.0
Mean for newly born pups...			41	98.75
January 14....	♂	yearling	112	128.0
March 5.....	♀	yearling	69	114.0
March 5.....	♂	yearling	102	129.0
March 5.....	♀	yearling	92	130.0
March 5.....	♀	yearling	111	145.0
March 5.....	♂	yearling	108	136.0
Mean for yearlings.....			99	130.3

¹ Straight line, tip of nose to tip of tail, animals lying on their bellies.

probably may be attributed to an error in reading the scales.) Considerable observation will be necessary to ascertain when the pup begins to maintain itself by feeding.

The mean weight of six yearlings was 99 pounds, and their mean length 130.3 cm. (Table 10). It is interesting to note that the length of yearlings increases little over that of the newly weaned pup and that newly weaned pups usually weigh considerably more than yearlings. Similar conditions have been shown in other pinnipeds (Scheffer and Wilke, 1953). This indicates that the adjustment from nursing to an independent existence, when the animal must obtain its own food, is strenuous. The substantial store of blubber is undoubtedly a valuable store of nourishment during early attempts to find food.

SUBADULTS AND ADULTS: A young seal, judged to be a yearling, weighed 119 pounds on July 21, 1957, shortly after capture. On September 2, 1957, it weighed 134 pounds and on February 5, 1958, 200 ± 25 pounds, estimated (G. H. Pournelle, *in lit.*). If a curve is projected on the basis of these weights, it appears possible that the monk seal may ap-

proach adult size in its third year. A rapid growth rate might be expected, since related forms, the Weddell and crabeater seals, are believed to attain adult size in 1 year (Bertram, 1940).

On February 2, 1957, four adult male monk seals were examined as they lay sleeping on a small islet at Midway. All were about the same size. The one estimated to be slightly largest was shot (now BDM 490). It was cut up and weighed in sections on a 100-pound capacity spring scale. Measurements and weights are recorded below.

Measurements:

Total length ¹	2,142 mm. (7 ft. ¼ in.)
Front flippers ²	369 mm.
Hind flippers ²	342 mm.
Tail.....	170 mm. (approx.)
Rectum to penile opening...	380 mm.
Girth behind flippers.....	1,300 mm.
Large intestine, length.....	1,410 mm.
Small intestine, length.....	2,200 cm. (64 ft. 8 in.)

Thickness of blubber,

mid-belly region:

outer layer.....	27-29 mm.
inner layer.....	15-16 mm.

Total..... 42-45 mm.

Weights (pounds):

Stomach and contents.....	8.5
Liver and gall bladder.....	11.5
Intestines.....	19.5
Kidneys.....	2.5
Heart.....	1.6
Remainder of carcass.....	336.4

Total..... 380.0

¹ Tip of nose to tip of tail, animal lying on its back.

² Flippers held at right angle to body, measured along anterior margin.

No adult females were collected. The length of a large living female measured as it lay flat on its belly on a smooth sand beach, was 7 feet 8 inches; her weight was estimated at 600 pounds. Fully adult females, in general, appeared larger than males. Pregnant and newly postpartum females are far more obese than any male seen. One large female was estimated to weigh about 575 pounds immediately after the birth of her pup. This

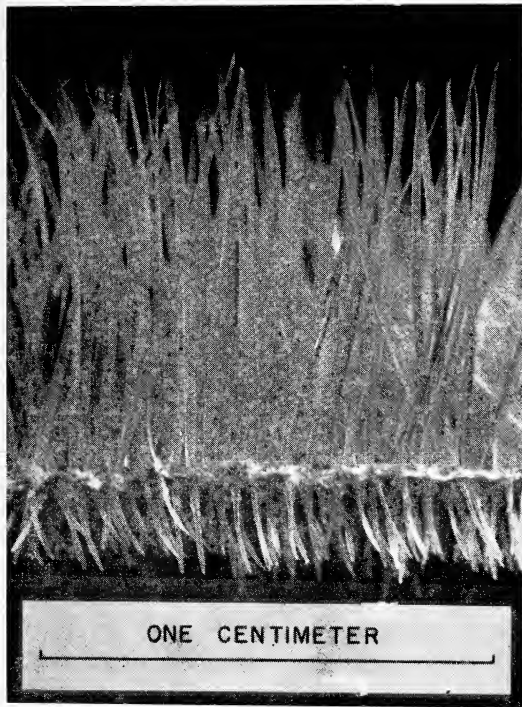


FIG. 15. Cross section of molted hair and epidermis from an adult monk seal. The old faded hair protrudes 8–10 mm. above and the roots 2 mm. below the thin epidermal tissue. Kure Atoll, June 5, 1957 (KWK 57-20-8).

estimate was first made visually. At the end of the nursing period, it was estimated that the mother's weight approximated that of the weighed adult male (380 pounds). Since her pup gained approximately 100 pounds during the 37-day nursing period and it is presumed that the mother lost about 2 pounds for every 1 gained by her pup (*cf.* Laws, 1953), we considered the original estimate quite valid.

ASSOCIATIONS WITH OTHER ORGANISMS

Parasites

Samples of all parasites found in an adult male monk seal, killed on February 2, 1957, at Midway Atoll, were preserved and distributed through Dr. R. A. Rausch to two other specialists. In the future, certain of their findings may be published. A general synopsis of the information now available is presented.

Nematodes, *Contracecum turgidum*: The esophagus (sample 1, USNM Helm. Coll. 38081) contained a number of minute larvae and a few adults which were much smaller than the approximately 200 individuals which occupied the stomach (sample 2, USNM Helm. Coll. 38080). In addition, a number of individuals were collected from the anterior and posterior portions of the small intestine. Specimens were identified by Mrs. M. B. Chitwood. This species was originally described by Chapin from material collected from the Hawaiian monk seal in 1925. The genus has been recorded from many pinnipeds of the Pacific coast.

Acanthocephalans, *Corynosoma* sp.: Specimens were collected from the anterior portion of the small intestine where they resembled grains of white sand attached to the mucosa. Dr. Yves J. Golvan suspects them of being undescribed. The genus is widely distributed in marine mammals.

Cestodes, *Diphyllobothrium* sp.: The small intestine was heavily infested with cestodes. Our field notes indicate that the smaller worms were found in the anterior part of the small intestine while the larger ones were in

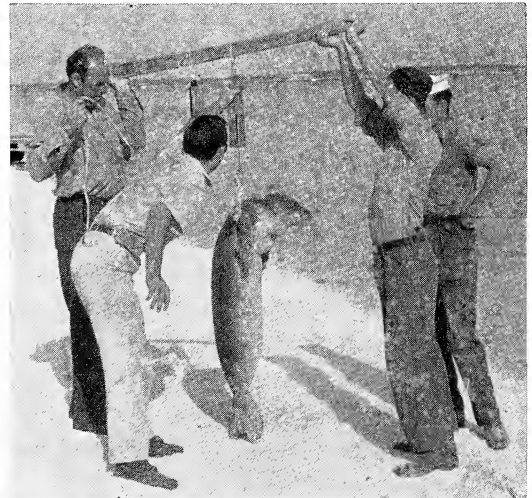


FIG. 16. Weighing male monk seal pup MS-12. Pups and yearlings were weighed on one or a combination of two 100-pound-capacity spring scales. Midway Atoll, May 29, 1957 (KWK 57-18-16).

the posterior. Dr. Rausch informs us that he has separated the specimens into three forms as yet unidentified.

Algae

Almost all seals observed in the field have areas of their pelage tinged greenish by a growth of minute green algae, *Pringsbeimiella scutata* (Reinke) Schmidt and Petrack (Fig. 17). According to Yale Dawson, who identified it, this algae is a widespread species epiphytic on various slender green algae. The size and shape of the seal hair seem to be ideal for the growth of this plant. This is apparently the first time it has been found growing on the hair of mammals. On the seals it grows most abundantly around the eyes, nos-

trils, and lips, in the axillae of the fore and hind flippers, between the digits, and along the side of the body. These are the parts of the pelage least subject to drying when the animals are on land, and for that reason are presumably most favorable for the growth of the algae. Animals remaining several days on land lost the greenish tinge. One very noticeable fact is that the yearling seals have a much more abundant growth of algae than do the adults. *Pringsbeimiella* differs greatly from the strands of *Enteromorpha* reported from the grey seal, *Halichoerus grypus* (Mackenzie, 1954), and the harbor seal, *Phoca vitulina* (Scheffer and Slipp, 1944), and from *Ectocarpus* found on fur seals.

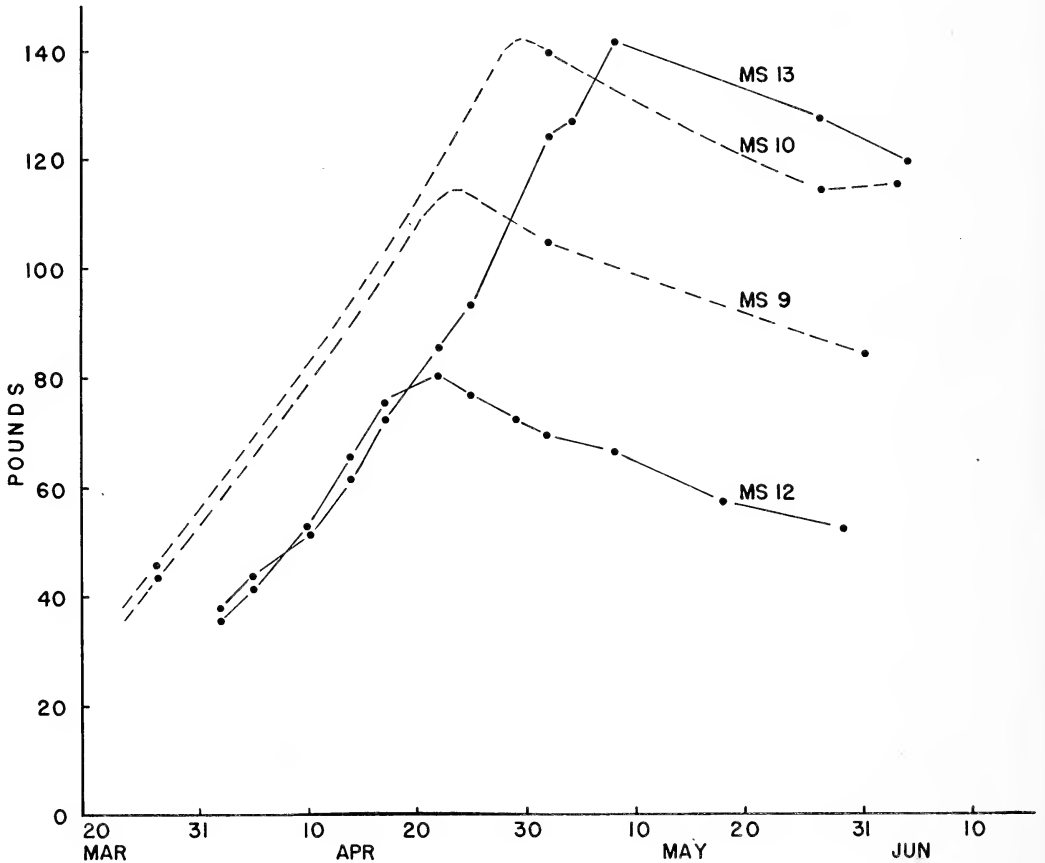


FIG. 17. Growth curves of four male Hawaiian monk seal pups from birth to several weeks after weaning. Dots indicate actual weights. Variation in the length of the nursing period appeared dependent on the obesity of the mother at parturition, the most obese mothers nursing their pups for the longest period.

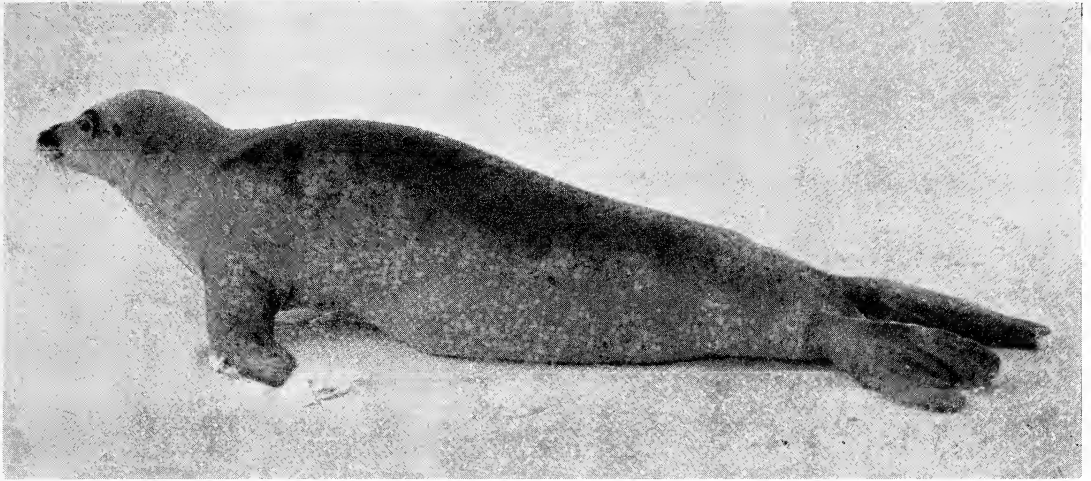


FIG. 18. Subadult monk seal. Dark patches above eye and on muzzle indicate green algae (*Pringsbeimiella*) growth. The characteristic mode of progression on land is demonstrated. Midway Atoll, February 2, 1957 (KWK 57-3-5).

Flies

Flies frequently cause seals considerable annoyance. They often cluster about the eyes of sleeping seals. On one occasion, a large female was resting under the *Scaevola* along the upper beach line. Swarms of flies clustered on one of her eyes; at intervals of several seconds, she brushed them away with her foreflipper. After this occurred several times, she crawled onto the open sand where the breeze was strong enough to keep the flies away. Flies swarmed around two open, festering wounds on the back of an old female hauled out on the beach.

On May 4, 1957, we collected several flies found swarming on a healthy subadult seal on Eastern Island. These were identified by Charles R. Joyce, as follows: *Lucilia graphita* Shannon, *Chrysomya megacephala* Fab., *Phoenicia sericata* (Meigen).

Birds

The islets and beaches where seals haul out are the nesting grounds of thousands of black-footed albatrosses (*Diomedea nigripes*) and Laysan albatrosses (*Diomedea immutabilis*). Thus, the birds are frequently in the proximity of seals. We watched an adult Laysan alba-

ross gaze curiously at a sleeping seal. After slowly walking around the animal, it paused near its head, then reached out and gingerly pecked the seal on the nose. Lurching violently, the seal awoke and the startled albatross took flight. A basking seal threatened a curious black-footed albatross with open jaws. An adult seal threatened an albatross chick which happened to be in its line of travel toward the sea. The chick returned the threats with an aggressive display of beak snapping. When only inches separated the two, the seal altered its course, avoiding the chick which it surely would otherwise have crushed.

On January 31, 1957, we observed a seal, presumably feeding in shallow water north of Eastern Island. Two great frigate birds (*Fregata minor*) were flying about 50 feet above it. Several times the birds dropped down to snatch bits of refuse from the surface—possibly the intestines of fish (the Mediterranean monk seal is said to remove the intestines by squeezing before swallowing the rest of the fish).

SUMMARY

1. The Hawaiian monk seal (*Monachus*

schauinslandi) is similar to the Weddell seal (*Leptonychotes weddelli*) in several aspects of behavior. The molt is epidermal, similar to that of elephant seals (*Mirounga*). Monk seals more nearly resemble the Lobodontinae and Cystophorinae than the Phocinae. It is suggested that the Hawaiian monk seal may be only racially distinct from the Caribbean monk seal (*M. tropicalis*).

2. The Hawaiian monk seal breeds only in the Leeward Chain of the Hawaiian Islands, on Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals. They have occasionally been reported from Maro Reef and Nihoa Island. In the main Hawaiian Islands, they are rarely seen. Sightings are recorded from Hawaii, Oahu, Kauai, and Lehua.

3. Monk seals appear to have few obvious adaptations to their tropical or subtropical environment. Like phocids of cooler regions, they are covered by a thick layer of blubber. A body temperature (35.5°C.), lower than temperatures recorded from seals inhabiting cooler climates, the black skin and black pelage of the pup may have significance in this respect.

4. Habitat requirements include shallow waters (usually near coral reefs) for feeding, sandspits and beaches for hauling grounds, and permanent islets or beaches above high tide for pupping areas.

5. Hawaiian monk seals were nearly exterminated during the nineteenth century, but have now successfully repopulated their former range. Aerial censuses and ground counts in 1956-57 placed the minimum population at 1,013 in the summer of 1957. This included 94 pups, but the count of pups was incomplete at some atolls. Other uncounted seals were undoubtedly at sea.

6. Sex was ascertained in a sample of 154 animals including all age groups. Of these animals, 75 were males and 79 females.

7. The annual reproductive rate (births per 100 animals older than pups) is rather low: about 22 per cent at uninhabited Kure Atoll,

and 8 per cent at Midway Atoll where the seals are subject to human disturbance. Field observations suggest that many adult females miss pregnancy each year.

8. Natural mortality among monk seals, both juvenile and adult, appears to be low. At Midway Atoll, six yearling seals were tagged and five pups were born in 1957, suggesting a high survival rate during the first year. A few monk seals carried large scars on their bodies; one apparently died of wounds inflicted by sharks.

9. At Midway Atoll, results of tagging indicate that all of the seals range widely in the lagoon, and share a common home range. Seasonally, seals are most numerous on land during winter months. Daily, they are most numerous on land during the afternoon.

10. While swimming, monk seals regularly use their front flippers, although their hind flippers and fishlike undulation of the body provide the chief means of propulsion.

11. Two distinct vocal sounds are uttered: a deep-throated, soft, bubbling sound (often with mouth closed), and various bellowing sounds.

12. Monk seals are genetically tame, but display threat behavior when closely approached or annoyed, both on land and in the water.

13. No marked social organization was observed. The seals are apparently sexually promiscuous. Courtship behavior was observed from early March to early July.

14. The most important food items in the contents of two seal stomachs were conger eels (*Ariosoma*) and moray eels (*Echidna* and *Gymnothorax*); other items included flatfish (*Bothus*) and cephalopods (octopi?). Apparently the monk seal is primarily a nocturnal bottom feeder, at least while frequenting atolls.

15. The single young is born sometime between late December or January and late June or early July, the majority during April and May. When newly born pups were observed, birth had taken place at night or early morn-

ing. In three cases the fetal membranes had been detached within a few hours after birth.

16. The mother nurses the pup from four abdominal nipples and apparently fasts during the entire nursing period. Weaning normally takes place when the pup is about 5 weeks old, at which time the mother deserts it.

17. The pup can swim at birth but may not normally take to water until the fourth day, after which it spends considerable time in the shallows daily.

18. When moving on land, or when out of sight of each other, mother and pup keep in contact vocally. The mother apparently recognizes her pup by smell. The pup follows its mother closely when she moves about on land and in the water.

19. The mother is affectionate towards her pup, and defends it aggressively from humans and from other seals (except other nursing females).

20. The milk teeth are resorbed before birth. The gums are smooth and toothless at birth. At 27 days after birth, all lower teeth and upper incisors, canines and posterior postcanines were erupted. At 46 days, all teeth were above the gums.

21. During the postnatal molt, the hairs are shed individually. This occurs from about age 20 to 40 days, varying with individuals.

22. The adult molt is epidermal, the outer layer of the epidermis sloughing off in large patches. This occurs between May and November, with the majority of animals molting in June. Parous females do not molt until after the pup is weaned.

23. At birth, pups weigh 35 to 38 pounds. In 5 weeks, they nearly quadruple their weight (average: 133 pounds). After weaning, weight decreases. The average weight of six yearlings was 99 pounds.

24. The growth of a young captive was rapid, indicating that adult size may be approached in the third year. A typical adult male, 7 feet long, weighed 380 pounds. Females average larger; a living 7-foot 8-inch

female's weight was estimated at 600 pounds; this animal was one of the largest we observed.

25. An adult male monk seal was heavily parasitized by *Contracaecum turgidum* and three species of *Diphyllbothrium*. An unknown species of *Corynosoma* was less abundant.

26. The pelage of many seals contains a growth of minute green algae, *Pringsheimiella scutata*. Several species of flies (*Lucilia graphita*, *Chrysomyia megacephala*, and *Phoenicia sericata*) cause seals considerable annoyance. There is negligible interspecific friction between albatrosses (*Diomedea nigripes* and *D. immutabilis*) and seals. Frigate birds (*Fregata minor*) were observed following feeding seals to gather scraps.

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Marine Mollusca of the New Hebrides

ALAN SOLEM¹

THIS PAPER presents a check list of the marine mollusks known from the New Hebrides Islands. In recent years there has been a revival of interest in Indo-Pacific marine shells and active research on their systematics and distribution is being carried on at several centers. Monographic treatments of families and genera are urgently needed, since the taxonomy of most groups is in chaotic condition. Until such monographic treatments become available, critical faunistic studies will be impossible.

Distribution records from faunal reports can be useful to monographers if the authority for identification is cited (see Solem, 1954, for use of such data). In a previous paper on the Solomon Islands fauna (Solem, 1953), no authorities were cited for the identifications. This omission seriously impaired the usefulness of that study and in the present paper is corrected in part. Both studies were carried out at the Chicago Natural History Museum while I was a graduate student at the University of Michigan. Since the summer of 1952 (when my paper of 1953 was submitted for publication) many nomenclatural changes have been recorded in the papers of Kuroda and Habe (1952), Kira (1955), and Demond (1957). These changes are incorporated below, although most of the identifications were completed in 1955. Preparation of the manuscript for publication has been delayed by a detailed study on the New Hebridean land mollusks (Solem, 1959).

MATERIAL STUDIED

The collection initiating this project was made by Robert E. Kuntz on the southeast

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coast of Espiritu Santo Island from October 1943 to January 1945. His 331 lots of marine shells represented 160 species and morphotypes. All NH and ML numbers refer to Kuntz collecting stations. Information about each site is found in Solem (1959: pl. 2, and Appendix I). About one half of the forms had not been previously reported from the New Hebrides. The Kuntz material is deposited in the University of Michigan Museum of Zoology with a set of duplicates in the Chicago Natural History Museum.

Some miscellaneous lots of New Hebridean marine shells were discovered in various museums and the records are incorporated below. Material from Tanga Island off Espiritu Santo (Museum of Comparative Zoology), Futuna Island (American Museum of Natural History), Rano Island off northeast Malekula (Chicago Natural History Museum), and Cape Lisburn, Espiritu Santo (gift of Harold Harry to Chicago Natural History Museum) was examined.

PREVIOUS STUDIES

Surprisingly little has been published on the New Hebridean marine fauna. Both Bougainville and Cook visited the islands in the late 1700's, but no New Hebridean mollusks are known to have been brought back from their voyages (von Martens, 1872a, 1872b). On August 24, 1829, George Bennett collected a living *Nautilus pompilius* at Dillon's Bay, Erromanga (Owen, 1832), and about the same time the "Astrolabe" scientists found 62 species of marine shells at Ticopia and Vanikoro in the neighboring Santa Cruz Islands (Quoy and Gaimard, 1832-1835). Dohrn (1864), H. Adams (1872), Baird (in Brenchley, 1873), Brazier (1894, 1896), Dautzenberg (1900), Fischer (1902), and Willey (1902) published brief notes or descriptions.

Mabille (1895) studied a small collection, Hedley (1899) included New Hebridean distribution records in his Funafuti report, C. R. Boettger (1916) listed a few marine shells, and Ingram and Kenyon (1946) recorded cowries from Espiritu Santo.

The only comprehensive studies are those of Fischer and Fischer-Piette (1938, 1939) on recent marine shells and of Abrard (1946) on fossils. Two short lists appearing in the *Minutes of the Conchological Club of Southern California*, no. 23 (1943) are ignored, since the identifications of one collection were found to be unreliable.

SYSTEMATIC LIST

The classification is slightly modified from Thiele (1929-1935). Specific and generic nomenclature follows recent Japanese usage, with the often more familiar synonyms usually being cited. Trinomials, when used, represent marked morphologic variants whose taxonomic status is uncertain. They do not represent "subspecies."

Identifications have been made from the Chicago Natural History Museum collection and have been checked against original illustrations whenever possible. For convenience, however, I have cited a reference figure from an easily available source, such as Hirase and Taki (1951) or Kira (1955), for many of the common species. Other reference figures are from the standard iconographies of Kiener, Reeve, Sowerby, Martini and Chemnitz (2nd edition), and the *Manual of Conchology*. A similar procedure was adopted by Demond (1957).

The following symbols indicate the sources of the species listed:

AMNH	American Museum of Natural History
Boettger	C. R. Boettger (1916)
Brazier	Brazier (1894, 1896)
CNHM	Chicago Natural History Museum
F	Fischer and Fischer-Piette (1938, 1939)

H	Donated by Harold Harry
Hedley	Hedley (1899)
IK	Ingram and Kenyon (1946)
Mabille	Mabille (1895)
MCZ	Museum of Comparative Zoology
ML	Collecting station on Espiritu Santo
NH	Same as ML
S	Schilder and Schilder (1952)

Class PELECYPODA Family ARCIDAE

- Anadara pilula* Reeve F
Anadara rhombea Born F
Anadara scapha Meuschen Kira (1955: pl. 43, fig. 12); NH 8
Arca imbricata imbricata Gmelin F
Arca imbricata avellana Lamarck (= *maculata* Sowerby) Reeve, *Arca*, pl. XI, fig. 71; NH 14, New Hebrides (Hedley)
Barbatia bicolorata Dillwyn (= *fusca* Bruguière, non Solander) F
Barbatia lima Reeve (= *decussata* of authors, non Sowerby) Kira (1955: pl. 42, fig. 12); Tangoa, Espiritu Santo
Barbatia ovata Gmelin (= *nivea* Chemnitz) Reeve, *Arca*, pl. XIV, fig. 90; NH 4, NH 5, NH 9, New Hebrides (F)

Family GLYCYMERIDAE

- Glycymeris (Veletuceta) reevei* Mayer F

Family NUCULIDAE

- Leda verconis* Tate Roy. Soc. So. Austral., Trans. 1891: 261, pl. 11, fig. 4 F

Family MYTILIDAE

- Brachidontes (Septifer) bilocularis* Linné Hirase and Taki (1951: pl. 18, fig. 2); NH 7, F
Brachidontes (Brachidontes) crebristriatus Conrad Dall, Bartsch, and Rehder (1938: pl. 8, figs. 5-8); ML 28
Modiolus auriculatus Krauss (= *moduloides* Röding?) F

Family VULSELLIDAE

- Isognomon isognomum* Linné F
Isognomon nucleus Lamarck F
Isognomon quadrangularis Reeve Immer
 (Boettger)
Isognomon sulcatum Lamarck Reeve, *Perna*,
 pl. 4, fig. 6; NH 9, NH 12, NH 14, F
Isognomon vitreum Reeve F

Family PINNIDAE

- Pinna rumphii* Hanley F

Family PECTENIDAE

- Aequipecten pallium* Linné F, Erromanga
 (Hedley)
Chlamys squamatus Gmelin F
Comptopallium radula Linné F
Cryptopecten inaequalis Sowerby F
Plicatula plicatus Linné Reeve, *Plicatula*, pl.
 II, fig. 5; NH 13, F
Spondylus ducalis Röding F
Spondylus linguafelis Sowerby F
Spondylus nicobaricus zonalis Lamarck F
Spondylus variegatus "Chemnitz" F

Family LIMIDAE

- Lima alata* Hedley F
Lima annulata Lamarck F

Family OSTREIDAE

- Ostraea cristagalli* Linné Reeve, *Ostraea*, pl.
 XXVIII, fig. 72; Havannah Harbour,
 Vate (Hedley)
Ostraea forskali Gmelin F
Ostraea paulucciae Crosse (= *palmipes* Sowerby)
 F
Ostraea plicatula Gmelin F

Family CORBICULIDAE

- Polymesoda (Geloina) cyprinoides* Quoy and
 Gaimard Martini and Chemnitz, IX(3):
 pl. 20, figs. 3, 4; ML 75
Polymesoda (Geloina) ingens Dautzenberg (= *cyprinoides*
 Quoy & Gaimard?) Dautzenberg (1900: pl. 5);
 Espiritu Santo (Dautzenberg, 1900)

Family CARDITIDAE

- Begonia (Mytilicardita) aviculina* Lamarck
 Reeve, *Cardita*, pl. IV, fig. 18; NH 9
Begonia (Mytilicardita) variegata Bruguière F
Venericardina ovalis Reeve F

Family LUCINIDAE

- Codakia (Codakia) tigerina* Linné F
Codakia (Jagonia) divergens Philippi New
 Hebrides (Hedley), F
Fimbria fimbriata Linné F
Loripes assimilis Angas F
Lucina (Lucina) edentula Linné F

Family CHAMIDAE

- Chama asperella* Lamarck F
Chama imbricata Broderip Zool. Soc. London,
 Trans. 1835: pl. 39, fig. 1; Aneiteum
 (Hedley)

Family CARDIIDAE

- Fragum fragum* Linné F
Fragum nivale Reeve F
Papyridea (Fulvia) australis Sowerby F
Trachycardium flavum dupuchense Reeve F

Family TRIDACNIDAE

- Hippopus hippopus* Linné Kira (1955: pl. 55,
 fig. 15); Tagoa, Espiritu Santo (MCZ)

Family VENERIDAE

- Circe (Circe) plana* Odhner K. vetensk. Akad.
 Handl., 52(16): pl. 1, figs. 23–25; NH 5
Dosinia aff. *angulosa* Philippi F
Gafrarium dispar mixtum Lamarck F
Gafrarium pectinatum Lamarck F
Gafrarium tumidum Röding (= *gibbium* Lamarck)
 Hirase and Taki (1951: pl. 33, fig. 3);
 NH 5, NH 9
Lioconcha castrensis Linné Kira (1955: pl. 57,
 fig. 3); ML 28, Aneiteum (Hedley), F
Lioconcha ornata Dillwyn (= *picta* Lamarck) F
Pitar (Lepidocardia) australica Reeve F
Pitar (Pitarina) citrina Lamarck F
Pitar (Paradione) erycina Linné F
Pitar (Lepidocardia) florida Lamarck F

- Pitar (Paradione) philippinarum* Hanley F
Tapes litteratus Linné F
Venerupis (Amygdala) variegata Sowerby Hirase and Taki (1951: pl. 40, fig. 6); NH 7, F
Venus (Periglypta) lacerata Hanley F
Venus (Leucoma) marica Linné F
Venus (Periglypta) puerpera Linné Hirase and Taki (1951: pl. 36, fig. 2); NH 9
Venus (Periglypta) reticulata Linné F

Family MESODESMATIDAE

- Mesodesma (Atactodea) glabratum* Gmelin F
Mesodesma (Davila) planum Hanley F
Mesodesma (Atactodea) striatum Lamarck Reeve, *Mesodesma*, pl. 2, fig. 10; NH 5, NH 9
Mesodesma (Atactodea) trigona Deshayes Reeve, *Mesodesma*, pl. III, fig. 19; Tangoa, Espiritu Santo (MCZ)

Family MACTRIDAE

- Cardilia semisulcata* Lamarck F
Mactra (Mactra) cuneata Gmelin F
Mactra (Mactra) kanakina Souverbie F
Mactra (Mactra) maculata Gmelin F

Family DONACIDAE

- Donax crenatus* Linné F
Donax tinctus Gould F

Family GARIDAE

- Asaphis (Asaphis) deflorata* Linné Vate (Hedley), Immer (Boettger), F
Sanguinolaria (Soletellina) elongata Lamarck (= *violacea* Lamarck) F

Family TELLINIDAE

- Angulus (Tellinides) apalinus* Gmelin F
Angulus (Exotica) clathrata Deshayes (= *rhomboides* Quoy & Gaimard) F
Angulus (Angulus) rubellus Deshayes F
Arcopagia (Arcopaginula) inflata Gmelin F
Arcopagia (Pinguitellina) robusta Hanley F
Arcopagia (Arcopagia) subelliptica Sowerby F
Cyclotellina (Cyclotellina) remies Linné F
Cyclotellina (Scutarcopagia) scobinata Linné

- Hirase and Taki (1951: pl. 44, fig. 1); NH 9, F

- Quadrans (Quidnipagus) palatam* Iredale (= *rugosa* Born) F
Strigilla (Strigilla) splendida Anton F
Tellina (Tellina) crucigera Lamarck F
Tellina (Pharaonella) perna Spengler F
Tellina (Tellinella) petalina Deshayes F
Tellina (Tellina) virgata Linné (= *jubar* Hanley) F

Family PHOLADIDAE

- Jouannetia (Triumphalia) globulosa* Quoy and Gaimard F

Family TEREDINIDAE

- Bankia bipalmulata* Lamarck Turtle Bay, Espiritu Santo (MCZ)

Class CEPHALOPODA

Family NAUTILIDAE

- Nautilus pompilius* Linné Tangoa, Espiritu Santo (MCZ), Dillon's Bay, Erromanga and Aneiteum (Bennett, 1860)

Class GASTROPODA

Subclass OPISTHOBRANCHIA

Family ACTAeonIDAE

- Pupa sulcata* Gmelin Man. Conch. (1)15: pl. 20A, figs. 39, 46-48; Aneiteum (Hedley)

Family BULLIDAE

- Bulla (Bulla) adamsi* Menke Man. Conch., (1)15: pl. 35, figs. 15, 16, 19, 20; Malekula (CNHM)

Family ATYIDAE

- Atys (Atys) naucum* Linné F
Haminoea crocata Pease F
Smaragdinella (Smaragdinella) viridis Rang F

Family OXYNOIDAE

- Oxynoe bargravesi* H. Adams H. Adams (1872: pl. 3, fig. 30); New Hebrides (type locality)

Subclass PULMONATA

Family SIPHONARIIDAE

Siphonaria laciniosa Linné Hirase and Taki (1951: pl. 121, fig. 11); NH 5

Subclass PROSOBRANCHIA

Family HALIOTIDAE

Haliotis (Sanhaliotis) dohrniana Dunker Man. Conch., (1)12: pl. 7, figs. 39–41; New Hebrides (type locality), Tangoa, Espiritu Santo (MCZ)

Haliotis (Haliotis) pustulata Reeve (= *dohrniana* Dunker?) Vate (F)

Haliotis (Haliotis) stomatiaeformis Reeve Tanna (F)

Haliotis (Sanhaliotis) varia Linné Man. Conch., (1)12: pl. 23, figs. 53–55; NH 13

Family FISSURELLIDAE

Clypidina lamberti Souverbie Tanna (F)

Diodora lineata Sowerby Man. Conch., (1)13: pl. 63, figs. 29, 30; NH 1, New Hebrides (CNHM)

Emarginula (Emarginula) scabricostata Adams Nguna (F)

Family PATELLIDAE

Patella (Scutellastra) stellaeformis Reeve Kira (1955: pl. 5, fig. 6); Cape Lisburn, Espiritu Santo (H), F

Cellana amusitata Reeve F

Cellana nigrolineata Reeve Immer (Boettger)

Cellana testudinaria Linné Vanua-Lava (F), Tanna (F)

Family TROCHIDAE

Chrysostoma paradoxum Born Hirase and Taki (1951: pl. 67, fig. 1); NH 12, NH 13, NH 14, Immer (Boettger)

Diloma (Melagraphia) constellata Souverbie Anelgauhaut Harbor, Aneiteum (Brazier)

Euchelus (Euchelus) atratus Gmelin Man. Conch., (1)11: pl. 38, fig. 22; NH 4, NH 5, NH 9, NH 11, NH 12, NH 13, Vate (F)

Gena (Plocamotis) lutea Adams F

Monilea (Talopena) lifuana Fischer Man. Conch., (1)11: pl. 41, figs. 6, 7; Aneiteum (Hedley)

Monodonta (Monodonta) canalifera Lamarck Immer (Boettger)

Stomatella (Stomatella) sulcifera Lamarck Malekula (F)

Stomatia (Stomatia) angulata Adams F

Stomatia (Stomatia) phymotis phymotis Helbing F

Stomatia (Stomatia) phymotis australis Adams Man. Conch., (1)12: pl. 54, figs. 1–3; NH 4

Tectus (Cardinalia) fenestratus Gmelin Kiener, *Trochus*, pl. 38, fig. 3; NH 4, NH 11, NH 13, NH 14, Espiritu Santo (F)

Tectus (Rochia) niloticus Linné Hirase and Taki (1951: pl. 65, fig. 6); NH 9, NH 12, NH 13, NH 14

Tectus (Tectus) pyramis Born (= *obeliscus* Gmelin) Hirase and Taki (1951: pl. 65, fig. 8); NH 8, Cape Lisburn, Espiritu Santo (H)

Tegula (Chlorostoma) pfefferi Dohrn (= *dohrni* Pilsbry) Man. Conch., (1)11: 189, pl. 61, figs. 28–29; New Hebrides (type locality), Anelgauhaut Harbor, Aneiteum (Brazier)

Trochus (Trochus) incrassatus incrassatus Lamarck F

Trochus (Trochus) incrassatus creniferus Kiener Kiener, *Trochus*, pl. 34, fig. 3; Cape Lisburn, Espiritu Santo (H)

Trochus (Trochus) maculatus maculatus Linné Hanley, *Ipsa Conchologia Linnaei*, pl. 3, fig. 7; NH 12, NH 13, Vate (F)

Trochus (Trochus) maculatus granosus Lamarck Kiener, *Trochus*, pl. 34, fig. 1; ML 6, NH 8, NH 9, NH 14

Trochus (Trochus) maculatus verrucosus Gmelin Kiener, *Trochus*, pl. 109, fig. 4; NH 5

Trochus (Infundibulum) tubiferus Kiener F

Family ANGARIIDAE

Angaria delphinus delphinus Linné Hirase and Taki (1951: pl. 71, fig. 8); NH 7, NH

8, NH 9, Vate (F)

Angaria delphinus atrata Reeve Espiritu Santo (F)

Family TURBINIDAE

Astraea (Calcar) stellaris Gmelin Man. Conch., (1)10: pl. 55, figs. 66-68; NH 9, Vate (F)

Liotia (Liotia) peronii Kiener F

Liotia (Arene) crenata Kiener Man. Conch., (1)10: pl. 36, figs. 12, 13; Aneiteum (Hedley)

Turbo (Marmarostoma) argyrostomus argyrostomus Linné Hirase and Taki (1951: pl. 73, fig. 4); NH 9

Turbo (Marmarostoma) argyrostomus margaritaceus Linné Man. Conch., (1)10: pl. 45, fig. 100; ML 6, NH 8, NH 9

Turbo (Marmarostoma) chrysostomus Linné Man. Conch., (1)10: pl. 40, fig. 19; NH 8, NH 12, NH 13, NH 14

Turbo (Marmarostoma) crassus Wood Man. Conch., (1)10: pl. 47, fig. 20; Tangoa, Espiritu Santo (MCZ), Vate (F)

Turbo (Olearia) marmoratus Linné Kira (1955: pl. 9, fig. 7); Tangoa, Espiritu Santo (MCZ)

Turbo (Turbo) petholatus Linné Hirase and Taki (1951: pl. 73, fig. 1); NH 8

Turbo (Lunella) porphyrites Gmelin Man. Conch., (1)10: pl. 50, fig. 58; NH 8, NH 9

Turbo (Marmarostoma) setosus setosus Gmelin Espiritu Santo (F)

Turbo (Marmarostoma) setosus patulus Philippi Man. Conch., (1)10: pl. 63, fig. 33; NH 8, NH 11

Family PHASIANELLIDAE

Phasianella (Orthomesium) variegata Lamarck Tanna (F)

Phasianella (Orthomesium) wisemanni Baird Brenchley (1873: pl. 38, fig. 34); Aneiteum (type locality), New Hebrides (CNHM)

Family NERITIDAE

The genus *Neritina* is not considered at

this time, since, like the Thiaridae, it primarily inhabits fresh or brackish waters.

Nerita (Theliostyla) albicilla Linné Hirase and Taki (1951: pl. 75, fig. 8); NH 1, NH 4, NH 9, NH 13, Erromanga (Hedley), Tangoa, Espiritu Santo (MCZ)

Nerita (Ritena) grossa Linné Man. Conch., (1)10: pl. 5, fig. 85; NH 7, Vate (F)

Nerita (Amphinerita) maxima Gmelin Martini and Chemnitz, II (11): pl. 6, figs. 1-5; Aneiteum (Hedley)

Nerita (Theliostyla) patula Recluz Man. Conch., (1)10: pl. 3, figs. 52, 55; NH 8

Nerita (Ritena) plicata Linné Martini and Chemnitz, II (11): pl. 10, figs. 7, 10; NH 5, NH 8, NH 9, NH 11, NH 12, NH 13, Erromanga (Hedley), Immer (Boettger), New Hebrides (F)

Nerita (Amphinerita) polita Linné Hirase and Taki (1951: pl. 75, fig. 13); ML 42, NH 1, NH 5, NH 7, NH 8, NH 9, NH 13, NH 14, Vate (F), Espiritu Santo (F), Erromanga (Hedley), Tangoa, Espiritu Santo (MCZ), New Hebrides (Mabille)

Nerita (Nerita) signata Lamarck (= *reticulata* Karsten) Man. Conch., (1)10: pl. 3, fig. 49; ML 28, NH 7, NH 9, NH 12, NH 13

Nerita (Ritena) undata Linné Man. Conch., (1)10: pl. 5, fig. 87; NH 1, NH 5, NH 7, NH 8, NH 9, NH 13, NH 14, Immer (Boettger)

Family LITTORINIDAE

Littorina (Melaraphe) mauritiana Lamarck Reeve, *Littorina*, pl. XVII, fig. 100; New Hebrides (Mabille)

Littorina (Melaraphe) coccinea Gmelin (= *obesa* Sowerby) Man. Conch., (1)9: pl. 43, fig. 53; Vate (Hedley)

Littorinopsis (Littorinopsis) scabra scabra Linné Hirase and Taki (1951: pl. 79, fig. 13); ML 6, ML 28, NH 11, 4KML, Surenda, Espiritu Santo (F), Hog Harbor, Espiritu Santo (MCZ), Immer (Boettger), Lagune d'Erakor, Vate (F)

Littorinopsis (Littorinopsis) scabra filosa Sowerby Man. Conch., (1)9: pl. 43, figs. 31, 31a; **ML** 6

Littorinopsis (Littorinopsis) scabra intermedia Philippi Reeve, *Littorina*, pl. VI, fig. 28a; New Hebrides (**Mabille**)

Littorinopsis (Littorinopsis) undulatus "Martyr" Gray Hirase and Taki (1951: pl. 79, fig. 11); **NH** 7, **NH** 8, **NH** 12

Echininus cumingi Philippi H. and A. Adams, Genera of recent shells, 3: pl. 33, fig. 3; **NH** 8, Vate (F), New Hebrides (**Mabille**)

Family RISSOIDAE

Rissoina ambigua Gould Vate (F), Tanna (F)

Rissoina exasperata Souverbie Vate (F)

Rissoina plicata Adams Vate (F)

Family SOLARIIDAE

Philippia hybridum Linné Sarakata, Espiritu Santo (F)

Philippia radiata Röding (= *cingulum* Kiener) Kiener, *Solarium*, pl. 3, fig. 6; **NH** 12, **NH** 13

Family VERMETIDAE

Vermetus dentifer Lamarck F

Family PLANAXIDAE

Planaxis (Quoyia) decollatus Quoy and Gaimard New Hebrides (**Mabille**)

Planaxis (Planaxis) lineatus DaCosta Hirase and Taki (1951: pl. 79, fig. 17); New Hebrides (**Hedley**)

Planaxis (Planaxis) nigra Quoy and Gaimard Reeve, *Planaxis*, pl. II, fig. 13; New Hebrides (**Mabille**)

Planaxis (Planaxis) sulcatus Born Hirase and Taki (1951: pl. 79, fig. 16); **ML** 6, Immer (**Boettger**)

Family POTAMIDIDAE

Terebralia palustris Bruguière Immer (**Boettger**)

Family CERITHIIDAE

The traditional generic usage is followed

here, rather than the newer concepts of Iredale and of most Japanese workers.

Aluco aluco Linné Hirase and Taki (1951: pl. 83, fig. 7); **NH** 1, **NH** 4; adults measure 49–66.4 mm. in length

Cerithium columna Sowerby Hirase and Taki (1951: pl. 83, fig. 9); **NH** 4, **NH** 8, **NH** 9, **NH** 13, **NH** 14, Vate (F)

Cerithium echinatum Lamarck Kiener, *Cerithium*, pl. 3, fig. 1; **NH** 9

Cerithium nodulosum Bruguière (= *Contumax decollatus* Hedley) Hirase and Taki (1951: pl. 83, fig. 8); **NH** 14

Cerithium consisum Hombron and Jacquinot (= *morus* Lamarck) Man. Conch., (1)9: pl. 24, figs. 29–33; **NH** 4, **NH** 5, **NH** 8, **NH** 9, **NH** 13

Cerithium consisum sejunctum Iredale (= *variegatum* Quoy and Gaimard) F

Cerithium consisum vittatum Sowerby F

Ischnocerithium rostratum Sowerby Man. Conch., (1)9: pl. 23, figs. 90, 91; Vate (F), New Hebrides (**Hedley**)

Liocerithium piperitum Sowerby Man. Conch., (1)9: pl. 27, fig. 31; **NH** 13, Vate (F)

Proclava zebra Kiener Man. Conch., (1)9: pl. 25, figs. 71, 72; New Hebrides (**Hedley**)

Rhinoclavis asperus Linné Hirase and Taki (1951: pl. 83, fig. 1); **NH** 5, **NH** 8

Rhinoclavis fasciatus Bruguière Man. Conch., (1)9: pl. 29, figs. 65–67; Segond Channel, Espiritu Santo (**MCZ**), Espiritu Santo (F)

Rhinoclavis pharos Hinds Man. Conch., (1)9: pl. 29, fig. 68; New Hebrides (**Hedley**)

Rhinoclavis sinense Gmelin (= *obeliscus* Bruguière) Hirase and Taki (1951: pl. 83, fig. 4); **NH** 4, **NH** 9, **NH** 13, F

Rhinoclavis vertagus Linné Espiritu Santo (F), Vate (F)

Semivertagus nesioticus Pilsbry and Vanatta (= *lacteus* Kiener and *collacteum* Iredale) Kiener, *Cerithium*, pl. 7, fig. 3; **NH** 12, **NH** 13

Family EPITONIIDAE

Epitonium (Limiscala) lyra Sowerby Sarakata, Espiritu Santo (F)

Cirsotrema (Coronoscala) perplexa Pease Sarakata, Espiritu Santo (F)

Family EULIMIDAE

Eulima bargravesi Brazier (= *porcellana* H. Adams, *preocc.*) Adams (1872: pl. 3, fig. 29); New Hebrides (type locality), Aneiteum (Brazier)

Family VANIKORIDAE

Vanikoro cancellata Lamarck Surenda, Espiritu Santo (F)

Family AMALTHEIDAE

Amalthea (Amalthea) australis Quoy and Gaimard (= *conica* Schumacher?) Man. Conch., (1)8: pl. 41, figs. 12, 13; NH 12, NH 13, NH 14, Tagoa, Espiritu Santo (MCZ)

Family CAPULIDAE

Capulus (Krebsia) intortus Lamarck Man. Conch., (1)8: pl. 39, figs. 75, 76; Aneiteum (Hedley)

Capulus (Capulus) violaceus Angas Man. Conch., (1)8: pl. 39, fig. 81; New Hebrides (Hedley)

Family STROMBIDAE

Canarium (Euprotomus) aurisdianae Linné (= *guttatus* Martini) Kira (1955: pl. 16, fig. 2); Cape Lisburn, Espiritu Santo (H), Espiritu Santo (F)

Canarium (Labiostrombus) canarium Linné Espiritu Santo (F)

Canarium (Canarium) dentatum Linné Kira (1955: pl. 15, fig. 3—as *tridentatum* Gmelin); NH 14

Canarium (Oostrombus) gibberulum Linné Man. Conch., (1)7: pl. 8, fig. 85; NH 1, NH 5, NH 9, NH 12, Vate (F), New Hebrides (Hedley)

Canarium (Canarium) labiatus Röding (= *ustulatus plicatus* Lamarck) Dodge (1946: figs. 3, 7; also 1956: 285); NH 9

Canarium (Euprotomus) latissimus Linné Espiritu Santo (F)

Canarium (Euprotomus) lentiginosus Linné Hirase and Taki (1951: pl. 86, fig. 4); NH 8, Tagoa, Espiritu Santo (MCZ), Espiritu Santo (F)

Canarium (Canarium) mutabilis Swainson (= *floridanum* Lamarck) Dodge (1946: figs. 4, 8); NH 4, NH 5, NH 9, NH 11, NH 12, NH 13, NH 14, Espiritu Santo (F), Cape Lisburn, Espiritu Santo (H), Vate (F), Erromanga (Hedley), Malekula (CNHM)

Canarium (Labiostrombus) variabile Swainson Man. Conch., (1)7: pl. 6, figs. 59, 60; NH 10, Cape Lisburn, Espiritu Santo (H)

Lambis truncata Solander (= *bryonia* Gmelin) Erromanga (Hedley)

Lambis scorpius Linné Hirase and Taki (1951: pl. 88, fig. 1); Cape Lisburn, Espiritu Santo (H)

Terebellum terebellum Linné Hirase and Taki (1951: pl. 89, fig. 1); NH 9, Erromanga (Hedley)

Family NATICIDAE

Natica (Natica) marochiensis Gmelin Man. Conch., (1)8: pl. 5, fig. 75; NH 7, NH 9, NH 12, New Hebrides (Hedley)

Specimens from NH 7 have the typical color pattern; those from NH 9 and NH 12 have two spiral bands of brown on a yellowish background.

Natica (Natica) solida Blainville Man. Conch., (1)8: pl. 20, fig. 98; NH 12

Natica (Natica) traillii Reeve F

Polinices (Polinices) albumen Linné Hirase and Taki (1951: pl. 91, fig. 7); NH 4 (juvenile), Cape Lisburn, Espiritu Santo (H)

Polinices (Polinices) flemingianus Récluz Hirase and Taki (1951: pl. 91, fig. 5); NH 5, NH 9, NH 12

Polinices (Mamilla) mamilla Linné (= *pyriformis* Récluz) Kira (1955c pl. 17, fig. 10); NH 4, NH 7, NH 10, NH 12

Polinices (Mamilla) melanostoma Gmelin Man. Conch., (1)8: pl. 21, fig. 14; NH 7, NH 11, Vate (F)

NH 11 is var. *melanostomoides* Quoy and

Gaimard which F reported as a distinct species from Vate.

Family OVULIDAE
(= AMPHIPERATIDAE)

Calpurnus verrucosus Linné Hirase and Taki (1951: pl. 94, fig. 20); Futuna (AMNH)

Ovula ovum Linné Espiritu Santo (F)

Family ERATOIDAE

Trivirostra oryza Lamarck New Hebrides (Hedley)

Family CYPRAEIDAE

No attempt has been made to utilize the elaborate subspecific categories proposed by the Schilders and many of their split genera are ignored. No reference figures are quoted.

Callistocypraea (*Chelyocypraea*) *testudinaria* Linné Aneiteum (Hedley)

Cypraea (*Lyncina*) *carneola* Linné Espiritu Santo (F, IK)

Cypraea (*Lyncina*) *lynx* Linné Second Channel, Espiritu Santo (MCZ), Cape Lisburn, Espiritu Santo (H), Espiritu Santo (F, IK), Erromanga (Hedley), Malekula (CNHM)

Cypraea (*Cypraea*) *tigris* Linné Espiritu Santo (F), Erromanga (Hedley)

Cypraea (*Lyncina*) *vitellus* Linné Second Channel, Espiritu Santo (MCZ), Espiritu Santo (IK), Vate (F)

Erosaria (*Ravitriona*) *caputserpentis* Linné ML 6, NH 14, Tangoa, Espiritu Santo (MCZ), Espiritu Santo (IK), Vate (F), Erromanga (Hedley)

Erosaria (*Erosaria*) *erosa* Linné NH 8, Espiritu Santo (F), Erromanga (Hedley)

Erosaria (*Erosaria*) *helvola* Linné Espiritu Santo (IK)

Erronea (*Erronea*) *errones* Linné Espiritu Santo (IK)

Erronea (*Blasicrura*) *hirundo* Linné Espiritu Santo (IK)

Erronea (*Blasicrura*) *neglecta* Sowerby Espiritu Santo (IK)

Luria (*Basilitriona*) *isabella* Linné NH 5, NH 14, Espiritu Santo (F, IK), Vate (F),

Tanna (F), Erromanga (Hedley), Aneiteum (Hedley)

Mauritia (*Arabica*) *arabica* Linné Tangoa, Espiritu Santo (MCZ), Cape Lisburn, Espiritu Santo (H), Espiritu Santo (F), Vate (F), Erromanga (Hedley), Aneiteum (Hedley)

Mauritia (*Arabica*) *depressa* Gray New Hebrides (Schilder and Schilder, 1952)

Mauritia (*Mauritia*) *mauritiana* Linné Tangoa and Second Channel, Espiritu Santo (MCZ), Espiritu Santo (F, IK), Vate (F), Erromanga (Hedley), Aneiteum (Hedley), Malekula (CNHM)

Monetaria annulus Linné NH 4, NH 5, NH 7, NH 8, NH 12, NH 13, NH 14, Tangoa and Second Channel, Espiritu Santo (MCZ), Espiritu Santo (F, IK), Malekula (CNHM)

Monetaria moneta Linné NH 4, NH 13, Second Channel, Espiritu Santo (MCZ), Erromanga (Hedley), Malekula (CNHM)

Nuclearia nucleus Linné Espiritu Santo (IK), Tanna (F), New Hebrides (Hedley)

Palmadusta asellus Linné Espiritu Santo (IK)

Palmadusta felina Gmelin Espiritu Santo (Schilder and Schilder, 1952)

Palmadusta fimbriata Gmelin Espiritu Santo (IK)

Palmadusta microdon Gray F

Pustularia childreni Gray Espiritu Santo (F, IK)

Pustularia cicerula Linné Espiritu Santo (IK), Aneiteum (Hedley)

Pustularia globulus Linné Tanna (F)

Pustularia mariae Schilder (= *annulata* Gray) Espiritu Santo (IK)

Staphylaea (*Staphylaea*) *limacina* Lamarck Espiritu Santo (IK)

Staphylaea (*Staphylaea*) *staphylaea* Linné Port Sandwich, Vate (Schilder and Schilder, 1952)

Talparia (*Arestorides*) *argus* Linné Espiritu Santo (F), Erromanga (Hedley), Aneiteum (Hedley)

Talparia (*Talparia*) *talpa* Linné Erromanga (Hedley)

Family CASSIDAE

Semicassis (Casmarea) vibex Linné Espiritu Santo (F), Vate (F)

Family CYMATIIDAE

Argobuccinum bituberculatum Lamarck Vate (F)

Charonia tritonis tritonis Linné Espiritu Santo (F)

Distorsio anus Linné Hirase and Taki (1951: pl. 96, fig. 4); NH 8, Espiritu Santo (F), Vate (F)

Gyrineum (Gyrineum) natator Röding (= *tuberculatum* Broderip) Man. Conch., (1)3: pl. 23, fig. 46; NH 9, NH 14

Gyrineum (Gyrinella) pusillum Broderip Man. Conch., (1)3: pl. 24, figs. 56, 57; NH 10

Lampusia chlorostoma Lamarck Man. Conch., (1)3: pl. 7, fig. 47; NH 9, Vate (F)

Lampusia rubecula Linné Espiritu Santo (F), Vate (F)

Ranularia (Gutturium) muricinum Röding (= *nonulus* Link, *tuberosa* Lamarck) Vate (F)

Family BURSIDAE

Bursa bufonia Gmelin Man. Conch., (1)3: pl. 21, figs. 21, 23; NH 5

Bursa granularis Röding (= *affinis* Broderip) Vate (F)

Ranella (Ranella) lampas Linné Espiritu Santo (F)

Family TONNIDAE

Tonna (Tonna) costatum Menke New Hebrides (F)

Tonna (Tonna) perdix perdix Linné Hirase and Taki (1951: pl. 93, fig. 7); NH 14, Espiritu Santo (F), Tangoa, Espiritu Santo (MCZ), Erromanga (Hedley)

Family MURICIDAE

Aspella (Favartia) tetragona Broderip Man. Conch., (1)2: pl. 36, fig. 424; NH 9

Chicoreus (Chicoreus) brunneus Link (= *adustus* Lamarck) Hirase and Taki (1951: pl. 109, fig. 4); NH 8, NH 9, NH 12, NH 14

Cronia (Usilla) margariticola Broderip (= *undata* Chemnitz) Man. Conch., (1)2: pl. 59, fig. 260; NH 9, NH 13

Drupa (Morula) anaxeros Dunker Man. Conch., (1)2: pl. 57, fig. 219; NH 9

Drupa (Morula) granulata Duclos (= *tuberculata* Blainville) Hirase and Taki (1951: pl. 110, fig. 15); NH 13, New Hebrides (F), Immer (Boettger)

Drupa (Drupina) grossularia Röding (= *digitata* Lamarck) Vate (F)

Drupa (Morula) marginatra Blainville Kiener, *Purpura*, pl. 7, fig. 16; NH 8

Drupa (Drupa) morum Röding (= *horrida* Lamarck) Hirase and Taki (1951: pl. 110, fig. 8); NH 11, Cape Lisburn, Espiritu Santo (H), Vate (F)

Drupa (Drupa) ricinus Linné Hirase and Taki (1951: pl. 110, fig. 11); NH 14, Cape Lisburn, Espiritu Santo (H), Vate (F)

Drupa (Drupa) rubuscaesium Röding (= *hystrix* of authors) Hirase and Taki (1951: pl. 110, fig. 9); NH 14

Drupa (Morula) uva uva Röding (= *morus* Lamarck) New Hebrides (Hedley)

Drupa (Morula) uva asperus Lamarck Man. Conch., (1)2: pl. 57, figs. 215, 216; NH 4

Drupella elata Blainville Kiener, *Purpura*, pl. 10, fig. 27; NH 8, NH 9

Maculotriton digitalis Reeve Man. Conch., (1)3: pl. 15, figs. 142, 143; Aneiteum (Hedley)

Mancinella hippocastaneum Linné Demond (1957: 313, fig. 22); NH 5, NH 7, NH 8, NH 13, Vate (F), Immer (Boettger)

Mancinella intermedia Kiener Man. Conch., (1)2: pl. 45, fig. 41; NH 11

Mancinella tuberosa Röding (= *pica* Blainville) Man. Conch., (1)2: pl. 46, fig. 46; NH 1, NH 4

Murex (Acupurpurea) ternispina Lamarck Malekula (F)

Nassa sertum Bruguière (= *francolinus* Bruguière) Vate (F)

Thais (Cymia) armigera Link Hirase and Taki (1951: pl. 110, fig. 2); NH 11

Family MAGILIDAE

Coralliobia (*Quoyula*) *madreporarum* Sowerby
Man. Conch., (1)2: pl. 47, figs. 389–391;
Vate (Hedley)

Coralliophila violacea Kiener (= *neritoidea* of
authors) Hirase and Taki (1951: pl. 111,
fig. 8); NH 10

Family COLUMBELLIDAE

Columbella (*Columbella*) *obtusa* Sowerby Man.
Conch., (1)5: pl. 59, figs. 65, 66; New
Hebrides (Hedley)

Columbella (*Nitidella*) *testudinaria* Link (= *pardalina* Lamarck) Martini and Chemnitz,
III(1d): pl. 6, figs. 8, 9; ML 41, NH 4,
NH 7, NH 14, Nguna (F), Ambrym and
Malekula (Hervier, 1899)

The typical form was found at ML 41 and
NH 14; a variety (with slightly concave spire,
orange-brown markings, and complete epi-
dermis) which is near *vulpeca* Sowerby was
found at NH 4 and NH 7.

Columbella (*Columbella*) *souverbiei* Crosse
J. Conchyliol., 13: pl. 5, fig. 9; Vate (F),
Tanna (F)

Columbella (*Columbella*) *versicolor* Sowerby
Hirase and Taki (1951: pl. 107, fig. 1);
NH 12, New Hebrides (Mabille)
Hervier (1899: 311) described a var. *he-
bridarum* from Ambrym Island.

Mitrella ligula Duclos New Hebrides
(Mabille)

Pyrene discors Gmelin (?) NH 10

According to Pace (1902: 416) this is the
most difficult group of Pacific Columbelloidea.
The identification is tentative.

Family BUCCINIDAE

Cantbarus (*Pollia*) *fumosus* Dillwyn Demond
(1957: 318, fig. 27); NH 1, NH 9, NH 13

Cantbarus (*Pollia*) *undosus* Linné Demond
(1957: 318, fig. 28); NH 9, NH 11, NH 13

Engina lauta Reeve Vate (F)

Engina lineata Reeve New Hebrides (Ma-
bille)

Engina mendicaria Linné Hirase and Taki
(1951: pl. 105, fig. 8); #5K, ML 41, NH 4,

NH 9, NH 12, NH 13, Vate (F), Immer
(Boettger)

Family NASSARIIDAE

Alectrion (*Alectrion*) *acuticosta* Montrouzier
J. Conchyl., 12: pl. 10, fig. 8; NH 7,
NH 9

Alectrion (*Zeuxis*) *lurida* Gould U. S. Explor.
Exped. Wilkes, Atlas, fig. 325; NH 7,
NH 9, NH 10

Alectrion (*Alectrion*) *monile* Kiener Kiener,
Buccinum, pl. 11, fig. 40; NH 7, NH 9,
NH 12, NH 13, NH 14, Vate (F)

Alectrion (*Zeuxis*) *mucronata* Adams Reeve,
Nassa, pl. 2, fig. 8; NH 14

Alectrion (*Alectrion*) *ornata* Kiener Kiener,
Buccinum, pl. 21, fig. 83; New Hebrides
(Mabille)

Alectrion (*Zeuxis*) *pictus* Dunker Reeve,
Nassa, pl. I, fig. 9; New Hebrides (Ma-
bille)

Alectrion (*Zeuxis*) *siquijorensis* H. Adams
Reeve, *Nassa*, pl. VIII, fig. 53; NH 10

Alectrion (*Zeuxis*) *taenia* Gmelin Vate (F)

Arcularia (*Arcularia*) *callospira* Adams
Reeve, *Nassa*, pl. X, fig. 66; NH 12, New
Hebrides (Mabille)

Arcularia (*Pliarcularia*) *globosa* Quoy and
Gaimard Reeve, *Nassa*, pl. X, fig. 62;
NH 1, NH 10, NH 12

Arcularia (*Arcularia*) *granifera* Kiener Man.
Conch., (1)4: pl. 8, figs. 39–41; New Heb-
rides (Hedley)

Arcularia (*Pliarcularia*) *thersites* Bruguière
Reeve, *Nassa*, pl. X, fig. 65; NH 9

Hebra muricata Quoy and Gaimard Reeve,
Nassa, pl. XI, fig. 73; NH 11, New Heb-
rides (Mabille)

Hebra subspinosa Lamarck Kiener, *Buccinum*,
pl. 26, fig. 103; ML 28, NH 7, Vate (F)

Hima (*Caesia*) *concinna* Powis Vate (F)

Hima (*Allanassa*) *eximia* H. Adams Adams
(1872: pl. 3, fig. 28); New Hebrides (type
locality)

Nassarius (*Nassarius*) *arcularia* Linné Reeve,
Nassa, pl. IV, fig. 25; NH 5, NH 7, NH 12,
Espiritu Santo (F), Vate (F)

- Nassarius (Phrontis) crassa* Koch Reeve, *Nassa*, pl. X, fig. 67; NH 7, NH 9, NH 12, NH 13, New Hebrides (**Mabille**)
- Niothia albescens* Dunker Reeve, *Nassa*, pl. XV, fig. 100; NH 7, NH 12, Vate (F, var. *bicolor* Hombron and Jacquinot)
- Niothia gemmulata* Lamarck (= *variiegata* A. Adams) Reeve, *Nassa*, pl. XII, fig. 83; New Hebrides (**Mabille**)
- Niothia pauperata* Lamarck Philippi, Abbild. Besch. neu. Conch., *Buccinum*, pl. 2, fig. 18; ML 28, Vate (F)

Family FASCIOLARIIDAE

- Fasciolaria coronata* Lamarck Espiritu Santo (F)
- Fasciolaria filamentosa* Röding Hirase and Taki (1951: pl. 99, fig. 12); Tangoa, Espiritu Santo (**MCZ**)
- Latirus polygonus* Gmelin Hirase and Taki (1951: pl. 100, fig. 1); NH 9, NH 13, Vate (F)
- Leucozonia (Mazzalina) smaragdula* Linné Man. Conch., (1)3: pl. 70, fig. 185; NH 12, NH 13, NH 14, Vate (F)
- Peristernia nassatula* Linné Hirase and Taki (1951: pl. 100, fig. 5); NH 9, NH 11, NH 12, NH 5 contained a form with elongate spire

Family OLIVIDAE

- Oliva (Galeola) carneola* Gmelin Tangoa, Espiritu Santo (**MCZ**)
- Oliva (Oliva) amethystina* Röding (= *guttata* Lamarck) Man. Conch., (1)5: pl. 19, figs. 64-74; Tangoa, Espiritu Santo (**MCZ**), New Hebrides (**Hedley**)
- Oliva (Oliva) irisans* Lamarck Espiritu Santo (F)
- Oliva (Oliva) ispidula* Linné Tangoa, Espiritu Santo (**MCZ**)
- Oliva (Oliva) maura* Lamarck Espiritu Santo (F)
- Oliva (Oliva) miniacea* Röding (= *erythrostroma* Meuschen) Espiritu Santo (F), Erromanga (**Hedley**)
- Oliva (Oliva) mustelina* Lamarck NH 10 (juvenile)

- Oliva (Oliva) rubrolabiata* Fischer J. Conchyl., 50: 409-411, pl. 8, figs. 12, 13; Marmaram, Malekula (type locality)
- Oliva (Oliva) reticulata* Röding (= *sanguinolenta* Lamarck) Espiritu Santo (F)
- Oliva (Galeola) tessellata* Lamarck Tangoa, Espiritu Santo (**MCZ**)
- Oliva (Oliva) tricolor* Lamarck New Hebrides (**Mabille**)

Family MITRIDAE

- Imbricaria conica* Schumacher Reeve, *Mitra*, pl. XXVII, fig. 216; NH 12
- Imbricaria vanikorensis* Quoy and Gaimard Hirase and Taki (1951: pl. 101, fig. 17); NH 14
- Mitra (Mitra) cardinalis* Gmelin Reeve, *Mitra*, pl. IV, fig. 26; NH 14
- Mitra (Mitra) mitra* Linné (= *episcopalis* Linné) Espiritu Santo (F)
- Mitra (Mitra) papalis* Linné Espiritu Santo (F)
- Mitra (Mitra) stictica* Link (= *pontificalis* Lamarck) Man. Conch., (1)4: pl. 32, fig. 3; Erromanga (**Hedley**)
- Pterygia dactylus* Linné Hirase and Taki (1951: pl. 101, fig. 16); NH 4
- Pterygia fenestratus* Lamarck Sowerby, Thes. Conch., IV, *Mitra*, fig. 363; New Hebrides (**Mabille**)
- Pusia muriculatus* Lamarck New Hebrides (**Mabille**)
- Scabricula (Chrysame) adusta* Lamarck Hirase and Taki (1951: pl. 101, fig. 3); NH 1
- Scabricula (Chrysame) aurantia* Gmelin New Hebrides (**Mabille**)
- Scabricula (Chrysame) chrysalis* Reeve Hirase and Taki (1951: pl. 101, fig. 2); NH 4, NH 9, NH 13
- Scabricula (Chrysame) tiarella* Adams (= *coronata* Lamarck, non Helbing) Reeve, *Mitra*, pl. XIV, fig. 104; NH 10, Vate (F)
- Scabricula (Chrysame) peregra* Reeve Surendo, Espiritu Santo (F)
- Strigatella (Strigatella) decurtata* Reeve Tangoa, Espiritu Santo (**MCZ**)

Strigatella (*Strigatella*) *litterata* Lamarck Hirase and Taki (1951: pl. 101, fig. 9); NH 8
Strigatella (*Strigatella*) *paupercula* Linné Reeve, *Mitra*, pl. XII, fig. 84; NH 9

Strigatella (*Strigatella*) *retusa* Lamarck Man. Conch., (1)4: pl. 46, fig. 343; NH 8, Vate (F)

Strigatella (*Strigatella*) *virgata* Lamarck Man. Conch., (1)4: pl. 46, fig. 341; NH 4, NH 8, NH 11

Vexillum (*Costellaria*) *cadaverosum* Reeve Reeve, *Mitra*, pl. XXI, fig. 160; NH 12

Vexillum (*Vexillum*) *gruneri* Reeve New Hebrides (F)

Vexillum (*Vexillum*) *placarium* Linné Reeve, *Mitra*, pl. VIII, fig. 56; NH 4, New Hebrides (F)

Family VASIDAE

Vasum (*Vasum*) *ceramicum* Linné Vate (F)

Vasum (*Vasum*) *turbinellum* Linné Hirase and Taki (1951: pl. 99, fig. 9); NH 14, Espiritu Santo (F)

Family HARPIDAE

Harpa amouretta Röding (= *minor* Lamarck) Hirase and Taki (1951: pl. 112, fig. 13); NH 14, Espiritu Santo (F)

Harpa ventricosa Lamarck Malekula (F)

Family CYTHARIDAE

Daphnella pupoidea H. Adams Adams (1872: pl. 3, fig. 27); New Hebrides (type locality)

Family TURRIDAE

Ancistrosyrinx (= *Kenyonia*) *pulcherrima* Brazier Brazier (1896: 346); New Hebrides (type locality)

Clavus (*Tyloia*) *unizonalis* Lamarck (= *vidua* Reeve) Martini and Chemnitz, IV(3): pl. 13, fig. 1; NH 4, New Hebrides (Mabille)

Drillia auriculifera Lamarck Vate (F)

Philbertia philippinensis Reeve Reeve, *Pleurotoma*, pl. XIII, figs. 109a, b; NH 1

Philbertia picta rubroguttata H. Adams Adams (1872: pl. 3, fig. 25); New Hebrides (type locality)

Philbertia pulcherrima H. Adams Adams (1872: pl. 3, fig. 26); New Hebrides (type locality)

Turris (*Turris*) *picturata* Weinkauff Martini and Chemnitz, IV(3): pl. 2, fig. 10; NH 13

Family CONIDAE

Conus acbatinus Gmelin Immer (Boettger)

Conus archiepiscopus Bruguière Kiener, *Conus*, pl. 96, figs. 1, 1a; NH 14, Malekula (CNHM)

Conus arenatus Bruguière Kiener, *Conus*, pl. 10, fig. 1; NH 12, Espiritu Santo (F)

Conus auratus Lamarck Man. Conch., (1)6: pl. 31, fig. 30; Erromanga (Hedley)

Conus catus Bruguière Kiener, *Conus*, pl. 43, figs. 1b, 1c (poor); ML 41, NH 14, Vate (F)

Conus ceylonensis var. ML 41 (worn)

Conus ceylonensis nanus Broderip Vate (F)

Conus chaldeus Röding (= *vermiculatus* Lamarck) Sowerby, *Thes. Conch.*, III: pl. 189, fig. 53; ML 41, NH 9

Conus coronatus Gmelin (= *miliaris* Bruguière) Sowerby, *Thes. Conch.*, III: pl. 194, fig. 278; ML 41, NH 4, NH 12, NH 14

Conus ebraeus Linné Hirase and Taki (1951: pl. 113, fig. 12); ML 41, NH 4, NH 5, NH 9, NH 12, Vate (F), Aore (MCZ), Immer (Boettger), Erromanga (Hedley)

Conus eburneus Bruguière Hirase and Taki (1951: pl. 113, fig. 15); NH 4, NH 12

Conus figulinus Linné Vate (F), Espiritu Santo (F)

Conus flavidus Lamarck Kiener, *Conus*, pl. 26, fig. 4; NH 4, NH 14

Conus geographus Linné Man. Conch., (1)6: pl. 28, fig. 84; Erromanga (Hedley)

Conus generalis Linné Kira (1955: pl. 36, fig. 21); Cape Lisburn, Espiritu Santo (H), Espiritu Santo (F)

Conus litteratus Linné Hirase and Taki (1951: pl. 113, fig. 16); NH 4, Cape Lisburn, Espiritu Santo (H), Espiritu Santo (F), Erromanga (Hedley)

Conus lividus Bruguière Kira (1955: pl. 37,

fig. 2); **ML** 41, **NH** 5, Espiritu Santo (**F**), Vate (**F**)

Conus magus decurtatus Dautzenberg (= *adansonii* Sowerby, non Lamarck) Sowerby, Thes. Conch., III: pl. 199, figs. 286-289; **NH** 4, **NH** 9, **NH** 12, **NH** 14

Conus magus striolatus Kiener Kiener, *Conus*, pl. 105, fig. 1; **NH** 13

Conus marmoreus Linné Kira (1955: pl. 36, fig. 6): **NH** 4, **NH** 12, **NH** 14, Espiritu Santo (**F**), Vate (**F**)

Conus miles Linné Vate (**F**)

Conus omaria Bruguière Espiritu Santo (**F**)

Conus pulicarius Bruguière Kira (1955: pl. 36, fig. 15); **NH** 4, **NH** 12, Cape Lisburn, Espiritu Santo (**H**), New Hebrides (**F**)

Conus rattus Bruguière Kiener, *Conus*, pl. 44, fig. 3; **ML** 41, **NH** 8, **NH** 14

Conus senator Linné Vate (**F**)

Conus striatus Linné Kiener, *Conus*, pl. 47, figs. 1, 1a; **NH** 4, Erromanga (**Hedley**)

Conus tessellatus Born Man. Conch., (1)6: pl. 2, figs. 26, 27; New Hebrides (**Hedley**)

Conus textile Linné Aneiteum (Bennett, 1860)

Conus tulipa Linné Kira (1955: pl. 37, fig. 19); Segond Channel, Espiritu Santo (**MCZ**), Espiritu Santo (**CNHM**), Erromanga (**Hedley**)

Conus vautieri Kiener Espiritu Santo (**F**)

Family TEREBRIDAE

Terebra chlorata Lamarck Hirase and Taki (1951: pl. 116, fig. 8); **NH** 13

Terebra cingulifera Lamarck Nguna (**F**)

Terebra dimidiata Linné Nguna (**F**), Vate (**F**), Erromanga (**Hedley**), Aneiteum (**Hedley**)

Terebra felina Dillwyn (= *tigrina* Gmelin) Man. Conch., (1)7: pl. 1, fig. 11; New Hebrides (**Hedley**)

Terebra maculata Linné Kira (1955: pl. 38, fig. 21); **NH** 15, Nguna (**F**)

Terebra striata Quoy and Gaimard (= *affinis* Gray) Man. Conch., (1)7: pl. 2, figs. 18, 22; New Hebrides (**Hedley**)

Terebra strigilata Linné Man. Conch., (1)7: pl. 10, figs. 84, 85; Cape Lisburn, Espiritu Santo (**H**)

Terebra subulata Lamarck Vanua Lava (**F**)

DISCUSSION

The 409 species and varieties named above are not presumed to form a complete list of the fauna. The Hadfield collection of shells from Lifu in the Loyalty group contained 860 species, and subsequent research has added many more to that number. There are eight turrids known from the New Hebrides and 196 from New Caledonia. The 22 Mitridae listed here are only a fraction of the 151 reported from New Caledonia, and similar comparisons can be made for nearly every family.

Since I have prepared a similar checklist of the Solomon Islands marine shells (Solem, 1953, 1958), a tabular comparison of the known faunas might be instructive. From Table 1 it can be seen that only a little more than one half of the New Hebridean species have been reported from the Solomons, and that more than one half of the Solomon Islands species are not yet known from the New Hebrides. This is the result of inadequate collecting in both areas and does not indicate any great faunal difference between the two areas. It is quite possible that many Indonesian species reach the Solomons and not the New Hebrides, but almost all of the species listed in these papers are distributed extensively throughout most of the Indo-Pacific region. Their presence in the Solomons and New Hebrides is to be expected, but the scanty literature dealing with the marine

TABLE 1

COMPARISON OF KNOWN MARINE MOLLUSKS OF SOLOMON ISLANDS AND NEW HEBRIDES ISLANDS

GROUP	SPECIES		
	Common to both	In New Hebrides only	In Solomons only
Bivalves	36	61	65
Prosobranchs	183	121	245
Others	4	4	4
Totals	223	186	320

mollusks of Melanesia makes worthwhile the recording of distributional data for even common species. Of the 160 species collected by Kuntz, 89 (55.6 per cent) were previously unreported from the New Hebrides. It is probable that additional collections will contain a similar proportion of previously unrecorded species and that the total number of marine mollusks will be well over 2,000 species.

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A Key to the Chaetognatha of the Tropical Eastern Pacific Ocean

PAUL N. SUND¹

THE INTER-AMERICAN Tropical Tuna Commission recently commenced a study of zooplankton collections from the tropical eastern Pacific Ocean to investigate the occurrence of planktonic organisms that can be used as biological indicators of water masses. This study is a part of the Commission's broader investigations of the relationship of the yellowfin and skipjack tunas and their food supply to the hydrographic regime within the eastern Pacific area.

The eastern tropical Pacific Ocean has been recently defined by Wooster and Cromwell (1958) as "the region lying between the Tropic of Cancer (23°27'N.) and the Tropic of Capricorn (23°27'S.) and extending westward from the coast of Central and South America to 130° W."

Two groups of animals which include species of known indicator value were selected for particular attention. These are the Euphausiacea and the Chaetognatha. The identities of the euphausiids were readily determined using the keys in the recent work of Boden, Johnson, and Brinton (1955). At the outset of our studies, the Chaetognatha proved to be quite difficult to identify because the published keys (e.g., Ritter-Zahony, 1911; Michael, 1908, 1911; Thomson, 1947) used characters that are often indistinguishable or whose determination is so time consuming that their use in studies of this sort was found impractical.

For these reasons it was decided to formulate a new key (of the type published by Fraser, 1952, for the chaetognaths of northern waters) that would allow rapid, but accurate, identification of a given specimen by using

characters that are readily distinguishable in preserved animals of good-to-fair condition. General discussions of the characters and their use for purposes of identification are presented by Fowler (1904, 1906) and Michael (1908).

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METHODS AND MATERIALS

The material was selected from the zooplankton collections made by University of California Scripps Institution of Oceanography research vessels during Eastropic Expedition, 1955. Figure 1 shows the locations of zooplankton stations from which the material for this study was taken. Holmes, Schaefer, and Shimada (1957) have outlined the methods and equipment employed in making these collections.

Specimens in good condition were identified and isolated from the Eastropic zooplankton. Upon accumulation of a number of these, the measurements and counts necessary to complete the armature formulae were made. All measurements were made with a calibrated ocular micrometer. These are presented in tabular form in the text, together with similar data obtained from specimens of known identity from eastern and central Pacific waters. The latter specimens were kindly donated to the writer by Dr. T. Tokioka of the Seto Marine Biological Laboratory, Japan; and Mr. T. Hida of Pacific Oceanic Fishery Investigations, U. S. Fish and Wildlife Serv-

¹ Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, La Jolla, California. Manuscript received January 15, 1958.

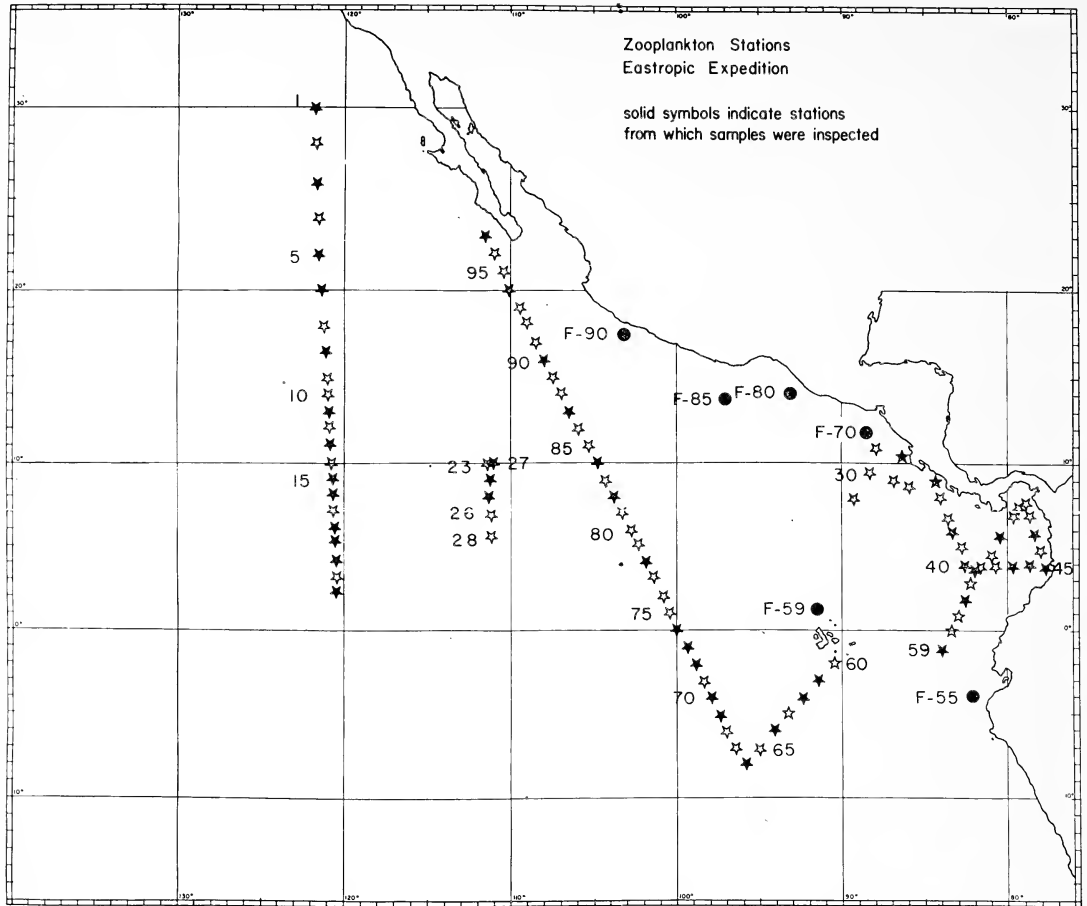


FIG. 1. Zooplankton stations occupied on Eastropic Expedition. Stars indicate stations occupied by RV Horizon; circles indicate those occupied by RV Spencer F. Baird. Modified from Holmes, Schaefer, and Shimada (1957).

ice, Honolulu, T. H. Of these, only those species represented in the Eastropic collections are considered in this publication. The armature formulae are included in this paper as they have been found useful in determining the variability within the limits of each species and in verifying the identity of juvenile and damaged specimens. For the measurements of the total length of the body and the tail segment, the caudal fin has been excluded as it is often damaged and its inclusion would lead to error.

DESCRIPTION OF THE SPECIES FOUND IN EASTROPIC COLLECTIONS

Several oceanographic investigations of the eastern Pacific have been made (Albatross,

Dana, Discovery, and Shellback expeditions), but published works considering the Chaetognatha from the area are very few. Of the 36 species considered valid by Tokioka (1952), the following 18 species have been recorded by Baldasseroni (1915), Michael (1908, 1911), and Bieri (1957): *Sagitta bedoti*, *S. bipunctata = californica*, *S. decipiens*, *S. enflata*, *S. ferox*, *S. hexaptera*, *S. lyra*, *S. minima*, *S. neglecta*, *S. pulchra*, *S. regularis*, *S. robusta*, *S. serratodentata*, *S. tenuis*, *Krohnitta pacifica*, *K. subtilis*, *Eukrohnia hamata*, and *Pterosagitta draco*.

In addition to these species, *S. serratodentata pacifica* and *S. pseudoserratodentata* have been identified from the Eastropic material.

Sagitta bedoti Béraneck*S. bedoti*, Bieri, 1957

Body firm, moderately opaque. Tail segment 17–27 per cent of total length of animal; hooks 6–7; anterior teeth 10–13; posterior teeth 20–29, or more. Anterior fins long, tapered, starting at ventral ganglion. Posterior and caudal fins close to, or touching, the seminal vesicles. Seminal vesicles oval. Intestinal diverticula absent. Collarrette obvious.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
12.0	22.5	7	12	29
11.0	23.6	6	13	27
10.5	21.9	7	11	25
9.9	21.2	7	10	24
8.3	26.5	7	11	27
7.4	22.9	7	10	20
<i>Tokioka's specimens:</i>				
10.4	23.2	6	11	28
9.5	21.1	7	12	28
8.5	17.7	6	10	23
7.9	24.0	7	10	22

Sagitta bipunctata Quoy et Gaimard = *S. californica* Michael*S. bipunctata* Michael, 1911*S. californica*, Bieri, 1957

Bieri (1957) presents arguments supporting the change of the name of the species referred to by several workers as *S. bipunctata* to *S. californica*. Until this point is satisfactorily settled, I prefer to use the older name, *S. bipunctata*; but also to record that here, these two terms refer to the same single species.

Body firm, moderately opaque. Tail segment 21–28 per cent of total body length; hooks 5–10; anterior teeth 4–7; posterior teeth 8–14. Anterior fins start at posterior end of ventral ganglion. Posterior fins do not reach seminal vesicles; wider and slightly longer than anterior fins, widest behind tail-septum. Caudal fin joins seminal vesicles. Collarrette present. No intestinal diverticula.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
16.3	27.6	8	4	8
11.0	24.5	10	7	14
9.3	21.5–24.7	5–9	4–5	9–12

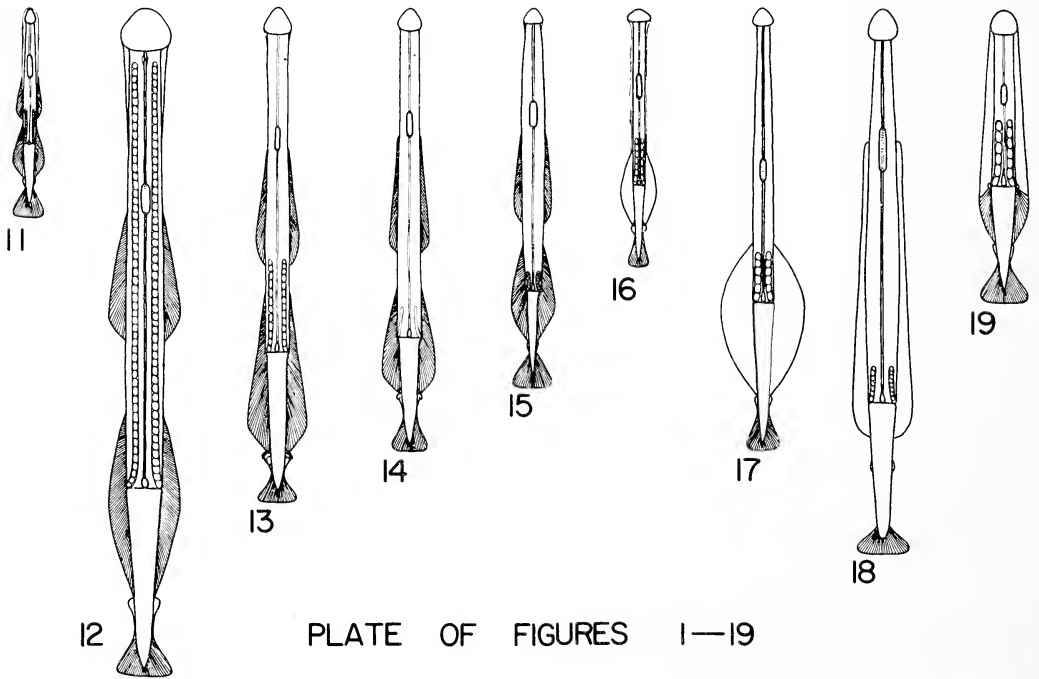
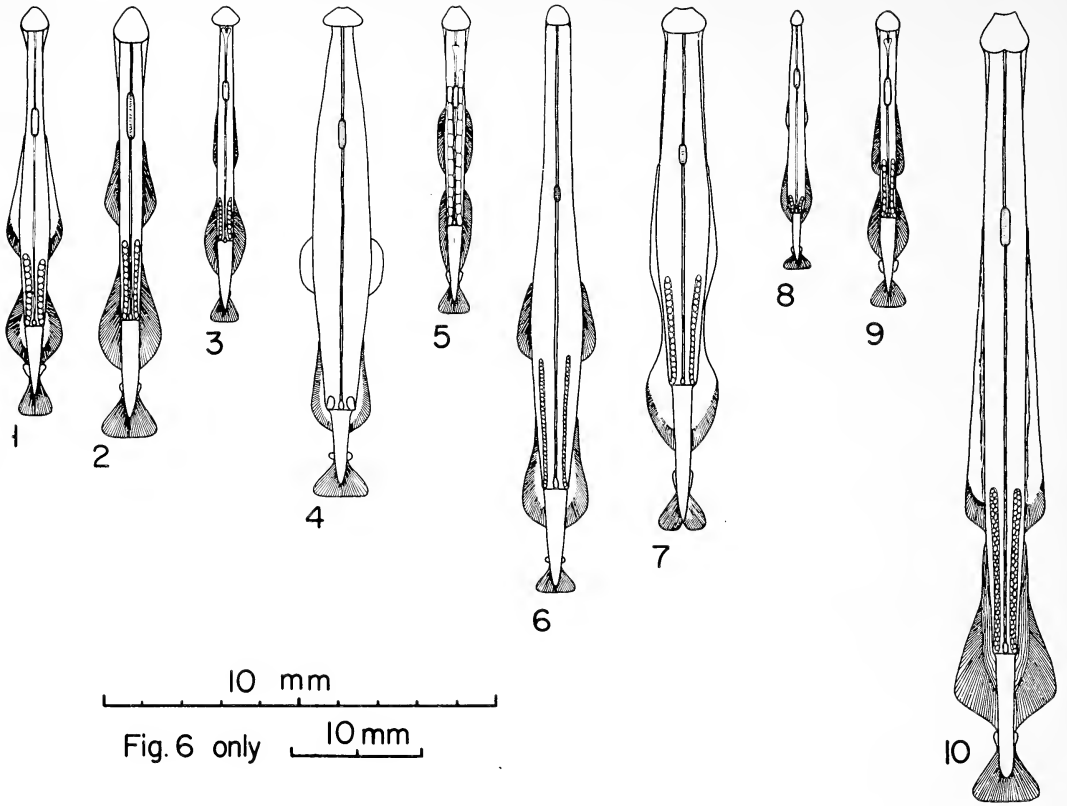


PLATE OF FIGURES 1—19

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
8.0	26.3	8	4	9
6.4	23.0	8	5	10
<i>Tokioka's specimen:</i>				
11.7	21.4	8	7	13
<i>Hida's specimens:</i>				
11.7	25.6	7	4	10
11.5	25.2	6	5	11
11.1	25.2	6	5	11
10.7	23.5-27.1	7-8	4-6	9

Sagitta decipiens Fowler, 1905

S. decipiens, Michael, 1908

Body delicate, moderately opaque. Tail segment 22-27 per cent of body length; hooks 5-7; anterior teeth 7-10; posterior teeth 13-20. Anterior fins start just posterior to ventral ganglion. Posterior fins widest at level of tail-septum, lying mostly on body segment, not reaching seminal vesicles. Caudal fin touching seminal vesicles. Intestinal diverticula present. Collarrete absent.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
11.0	23.0	5	9-10	17
10.0	23.0	6	8	17
9.2	25.0	5	7	17
8.8	22.7-23.8	6-7	8-9	13-20
8.6	26.7	6	9	16

EXPLANATION OF PLATE I

(All figures drawn from preserved material, some with the aid of photographs; semidiagrammatic.)

FIG. 1. *S. bedoti*, 10.0 mm. specimen.

FIG. 2. *S. bipunctata*, 10.6 mm. specimen.

FIG. 3. *S. decipiens*, 7.8 mm. specimen.

FIG. 4. *S. enflata*, 12.6 mm. specimen.

FIG. 5. *S. ferox*, 7.6 mm. specimen.

FIG. 6. *S. hexaptera*, 44.9 mm. specimen.

(Note change of scale.)

FIG. 7. *S. lyra*, 13.2 mm. specimen.

FIG. 8. *S. minima*, 6.5 mm. specimen.

FIG. 9. *S. neglecta*, 7.3 mm. specimen.

FIG. 10. *S. pulchra*, 19.7 mm. specimen.

FIG. 11. *S. regularis*, 5.1 mm. specimen.

FIG. 12. *S. robusta*, 17.0 mm. specimen.

FIG. 13. *S. serratodentata pacifica*, 12.5 mm. specimen.

FIG. 14. *S. pseudoserratodentata*, 11.2 mm. specimen.

FIG. 15. *S. tenuis*, 9.5 mm. specimen.

FIG. 16. *K. pacifica*, 6.5 mm. specimen.

FIG. 17. *K. subtilis*, 11.2 mm. specimen.

FIG. 18. *E. hamata*, 13.6 mm. specimen.

FIG. 19. *P. draco*, 7.2 mm. specimen.

Sagitta enflata Grassi, 1883*S. enflata*, Michael, 1908, 1911; Bieri, 1957*S. inflata*, Baldasseroni, 1915

Body flaccid, transparent, with marked constriction at the tail-septum. Tail segment 14–18 per cent of total length; hooks 8–9; anterior teeth 4–10; posterior teeth 7–15. Anterior fins rounded, removed from ventral ganglion by a distance greater than the length of the fin, narrower than posterior fins. Posterior fins do not touch seminal vesicles, widest at level of tail-septum, or a little anterior. Caudal fin joining seminal vesicles. No collarette. No intestinal diverticula. Seminal vesicles round. Ovaries short.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
11.8	16.1	8–9	9–10	13
11.3	16.5	9	7	13
10.1	15.7	8	6	10
10.0	14.0	9	7	11
6.0	16.3	9	4	7
<i>Hida's specimens:</i>				
15.6	17.9	9	10	12
15.4	15.6	9	10	15
14.3	16.1	9	6	12
12.6	15.1	9	6	13
12.0	15.0	9	7	11

Sagitta ferox Doncaster, 1903*S. ferox*, Bieri, 1957

Body firm, opaque, short and robust, of equal width for most of the length of body segment. Tail segment 22–28 per cent of total length; hooks 6–7; anterior teeth 6–13; posterior teeth 4–12. Anterior fins reach the posterior end of ventral ganglion. Posterior fins and tail fin close to, or touching, seminal vesicles. Posterior fins longer than anterior fins. Collarette present. Intestinal diverticula present; often removed from neck. Seminal vesicles angular, with anterior edge slanting postero-laterally. Ovaries when ripe containing cuboidal ova that fill body cavity.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
9.0	24.4	6	10	8
8.4	26.2	7	8	10
8.2	24.4	7	12	9
7.8	24.4	7	8	12

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
7.2	26.4	7	8	10
7.1	25.4	7	7-8	11
7.0	25.7	7	6-7	9
6.8	26.4	7	6	9
<i>Tokioka's specimens:</i>				
7.8	24.3	7	8	11
7.5	22.7-25.2	7	13	10
7.3	27.4	7	10	..
7.2	26.5	7	13	11
7.0	25.8	7	6	4

Sagitta hexaptera d'Orbigny, 1834

S. hexaptera, Michael, 1908, 1911; Baldasseroni, 1915; Bieri, 1957

Body large, transparent. Tail segment 15-22 per cent of total length of body; hooks 4-8; 1-4 anterior teeth; posterior teeth 1-4. Anterior fins widely separated from ventral ganglion; narrow and rounded. Posterior fins not joining seminal vesicles. Caudal fin close to, but not joining, seminal vesicles. Ovaries narrow, containing round ova, extending to posterior end of anterior fin when mature.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
44.5	15.7	6	3	..
23.7	17.8	7	3	4
19.0	19.0	7	3	4
<i>Tokioka's specimens:</i>				
34.8	19.8	4	3	2
34.6	18.8	2 (?)	1	1
23.5	21.3	6	3	1
22.3	19.3	7	4	2
14.3	20.9	7	3	3
<i>Hida's specimens:</i>				
36.5	18.4	8	2	3
31.4	18.8	6	2	3

Sagitta lyra Krohn, 1853

S. lyra, Michael, 1911; Baldasseroni, 1915; Bieri, 1957

Body large, flaccid, opaque. Tail segment 10–19 per cent of total length; hooks 6–10; anterior teeth 4–5; posterior teeth 2–9. Anterior fins reaching ventral ganglion, or further anterior; connected to the posterior fins by a "fin-bridge." Posterior fins close to, or touching, seminal vesicles. Caudal fin separated from seminal vesicles. Intestinal diverticula absent.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
29.1	10.3	9	5	6
29.0	13.1	10	5	7
25.8	14.7	10	5	9
25.0	14.8	10	4	6
21.2	16.5	9	5	7
19.8	17.7	10
16.0	17.8–18.8	10	4	6
<i>Hida's specimens:</i>				
41.5	12.1	6	4	5
40.0	13.3	8	5	2

Sagitta minima Grassi, 1881

S. minima, Bieri, 1957

Body small, transparent, with marked constriction at the tail-septum. Tail segment 16–24 per cent of total length; hooks 5–8; anterior teeth 2–5; posterior teeth 3–11. Anterior fins not rayed, narrow, tapered, but rounded; removed from ventral ganglion. Posterior fins not reaching seminal vesicles. Caudal fin connected to seminal vesicles. No intestinal diverticula. Ovaries short; when mature, they appear to contain 3–5 large, round ova.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
6.6	18.3	7	4	10
5.8	21.6	7	4	8
5.6	20.7	7	4	11
5.5	18.2–23.6	7–8	3–4	9–11
5.4	19.4–23.6	7–8	4	9–11
5.3	21.7	8	4	11
5.1	23.5	8	5	10–11
4.9	23.7	7	2	9
4.6	23.9	8	5	10–11
<i>Tokioka's specimens:</i>				
7.1	16.9	5	3	4
6.3	20.6	6	3	6

Tokioka's specimens:

6.1	19.7	6	..	6
5.8	18.9	5	5	9
4.4	22.7	5	..	3

Sagitta neglecta Aida

S. neglecta, Michael, 1908; Baldasseroni, 1915; Bieri, 1957

Body firm, semiopaque. Tail segment 27–31 per cent of total length; hooks 6–8; anterior teeth 5–7; posterior teeth 13–17. Anterior fins start at ventral ganglion. Posterior fins reach seminal vesicles. Caudal fin separated from seminal vesicles by a distance equal to about ½ length of seminal vesicles. Seminal vesicles rounded. Ovaries containing rounded ova, extending anterior to posterior border of anterior fins. Collarlette present. Intestinal diverticula present.

Few specimens of *S. neglecta* were found in the Eastropic material; only one of these was in such condition that a complete formula could be obtained.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
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Eastropic specimen:

7.3	27.4	7	5	17
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Sagitta pulchra Doncaster, 1902

S. pulchra, Michael, 1908; Baldasseroni, 1915; Bieri, 1957

Body firm, moderately opaque; usually slim, but can be robust and quite transparent; with a marked constriction often present at tail-septum as seen from side. Tail segment 16–24 per cent of total length; hooks 6; anterior teeth 5–9; posterior teeth 8–12. Anterior fins tapered, reaching posterior end of ventral ganglion. Posterior fins shortly separated from seminal vesicles; widest posterior to the tail-septum. Caudal fin joining seminal vesicles. Collarlette present, readily visible. Intestinal diverticula absent. Seminal vesicles shaped as ovals; ovaries with small, round ova.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
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Eastropic specimens:

20.3	16.3	6	7	12
20.0	16.5	6	7	9
19.5	16.4	6	9	11
16.7	18.0	6	8	10
14.9	17.5	6	7	9
13.9	18.7	6	6	11
10.1	19.8	6	7	10

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Tokioka's specimens:</i>				
15.8	17.1	6	5	10
15.6	23.1	6	..	8
14.3	16.1	6	7	10
12.9	18.6	6	6	11
9.4	20.2	6	6	10
9.3	22.6	6	6	9
7.8	23.1	6	6	10

Sagitta regularis Aida, 1897

S. regularis, Bieri, 1957

Body firm, moderately opaque. Tail segment 29-34 per cent of total length; hooks 7-8; anterior teeth 2-4; posterior teeth 4-7. Anterior fins start at posterior end of ventral ganglion. Small interval between anterior and posterior fins. Posterior fins wider than anterior fins. Voluminous collarette usually present, covering head and most of body. No intestinal diverticula.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
5.8	32.8	7	3	5
5.6	32.1	8	4	6
5.3	32.1	8	3	5
5.2	30.8-32.7	7	3-4	4-6
5.1	31.4	8	4	7
5.0	32.0-34.0	7	2-4	4-5
4.8	29.2-31.3	7-8	3	5

Sagitta robusta Doncaster, 1903

S. robusta, Baldasseroni, 1915; Bieri, 1957

Body very opaque, firm; of uniform width from neck to tail-septum. Tail segment 24-28 per cent of total length; hooks 5-7; anterior teeth 6-11; posterior teeth 8-15. Anterior fins start at posterior end of ventral ganglion. Posterior and caudal fins both reaching seminal vesicles. Seminal vesicles long-tapered posteriorly. Ovaries long (when fully mature they may extend to the neck), containing eggs of moderate size. Intestinal diverticula present, but specimens are often too opaque for them to be seen.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
13.7	25.6	7	8	8

Eastropic specimens:

13.6	28.0	6-7	7	12
13.2	27.3	7	10	14
12.7	26.0	5-7	10-11	14-15
12.5	25.6	6-7	10	13
9.5	26.3	6	9	12-13
9.3	28.0	7	6-7	10
8.6	25.6	6	11	12

Tokioka's specimen:

16.4	26.6	6	8	8
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Hida's specimens:

13.0	26.9	6	9	14
11.9	24.4	7	10	12
11.1	27.0	6	8	13
10.0	27.0	7	8	12

Sagitta serratodentata pacifica Tokioka, 1940*S. pacifica*, Bieri, 1957

The nomenclature employed for the *S. serratodentata* group is that suggested by Tokioka (1952). The synonyma are discussed by Furnestin (1953).

Body firm, opaque. Tail segment 22-25 per cent of total length; hooks 5-7; anterior teeth 5-11; posterior teeth 8-24. Anterior fins tapering, narrower than posterior fins; extending anteriorly to posterior end of ventral ganglion. Posterior fins widest behind tail-septum; close to, or touching seminal vesicles. Seminal vesicles greatly expanded anteriorly, armed laterally with 3-10 chitinous spines. Ovaries containing large cuboidal ova. Collarlette small, or absent. Intestinal diverticula absent.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
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Eastropic specimens:

12.5	23.2	6	10	17
12.4	22.5	6	11	23
11.4	22.0	6	10	19
10.8	24.0	5	8	19
10.6	23.5	6	9	20
10.5	22.9	..	8	15
10.0	25.0	6	7	15
9.6	20.8	7	8	13

Tokioka's specimens:

13.0	23.5	5	7	13
12.4	23.4	5	9	18
12.2	23.0	7	9	18
12.0	24.2	6	9	17

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Tokioka's specimens:</i>				
11.3	24.8	6	9	18
11.1	23.4	5	7	12-13
10.5	23.9	6	9	16
9.0	23.4	6	6	9
8.9	24.8	7	7	13
8.0	22.5	6	5	8
<i>Hida's specimens:</i>				
12.3	22.8	5	9	16
11.5	23.0	6	..	24
11.2	23.1	7	8	19
11.1	24.3	5	10	20
10.5	24.7	7	8	14

Sagitta pseudoserratodentata Tokioka, 1939

Tail segment 26-28 per cent of total length; hooks 6-7; anterior teeth 5-6; posterior teeth 7-12.

The features of this species are similar to those of *S. s. pacifica*, except that the seminal vesicles are unarmed, and the anterior edge of the vesicles slopes posterolaterally to a rounded point, from which the longer posterior border extends backwards and medially to rejoin the body wall. The percentage of the total length that the tail segment occupies is greater for specimens of equal size in *S. pseudoserratodentata* than in *S. s. pacifica*, and the number of teeth is less than in *S. s. pacifica* (see armature formulae tables).

S. pseudoserratodentata seems to be mature at a shorter total length than *S. s. pacifica*.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
7.1	26.7	6	5	9
6.8	26.5	7	5	7
6.2	27.4	6	6	12

Sagitta tenuis = *friderici*

S. tenuis Conant, 1896

S. friderici Ritter-Zahony, 1903

S. tenuis, Bieri, 1957

Body firm, translucent. Tail segment 21-26 per cent of total length; hooks 5-8; anterior teeth 2-5; posterior teeth 4-9. Anterior fins close to, but not reaching posterior end of ventral ganglion. Posterior fins close to, or touching seminal vesicles. Caudal fin reaching seminal

vesicles. Ovaries similar in appearance to those of *S. enflata*. Collarette present but extremely small; often missing in damaged specimens. Intestinal diverticula absent. Teeth wide-based, tapering sharply to a point; tips widely separated.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
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Tokioka's specimens:

10.3	22.8	8	5	9
9.4	21.6	8	4	9
7.3	20.6	8
4.7	23.7	6	3	4
3.9	25.6	5	2	4

The formulae for *S. tenuis* = *friderici* identified from the Eastropic material have been omitted because the specimens were in such poor condition that accurate measurements could not be made. The specimens for which the formulae are given above were labelled by Tokioka as *S. friderici*. The status of the two species is still doubtful, especially concerning specimens from Pacific waters (Tokioka, 1955). The specimens so far identified from the Eastropic material were immature and in poor condition and provide no basis for a discussion of the validity of this species at this time. Bieri (1957) gives the impression that the two are synonymous, but his final interpretations must await the publication of his findings.

Krohnitta pacifica Aida, 1897

K. pacifica, Bieri, 1957

Body moderately firm, translucent-to-opaque. Single pair of lateral fins long and tapering; fins extend anteriorly from seminal vesicles over posterior $\frac{1}{3}$ of trunk; widest behind septum. Collarette present, extending as narrow band from neck to anterior edge of fins. Tail segment 28–38 per cent of total length; hooks 6–9; teeth 7–15. Lateral and caudal fins joining seminal vesicles. Ovaries with cuboidal ova. Intestinal diverticula absent.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	TEETH
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Eastropic specimens:

7.2	31.9	7	11
6.8	33.8	7	13
6.6	31.8–31.9	7	13
6.4	35.9–37.5	7	14–15
6.3	30.1	7	12

Tokioka's specimens:

7.1	28.1	9	12
7.0	28.6	9	12
4.2	31.0	6	7–8

Krohnitta subtilis Grassi, 1883

Eukrohnita subtilis, Michael, 1908, 1911

Body long, thin, moderately transparent, delicate. Tail segment 30–34 per cent of total length; hooks 5–8; teeth 8–12. Lateral fins wide, rounded, often subcircular; extending from seminal vesicles over posterior $\frac{1}{3}$ of trunk; widest at level of tail-septum. Collarette and intestinal diverticula absent. Caudal fin touching seminal vesicles. Ovaries with rounded ova.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	TEETH
<i>Eastropic specimens:</i>			
12.5	32.0	7	11
10.2	31.3	7	11
10.0	30.0	8	12
<i>Tokioka's specimens:</i>			
11.3	34.1	6	8
10.6	32.0	6	9
10.2	32.4	5	9
9.1	34.0	6	..
<i>Hida's specimens:</i>			
10.9	30.0–32.0	7	9
10.4	31.2	7	11
9.2	30.5–31.2	7	11

Eukrohnia hamata Möbius, 1875

E. hamata, Michael, 1908, 1911

Body flaccid, opaque, wide. Single pair of lateral fins extending from behind tail-septum to ventral ganglion, not reaching seminal vesicles. Tail-septum 20–26 per cent of total length; hooks 8–9; single row of teeth, 6–17 in number. Tips of hooks curved inward. Intestinal diverticula absent. Collarette absent.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	TEETH
<i>Eastropic specimens:</i>			
10.7	23.4	8	17
7.0	22.9	8	6
<i>Hida's specimens:</i>			
13.9	21.5	9	10
13.7	25.5	9	9
13.2	20.5	9	6
10.7	23.4	9	6

Pterosagitta draco Krohn, 1853

Spadella draco, Michael, 1908, 1911

P. draco, Baldasseroni, 1915; Bieri, 1957

Body opaque, firm. Tail segment 32–38 per cent of total length; hooks 8–9; anterior teeth

4-9; posterior teeth 8-17. Single pair of lateral fins restricted to tail segment; wide, with rounded lateral borders; reaching seminal vesicles. Caudal fin close to, but not touching, seminal vesicles. No intestinal diverticula. Collarlette voluminous, all or part frequently missing, extending from head to anterior border of fins, confluent with fins.

BODY LENGTH IN MM.	LENGTH OF TAIL SEGMENT (IN % OF TOTAL BODY LENGTH)	HOOKS	ANTERIOR TEETH	POSTERIOR TEETH
<i>Eastropic specimens:</i>				
7.1	35.2	8	6-7	12
5.8	36.2	8	6	15
5.6	37.8	9	6	15
5.1	37.2	9	6	17
4.9	32.6	8	5	13
4.4	38.6	9	6	8
4.0	35.0	9	4	..
<i>Hida's specimens:</i>				
7.6	34.2	9	9	15
6.9	34.7	9	9	17
6.8	35.2	9	7-8	11-14
6.3	36.6	9	7	..
6.2	37.0	9	7	17

KEY TO THE PLANKTONIC GENERA AND SPECIES OF CHAETOGNATHA PRESENT
IN THE EASTERN TROPICAL PACIFIC

Key to the Genera of Chaetognatha

1. A single pair of lateral fins 2
1. Two pairs of lateral fins, which are sometimes connected **Sagitta**
2. Two rows of teeth; one pair of lateral fins restricted to the tail segment, appearing as a continuation of a voluminous collarlette (one species only: *P. draco*) **Pterosagitta**
2. One row of teeth; one pair of lateral fins extending over the trunk and tail segments . . . 3
3. Single pair of lateral fins extending from seminal vesicles over the posterior 1/3 of the trunk segment. Teeth long, tapered, tips converging **Krohnitta**
3. Lateral fins slender, not reaching seminal vesicles, extending anteriorly to ventral ganglion. Teeth short, not converging (one species only: *E. hamata*) **Eukrohnia**

Key to the Genus Krohnitta

1. Body slender, transparent; fins very wide, rounded, widest at level of tail-septum; short ovary with rounded ova; collarlette absent **subtilis**
2. Body robust, opaque; fins not rounded, widest behind tail-septum; ovaries contain large cuboidal ova; collarlette sometimes evident as a narrow band of epidermal thickening extending from neck to anterior edge of fins **pacifica**

Key to the Genus Sagitta

1. Anterior fins start some distance posterior to ventral ganglion 2

1. Anterior fins start at level of posterior end of ventral ganglion, or farther anterior. 7
2. Lateral fins joined by "fin bridge"; caudal fin bilobed. *lyra*
2. Lateral fins not joined. 3
3. Anterior fins rounded, widely separated from ventral ganglion. 4
3. Anterior fins tapering; distance between anterior fins and ventral ganglion not great (distance is less than that equal to a length of the ventral ganglion). 5
4. Teeth numerous; hooks 8-10; small-to-middle size species. *enflata*
4. Teeth few, protruding; large species. *hexaptera*
5. Moderately opaque species; delicate, of medium length; intestinal diverticula present. *decipiens*
5. Small, transparent species; no intestinal diverticula. 6
6. Tail segment tapers sharply posterior to tail-septum, marked constriction at septum; 3-5 large, round ova in mature specimens; lateral septa connecting gut to body wall sometimes evident; posterior fins widely separated from seminal vesicles. *minima*
6. Constriction at tail-septum not great; ovaries club-shaped; posterior fins close to, but not touching, seminal vesicles; caudal fins touching seminal vesicles. *tenuis* = *friderici*
7. Posterior fins joining, or close to seminal vesicles. 8
7. Posterior fins not joining seminal vesicles; no intestinal diverticula; seminal vesicles head-shaped anteriorly; 9-10 hooks. *bipunctata*
8. Voluminous collarette covering head and most of body. *regularis*
8. Collarette not covering head. 9
9. Posterior teeth less than 20; intestinal diverticula may, or may not be present. 10
9. Posterior teeth 20-30; intestinal diverticula absent; anterior fins tapering, reaching ventral ganglion; collarette obvious. *bedoti*
10. Intestinal diverticula absent. 11
10. Intestinal diverticula present. 13
11. Posterior fins shorter than anterior fins; widest behind tail-septum; collarette of moderate size; anterior fins tapering, reaching ventral ganglion; hooks 6; posterior teeth 8-12. *pulchra*
11. Posterior fins longer than anterior fins, or of about same length. 12
12. Posterior fins widest well behind tail-septum, jaws serrated, 6-7 in number. *serratodentata* group
 - a. Posterior fins close to seminal vesicles; seminal vesicles armed with spines anterolaterally, sometimes with a membrane connecting the anterior free end to the body; short space separating caudal fin and seminal vesicle; 12-15 mm. maximum length when mature. *S.s. pacifica*
 - b. Seminal vesicle triangular in shape, anterior border slants posterolaterally; 10-12 mm. maximum length when mature; (common in California current). *S. pseudoserratodentata*
13. Seminal vesicles close to but not in contact with caudal fin, separated by distance equal to about ½ length of seminal vesicle. *neglecta*
13. Seminal vesicles touch caudal fin. 14
14. Body very opaque, of uniform width from neck to tail-septum; collarette extends from neck to anterior fins; ovaries extending to neck, containing eggs of moderate size; intestinal diverticula not obvious due to opacity of species. *robusta*
14. Body moderately transparent, of uniform width from ventral ganglion to tail-septum; ovaries containing large eggs that fill body cavity; intestinal diverticula obvious. *ferox*

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Notes on Indo-Pacific Scleractinian Corals

Parts I and II

Part I. *Oryzotrochus*, a New Genus of Turbinolian Coral

JOHN W. WELLS¹

IN 1954 the writer spent a few days studying part of the coral collections of the Australian Museum. Among much undetermined material was a lot consisting of two species of very small turbinolian corals from a dredge haul (source unknown) made at the northern end of the Great Barrier Reef. One species was *Holcotrochus scriptus* Dennant 1902, a most peculiar form previously recorded only from the Lower Miocene and Pliocene of South Australia and from depths of 38–185 meters off South Australia. It was represented by some 20 individuals, 1 of which is illustrated in Figures 6 and 7. The other species, represented by 100 specimens, mostly more or less damaged, proved to be a new turbinolian genus, here called *Oryzotrochus* in allusion to its resemblance to a rice grain.

Special thanks are due to F. J. McNeill of the Australian Museum for permission to re-

tain several specimens for description.

Family CARYOPHYLLIIDAE

Subfamily TURBINOLIINAE

Oryzotrochus gen. nov.

Small, solitary, free, conical corals. Wall imperforate, externally costate with prominent, high, smooth costae. Septa exsert, smooth margined, lightly granulated laterally. Pali absent. Columella small and styliform.

This genus is obviously very closely allied to the well-known Tertiary (Eoc.-Mioc.) genus *Turbinolia*,² from which it is distinguished only by the absence of mural perforations or external intercostal pits. The more apparent differences from other conical turbinolians are brought out in the following artificial key.

- A. Wall perforate or with deep intercostal pits:
 - 1. Pali absent:
 - a. Columella spongy **Bothrophoria** Felix (U. Cret.)
 - b. Columella styliform:
 - aa. Costae smooth **Turbinolia** Lamarck (Eoc.-Mioc.)
 - bb. Costae hispid **Batotrochus** Wells (Rec.)
 - 2. Pali present:
 - a. 1 crown of 6 before second cycle; costae smooth **Conocyathus** d'Orbigny (Eoc.-Rec.)
 - b. Pali weakly developed; costae hispid **Trematotrochus** Tenison-Woods (Olig.-Rec.)
- B. Wall imperforate:
 - 1. Paliform lobes absent **Oryzotrochus** n.g. (Rec.)
 - 2. Paliform lobes present **Notocyathus** Tenison-Woods (Eoc.-Rec.)

¹Department of Geology, Cornell University, Ithaca, N. Y. Manuscript received February 17, 1958.

²*Turbinolia australiensis* Gardiner 1939 (*Discovery Reports*, vol. 18, p. 332, pl. 21, figs. 1, 2), from Port Jackson, N. S. Wales, is *Conocyathus zelandiae* Duncan 1876.

Type species: *Oryzotrochus stephensoni* n. sp.

Oryzotrochus stephensoni sp. nov.

Figs. 1–5

With the characters of the genus as diagnosed above. Septa 12 in number, in two cycles, thin, upper margins evenly arched and equally exert over the wall and dropping steeply to level of the columella about halfway between wall and axis. Septa generally all extending to and fusing with the columella, but secondaries in one or two systems may join primaries short of the columella. Costae corresponding to all septa, equal, high, smooth-margined, separated by relatively broad and flat interspaces. An irregular row of very small buttresslike expansions on each side of each costa at junction with the wall. Primary costae distinct to the base; secondary costae arising just short of the base. Columella

a slender style elevated about to height of exert septal margins.

Dimensions

	CALICULAR		
	HEIGHT	DIAMETER	
Holotype	3.5 mm.	1.7	(Figs. 3, 4)
Paratype	3.0	1.5	(Fig. 5)
Paratype	3.3	1.6	(Fig. 1)
Paratype	2.4	1.5	(Fig. 2)

Named for W. Stephenson, Professor of Zoology, University of Queensland.

Holotype and figured paratypes to be deposited in the U. S. National Museum. Remaining paratypes are in the Australian Museum.

Locality

Murray Islands (9°55'S., 144°02'E.), near northern end of Great Barrier Reef, Queensland, 9–15 meters.

Part II. A New Species of *Turbinaria* from the Great Barrier Reef

AT LEAST 350 species representing 57 genera of reef-building scleractinian corals are now known from the Great Barrier Reef area (Wells, 1955: 21). It would seem ungracious to add a new species to this burdensome total, especially to a genus with 34 species already reported from this region, many of them of doubtful validity, but the form described below is so distinct that it cannot be referred to any known species of *Turbinaria*.

Family DENDROPHYLLIIDAE

Genus TURBINARIA Oken 1815

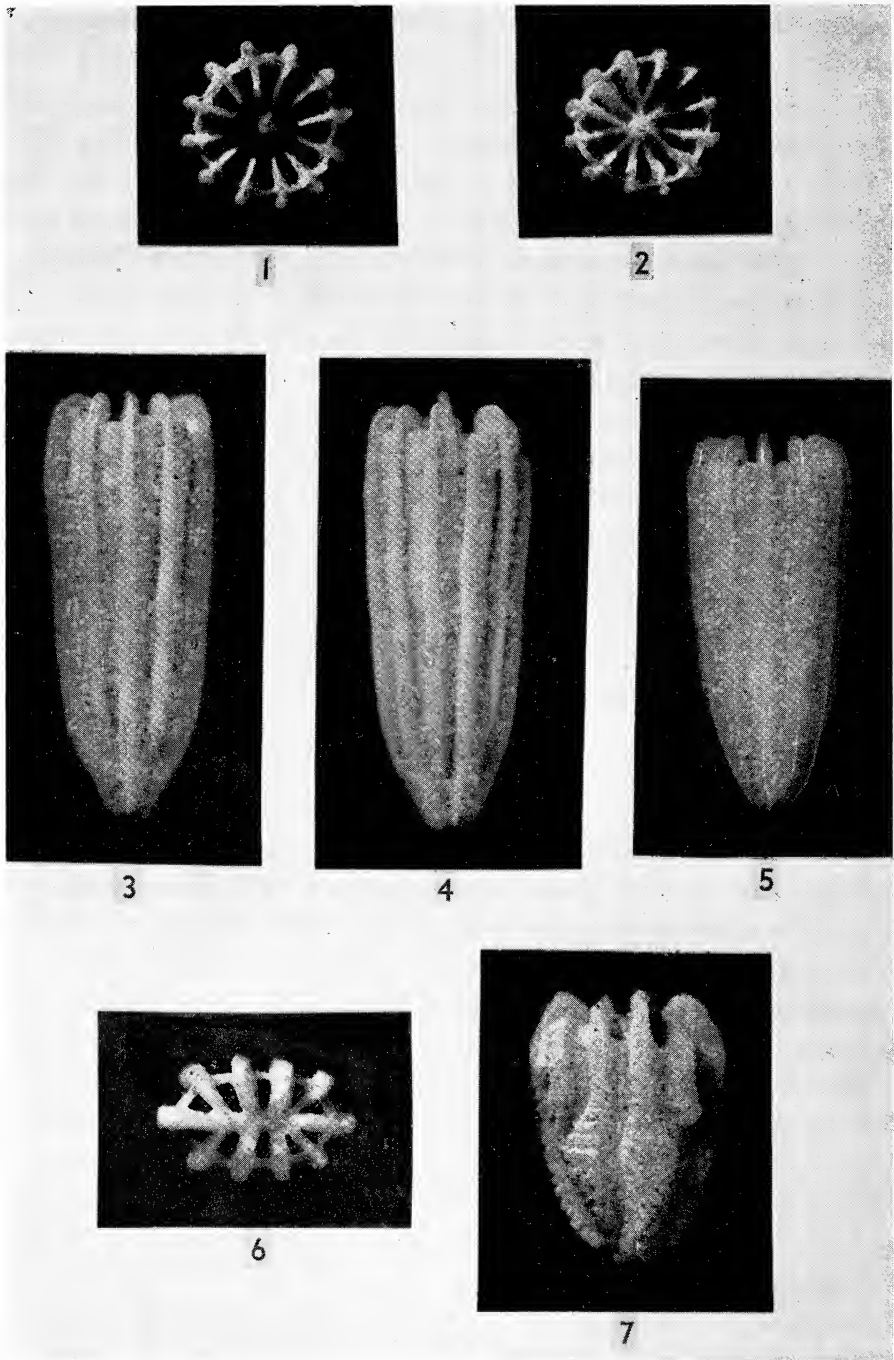
Turbinaria heronensis sp. nov.

Figs. 1–4

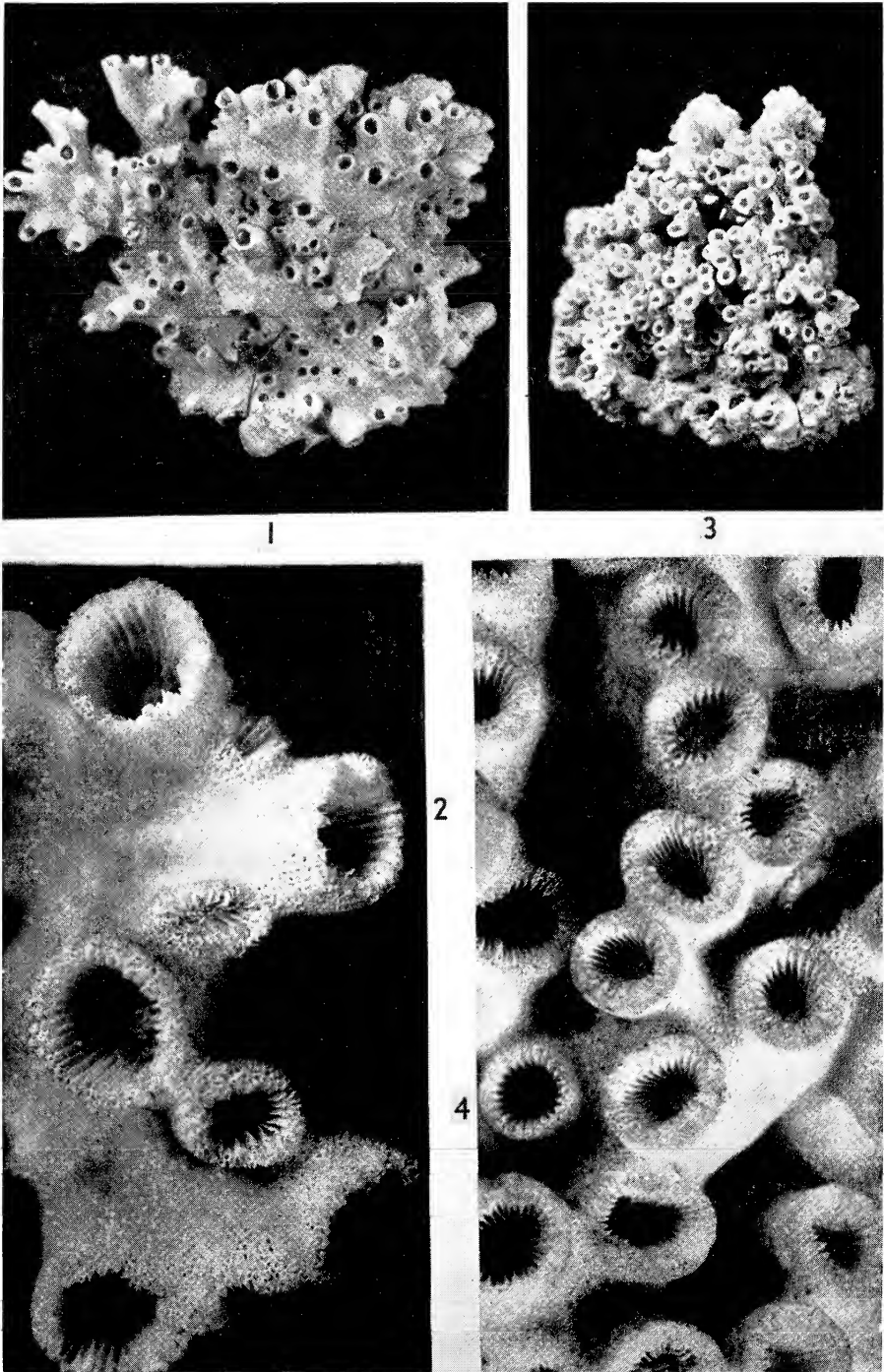
Corallum bushy, to 20 cm. in height, formed by erect branches arising from a small, encrusting base. Corallites tending to develop irregularly on opposite sides of flattened and

twisted branches, new extratentacular buds appearing in the plane of the branches between the previously formed and the next previously formed corallites. Corallites cylindrical, rarely more than 10 mm. long without buds, averaging 4 mm. in diameter. Wall spongy. Calices deep (3 mm.), circular, averaging 3 mm. in internal diameter. Septa thick peripherally in the wall, thin axially, upper margins dropping abruptly to the level of the columella, 36 to 40 in number, irregularly arranged, with 24 to 30 extending to the columella, the remainder fusing to lower cycles of septa. Columella a deep, chioraceous, trabecular column about half the internal diameter of the corallites. Coenosteum and exterior of free parts of corallites very compact but porous, the surface appearing smooth, but very finely vermiculo-echinulate.

This species is readily distinguished from practically all other known recent species of



FIGS. 1-5. *Oryzotrochus stephensoni* n. gen., n. sp. 1, 2, Calicular aspect of two paratypes. 3, 4, Lateral aspects of holotype. 5, Lateral aspect of paratype. 6, 7, *Holcotrochus scriptus* Dennant. Calicular and lateral aspects. (All figures 15X.)



FIGS. 1, 2. *Turbinaria heronensis* n. sp. 1, Lateral aspect of holotype corallum, $\times 0.4$. 2, Calices of same, $\times 4$. 3, 4. *T. heronensis*. 3, Calicular aspect of rough-water facies (paratype), $\times 0.4$. 4, Calices of same, $\times 4$.

Turbinaria by its subramose growth form. The growth form in *Turbinaria* is characteristically crateriform to foliate, with barely protuberant corallites. The only other subramose species is *T. ramosa* Yabe and Sugiyama (1941, p. 89, pl. 100, figs. 2, 2a, 2b) from Kyushu, Japan, but in this species the corallites taper slightly toward the calice, the calices are slightly smaller (2.5–3 mm.) with only 14 to 16 thick, wedge-shaped septa, and the columella is sublamellar. The most significant difference lies in the smaller number of septa in the Japanese coral. There is a slight resemblance to the allied genus *Duncanopsammia* in the calicular characters and even less in the mode of growth.

The typically loosely ramose form (Fig. 1) of *T. heronensis* grows in relatively sheltered sites amongst other corals on reef flats. Stunted, compact, fasciculate colonies (Fig. 3) are occasionally found in rough-water environments near reef margins. The polyps are an unpleasant sulphur yellow, set in yellow-brown coenosarc.

A number of specimens of this coral have been seen in collections from the Great Barrier Reef, but very few had definite localities.

The living specimens were collected by the writer in 1954 at Heron Island, Queensland. Holotype and figured paratype are to be deposited in the U. S. National Museum.

Localities

Great Barrier Reef, Queensland; windward reef flat, Heron Island (23° 25' S.), Capricorn Group (holotype); windward reef margin, Heron Island (paratype: rough-water facies); Low Isles (16° 25' S.) (Australian Museum); South Molle Island (20° 15' S.), Whitsunday Group (in private collection at S. Molle); "East of Port Curtis" (probably from Capricorn or Bunker Group, 23° 30' S.) (Australian Museum No. 4955).

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Occurrence of Gibbsite Amygdules in Haiku Bauxite Area of Maui¹

G. DONALD SHERMAN and HARUYOSHI IKAWA²

AREAS OF BAUXITE DEPOSITS have been discovered on the islands of Kauai, Maui, and Hawaii of the Hawaiian Islands. These deposits have been described by Sherman (1957) and Fellom (1957). In many of these deposits the free aluminum oxide occurs as a constituent of irregular-shaped nodules varying in size from 1/100 inch to over 6 inches in their longest dimensions. The alumina content of these nodules as determined in the laboratories of the Hawaii Agricultural Experiment Station ranges from 40 per cent to 62 per cent. Iron oxide was found to be the other major constituent of these nodules ranging from a little over 2 per cent to 40 per cent. Mineralogical analysis of the nodules has identified the minerals as gibbsite, the trihydrate of aluminum oxide, and goethite, an iron oxide.

Recently, layers of pea-sized gibbsite amygdules were found in several of the deep road-cuts occurring on the new highway to Hana, 3-5 miles east of Pauwela, Maui. The white gibbsite amygdules are exposed in the banks of the road-cuts as irregular layers from 12 to 20 feet below the surface soil. These layers are easily recognized because the numerous white amygdules occur in dark gray brown rocks which are completely weathered. These weathered rocks still retain the structure of the original parent rock. The material is soft and when crushed between one's fingers it

readily breaks down to a clayey material, and the hard round amygdules. The amygdules are shown in Figure 1.

A close examination of the amygdules revealed that they have been developed by the precipitation of hydrated aluminum oxide in the cavities of the parent rock. The unfilled cavities can be found in adjacent parent rock and in the unweathered rock of the same formation. The cavities were formed by gas bubbles in the original lava. The precipitation of the aluminum oxide initially occurred on the wall of the cavity. Subsequent precipitation of additional aluminum oxide has continued until the cavity was completely filled. The contents of the cavity harden to form a resistant amygdule. The size and shape of the cavity determine the physical shape of the amygdule. The aluminum is transported in percolating waters to the cavity as aluminum hydroxide and is precipitated as the hydroxide on exposure to air in the cavity. It then is converted to trihydrate of aluminum oxide on aging in a drier atmosphere. The evidence for the mode of deposition of the aluminum oxide in the cavities is as follows: (a) the occurrence of similar unfilled cavities having similar shapes and volume in the adjacent weathered material, (b) the concentric deposition layers of the amygdule, (c) the occurrence of hollow amygdules which would indicate the initial precipitation of the hydrated oxide on the wall of the cavity (several of the amygdules in Fig. 1 have hollow centers), and (d) the observation of the formation of aluminum and iron oxides on exposure of seepage waters exuding from ditch and road cuts during the wet season.

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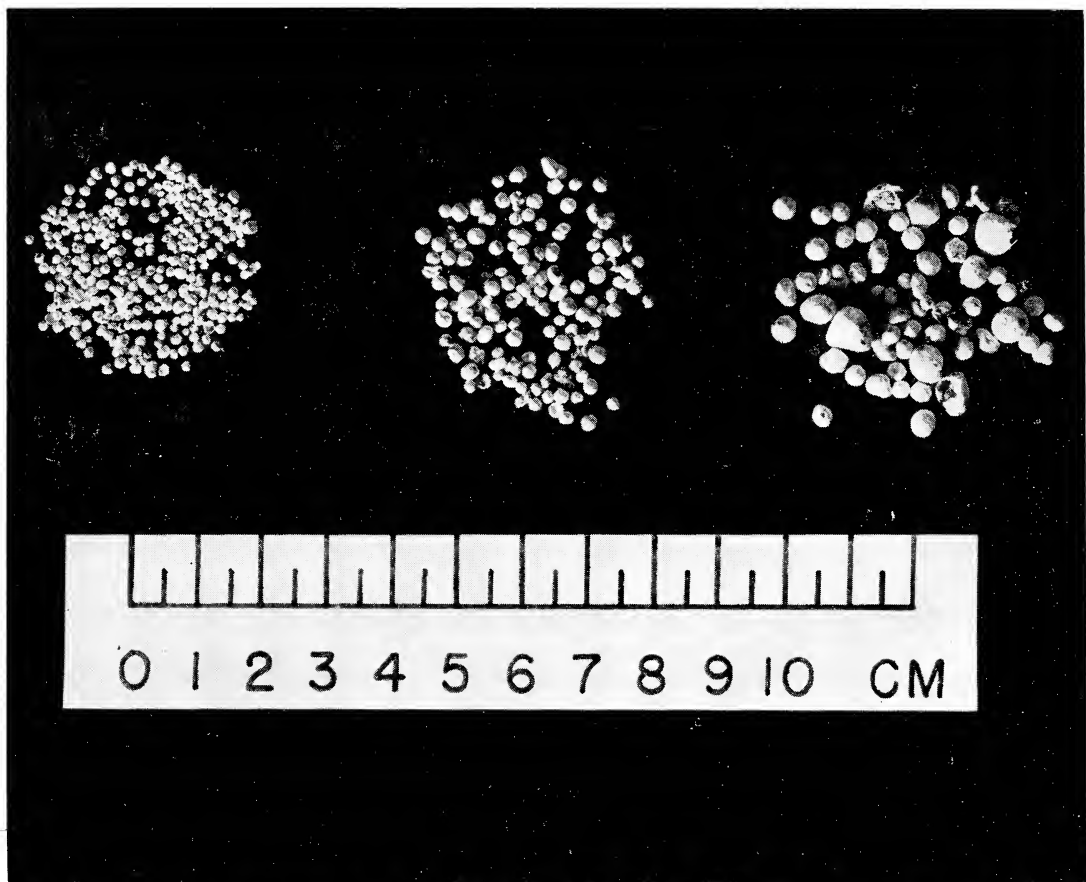


FIG. 1. Samples of gibbsite amygdules from Haiku bauxite area east of Pauwela, Maui. Samples on the right show outer skin of amygdule, some of which are hollow in the center.

Samples of the weathered rock containing the amygdules were collected to determine their chemical and mineral compositions. The amygdules were separated by dry-screening on a 20-mesh sieve and then any adhering matrix was removed by washing with distilled water. The samples of matrix and amygdules were dried and weighed. The chemical analysis of the samples of matrix and amygdules was made by procedures described by Piper (1944). The identification of the minerals in both the matrix and the amygdules was made by differential thermal analysis procedures proposed by Norton (1939). The samples were ground to pass through a 100-mesh sieve before analysis.

The chemical composition of the amy-

gdules and their respective matrices is presented in Table 1. The samples of amygdules have a very uniform chemical composition which averages as follows: 1.6 per cent SiO_2 ; 61.7 per cent Al_2O_3 ; 5.8 per cent Fe_2O_3 ; 0.8 per cent TiO_2 ; and, a loss on ignition of 30.9 per cent. The chemical composition of the amygdules approaches that of the mineral gibbsite, the trihydrate of aluminum oxide. The theoretical analysis of gibbsite is approximately 66 per cent Al_2O_3 and a loss on ignition of 34 per cent. The average composition of the matrix is as follows: 2.5 per cent SiO_2 ; 27.9 per cent Al_2O_3 ; 44.0 per cent Fe_2O_3 ; 9.6 per cent TiO_2 ; and a loss of ignition of 15.0 per cent. The variation in chemical analysis of the samples of amygdules and matrix is

extremely uniform. The remarkable fact brought out by the analyses is that the amygdules have a high concentration of aluminum oxide while the matrix has a high concentration of iron and titanium oxides. The silica content of both materials is very low. This same observation has been made in other types of precipitation of gibbsite from percolating waters.

The data presented in Figure 2 were obtained from the differential thermal analysis of a representative sample of the amygdules and the matrix. The strong endothermic peak occurring in these curves at temperatures between 350° C. and 375° C. is due to the minerals gibbsite and goethite. The endothermic action of gibbsite is much stronger than goethite, thus it is safe to identify the aluminum oxide mineral of the amygdule as gibbsite, the trihydrate of aluminum oxide.

The occurrence of gibbsite amygdules in the Hawaiian bauxite deposits is of considerable interest. Prior to their discovery, the gibbsite had been found only in nodular form and in sheets of aluminum oxide with iron oxide in seepage channels of percolating water. Pisolitic deposition of gibbsite has been described by Alexander *et al.* (1955). In the soils above the decomposed layer, the amygduloidal gibbsite occurs in aggregates and thus might easily be described as being a pisolitic occurrence of gibbsite.

Their observed gibbsite fills in spaces left

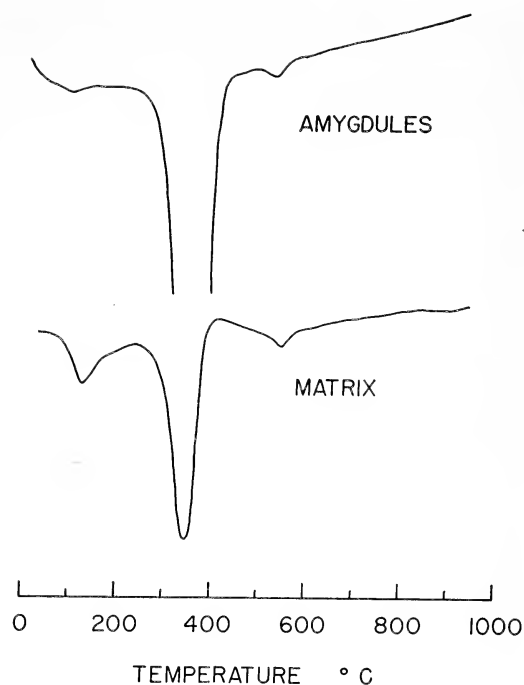


FIG. 2. The representative differential thermal analysis curves of a sample of amygdule and the matrix. Amygdules are from the Haiku bauxite area east of Pauwela, Maui.

by shrinkage in the hardening of laterite. The recently discovered bauxite of Cape York, Australia, is a pisolitic type of concentration. Its development has been attributed to the flooding of the coastal areas during the cyclones of the monsoon season and its subsequent drying. The development of pisolites

TABLE 1
THE CHEMICAL COMPOSITION OF GIBBSITE AMYGDULES AND THEIR MATRICES
FROM THE HAIKU BAUXITE AREA EAST OF PAUWELA, MAUI
(Samples from road-cuts on Hana road)

SAMPLES	SAMPLE PER CENT	SiO ₂ PER CENT	Al ₂ O ₃ PER CENT	Fe ₂ O ₃ PER CENT	TiO ₂ PER CENT	LOSS ON IGNITION PER CENT
Amygdules A.....	51.1	1.54	61.72	5.64	0.80	30.96
Matrix A.....	48.9	2.43	28.68	45.37	9.43	15.11
Amygdules B.....	49.5	1.65	61.60	5.83	0.73	31.06
Matrix B.....	50.5	2.65	27.80	46.30	9.62	14.92
Amygdules C.....	50.4	1.72	61.72	6.08	0.88	30.60
Matrix C.....	49.6	2.52	27.24	46.42	9.62	14.84

and amygdules of gibbsite depends upon wet and dry conditions to provide the means of movement of the alumina in order to produce the rhythmic precipitation which is so characteristic of their structure.

SUMMARY

The occurrence of gibbsite amygdules in a bauxite deposit of the Haiku area of Maui has been described. The amygdules are formed by the rhythmic precipitation of hydrated aluminum oxide in cavities which are relics of the parent rock. These cavities were probably gas bubbles in the original lava. The amygdules contain approximately 62 per cent Al_2O_3 , 6 per cent Fe_2O_3 , and trace amounts of silica and titania. The hydrated aluminum oxide has been identified as gibbsite by differential thermal procedures.

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A Survey for Alkaloids in Hawaiian Plants. I

CARL E. SWANHOLM,¹ HAROLD ST. JOHN,²
and PAUL J. SCHEUER¹

ALTHOUGH PLANT ALKALOIDS have been isolated and studied for over 150 years, only a small percentage of the recorded plant species have been investigated and even fewer of the isolated compounds have been carried to full elucidation of their structures. Willaman and Schubert (1955) in their valuable survey of alkaloid-containing plants state that by the end of 1952 about 950 alkaloids were isolated and named and that 1,202 plant species were known to contain alkaloids. Up to that time only about 2 per cent of all recorded plant species had been as much as tested for alkaloids.

The widely varying pharmacological properties of alkaloids always have been a major point of interest and have helped to attract organic chemists to this field of research. This viewpoint, however, was losing ground steadily in the face of mounting successes scored by synthetic drugs. The demonstration by Müller, Schlittler, and Bein (1952) that the alkaloid reserpine was responsible for the hypotensive action of the Indian snakeroot, *Rauwolfia serpentina* Benth., instilled new vigor into natural products research. As a consequence of this work many members of the genus *Rauwolfia* and related genera in the plant family Apocynaceae from all parts of the tropics have been investigated. This recent research has also prompted the chemical study of three of the reported seven Hawaiian *Rauwolfia* species (Gorman *et al.*, 1957).

In order to utilize plant sources for the isolation of alkaloids effectively it is necessary to survey a given flora, and base subsequent

detailed work on the results of such a survey. A number of native floras have been investigated in recent years from this point of view. The most notable of these have been carried out in Australia (Webb, 1949, 1952), and more recently in Papua–New Guinea (Webb, 1955).

Hawaii's flora is unique in two respects: It offers widely diverse vegetational types located within small geographical areas, and its native flora is over 90 per cent endemic, one of the highest endemisms in the world. Yet, except for the recent *Rauwolfia* research (Gorman *et al.*, 1957) and a few isolated instances in the past (e.g., Folkers and Koniuszy, 1939), Hawaii's flora has not been the subject of chemical study, nor has it even been surveyed for alkaloids. The pioneering research of Bushnell and co-workers (1950) drew attention to the antibacterial properties of some plants found in Hawaii and to the important link between Hawaiian flora and native Hawaiian *materia medica*.

The present work is concerned with a survey of some Hawaiian plants for their alkaloid content. While the 96 species tested represent only a small fraction of the recorded species, it is hoped that this work will constitute only the beginning of more extensive surveys in the future.

METHODS

This study was patterned after the survey carried out by Webb (1949, 1952) in Australia. The floristic books by Hillebrand (1888) and by Rock (1913) were used in the study of the indigenous plants of Hawaii. An attempt was made to test indigenous plants predominantly, although some introduced species have been included. A majority of the tests were carried out on freshly collected specimens. To ascertain that herbarium speci-

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mens gave valid results, several cross checks were made. All identifications of plants were made by H. St. John.

EXTRACTION OF PLANT MATERIAL. Two methods of extraction were used. In the first method about 5 grams of chopped or ground dried plant material was extracted with 1 per cent hydrochloric acid at 80° C. for 4–6 hours. The resulting solution was filtered through fine paper and the filtrate was tested with the alkaloid reagents.

In the second method about 5 grams of chopped or ground dried plant material was extracted with Prollius fluid (*vide infra*) for 56 hours at room temperature with occasional stirring. The organic layer was separated and evaporated to dryness at room temperature. The residue was dissolved in 1 per cent hydrochloric acid by heating to 80° C. for 1 hour. The resulting solution was filtered through fine paper and the filtrate tested with the alkaloid reagents.

The second method was used to supplement the first when sufficient plant material was available. It proved useful in clarifying tests which had doubtful results on the basis of the first method alone.

REAGENTS. The following formulations

of the alkaloid test reagents were based on Henry's directions (1929) with certain modifications.

Prollius Fluid. Ether, chloroform, alcohol, and ammonia were mixed in the ratio of 25:8:2.8:1 (by volume).

Mayer's Reagent. Dry mercuric chloride (6.8 g.) and potassium iodide (25 g.) were dissolved separately in water and diluted to make one liter of solution.

Hager's Reagent. A saturated aqueous solution of picric acid.

Wagner's Reagent. Iodine (13 g.) was dissolved in 1 N aqueous potassium iodide to make one liter of solution.

Dragendorff's Reagent. Neutral bismuth nitrate (20 g.) was dissolved in 30 g. cold conc. nitric acid (30 per cent). The solution was filtered and 68 g. potassium iodide in 60 ml. water was added. The resulting solution was allowed to stand for 24 hours, was filtered and diluted to 250 ml. with water.

Silicotungstic Acid Reagent. An aqueous solution of the acid, 0.1 N.

Sonnenschein's Reagent. A warm 4 N solution of disodium hydrogen phosphate was acidified with conc. nitric acid (pH 3). A slight excess of a saturated solution of ammonium

KEY TO ABBREVIATIONS IN TABLE I

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

BINOMIAL	The accepted botanical name. The authority is omitted to conserve space. An asterisk (*) indicates introduced species.
LOCAL NAME	The Hawaiian or vernacular name, if known.
LOCALITY	The nearest town or other prominent map feature.
DATE COLLECTED	Date of actual collection in the field.
DATE TESTED	Date of actual application of spot tests.
PLANT PART(S)	B—bark, Br—branchlet, F—fruit, Fl—flower, H—herb or whole plant, L—leaf, R—root or underground part, S—seed, St—stem, W—wood, I—immature, M—mature.
ALKALOID REAGENTS	M—Mayer's, P—Picric Acid (Hager's), I—Iodine (Wagner's), D—Dragendorff's, S—Sonnenschein's, T—Silicotungstic Acid.
PRECIPITATES	With hydrochloric acid (HCl) or Prollius extracts (organic solvents and ammonia), classified on a tr (trace), + (light), ++ (heavy) basis. A — indicates no precipitation and a ? indicates that the test was meaningless.

TABLE I
RESULTS OF SPOT TESTS FOR ALKALOIDS
(Plants are listed alphabetically within each taxon.)

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	
						HCl	Prollius
AMARANTHACEAE							
<i>Charpentiera obovata</i>	Papala	Kawaiiki trail, Oahu	23 Jul 57	14 Aug 57	Br, L, St	S+, D+, I+, M+, T+, P+	
<i>C. ovata</i>	Papala	Manoa Cliff trail, Oahu	6 Aug 57	19 Aug 57	L, St	S++, D++, I++, M++, T++, P++	S-, D-, I-, M-, T-, P-
ANACARDIACEAE							
<i>Schinus terebinthifolius</i> *	Wilelaiki, Christmas Berry	Tantalus, Oahu	21 Dec 56	1 Oct 57	B, Br, F	Str, D-, I-, M-, T+, P-	
APOCYNACEAE							
<i>Allamanda cathartica</i> var. <i>Hendersonii</i> *	Lani-ali'i, Allamanda	UH campus, Oahu	24 Feb 57	19 Mar 57	F, L, R, St	S-, D++, I++, M-, T-, P-	S++, D++, I++, M++, T++, P++
<i>Alyxia olivaeformis</i>	Maile	Koolau, Oahu	28 Oct 56	4 May 57	Br, F, L, St	S+, D++, I+, M++, T+, P++	S++, D++, I++, M++, T++, P++
<i>Ocrosia sandwicensis</i>	Holei	Laie trail, Oahu	— Oct 56	20 Mar 57	B, R	S++, D++, I++, M++, T++, P++	S++, D++, I++, M++, T++, P++
<i>O. sandwicensis</i>	Holei	Pupukea-Kahuku, Oahu	2 Oct 57	4 Oct 57	IF, MF	M+, T++, P+	S++, D++, I++, M++, T++, P++
<i>Rauwolfia Degeneri</i>	Hao	Mokuleia, Oahu	?	1 May 57	B	M++, T++, P++	M++, T++, P++
<i>R. mauensis</i>	Hao	Hana district, Maui	?	1 May 57	B	S+, D+, I+, M+, T+, P-	S+, D+, I+, M+, T+, P+
<i>R. sandwicensis</i>	Hao	Aiea trail, Oahu	?	1 May 57	B	S++, D++, I++, M++, T++, P++	S++, D++, I++, M++, T++, P++
AQUIFOLIACEAE							
<i>Ilex anomala</i>	Kawa'u	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+, D+, I+, M+, Ttr, P-	Str, D+, I+ M?, T+, P-
ARALIACEAE							
<i>Tetraphlasandra</i> sp.	Ohe	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+, D+, I+, M+, T++, P?	
BORAGINACEAE							
<i>Heliotropium anomalum</i>	Hinahina	Mokapu Point, Oahu	20 Jul 57	13 Aug 57	Br, L, Fl, R	Str, D-, Itr, M-, Ttr, Ptr	
CAPRIFOLIACEAE							
<i>Lonicera japonica</i>	Honekakala, Honeysuckle	Aiea trail, Koolau, Oahu	6 Jan 57	1 Oct 57	F, L, St	S+, D+, Itr, M-, T+, P-	

TABLE I—Continued

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	
						HCl	Prollius
CHENOPODIACEAE <i>Chenopodium oahuense</i> ...	'Aweoweo, 'Aheabea	Pohakea Pass, Oahu	26 Nov 56	4 May 57	Fl, L, St	S++ , D+++ , I++ , M+ , T+++ , P+	
COMPOSITAE <i>Artemisia australis</i>	'Ahinahina	Manoa Cliff trail, Oahu	6 Aug 57	19 Aug 57	Br, L	S+ , D- , I- , M- , T+ , P-	
<i>Dubautia plantaginea</i>	Na'ena'e	Pupukea, Oahu	28 Oct 56	4 May 57	F, L, St	S+++ , D+++ , I++ , M+ , T+++ , P+	
<i>Lipochaeta integrifolia</i> ...	Nehe	Mokapu Point, Oahu	20 Jul 57	11 Aug 57	Br, F, L	Str, Dtr, I- , M- , Tr, P-	
CONVOLVULACEAE <i>Ipomoea alba</i>		Manoa Cliff trail, Oahu	6 Aug 57	19 Aug 57	F, L, St	S+++ , D+++ , I+++ , M+++ , T+++ , P+	
<i>I. pes-caprae</i>	Pohuehue	Mokapu Point, Oahu	20 Jul 57	13 Aug 57	Fl, L, St	Str, Dtr, Itr, M- , T+ , P-	
<i>Jacquemontia sandwicensis</i>	Pa'u-o-Hi'i-aka, Kakua-o-Hi'i-aka	Barbers Point, Oahu	16 Dec 56	4 May 57	Br, Fl, L, St	S+ , D+ , I+ , M+ , T+ , P+	S+++ , D+++ , I+++ , M+ , T+++ , P+++
CYPERACEAE <i>Cladium Meyenii</i>	'Aha-niu	Aiea trail, Koolau, Oahu	6 Jan 57	30 Sep 57	F, Fl, L, R, St	S- , D- , I- , M- , T- , P-	
<i>Gabnia gabniaeformis</i> ..	Uki ?	Aiea trail, Oahu	6 Jan 57	4 May 57	L, R, St	S+ , D- , I- , M- , T+ , P-	S+ , D- , I- , Mtr, Tr, P-
DIOSCOREACEAE <i>Dioscorea bulbifera</i>	Hoi	Waiahole trail, Oahu	2 Mar 57	20 Mar 57	Aerial bulblet	S+++ , D+++ , I+++ , M+ , T+++ , P+	S+ , D+ , I+ , M- , Tr, P-
<i>D. bulbifera</i>	Hoi	Manoa Cliff trail, Oahu	6 Aug 57	19 Aug 57	L, R, St	S+++ , D+++ , Itr, M- , T+++ , P-	S- , D- , I- , M- , T- , P-
<i>D. pentapphylla</i>	Pi'a	Kawaiki ditch trail, Oahu	23 Jul 57	14 Aug 57	L, St	S+ , D+ , I+ , M- , T+ , P-	
EBENACEAE <i>Diospyros ferrea</i> var. <i>sandwicensis</i>	Lama	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	L, St	S- , D- , I- , M- , T- , P-	
<i>D. ferrea</i> var. <i>sandwicensis</i>	Lama	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+ , D- , I- , M- , T+++ , P-	

<i>D. Hillebrandii</i>	Lama	Kawaiki ditch trail, Oahu	23 Jul 57	23 Aug 57	Br, IF, L, St	Str, D-, I-, M-, T+, P-	S-, D-, I-, M-, T+, P-
EPACRIDACEAE							
<i>Syphelia Tameiameiae</i>	Pukiawe	Kawaiki ditch trail, Oahu	7 Oct 56	4 May 57	F, L, St	S-, D-, I-, M-, T-, P-	S-, D-, I-, M-, T+, P-
EUPHORBIACEAE							
<i>Aleurites moluccana</i>	Kukui, Candle-nut tree	UH campus, Oahu	24 Feb 57	19 Mar 57	F	S+, D+, I?, M+, T+, P+, Ptr	S-, D-, I-, M-, T-, P-
<i>A. moluccana</i>	Kukui, Candle-nut tree	UH campus, Oahu	24 Feb 57	19 Mar 57	B, Br, L, St	S-, D-, I+, M-, T-, P-	S+, D+, I+, M-, T+, P?
<i>Antidesma platyphyllum</i> .	Ha'a, Hame	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	Str, Dtr, Itr, M-, T+, P-	S-, D-, I-, M-, T-, P-
<i>A. pulvinatum</i>	Mehame, Hame	Kawaiki ditch trail, Oahu	23 Jul 57	14 Aug 57	L, St	S+, Dtr, I-, M-, T+, P-	
<i>Euphorbia celastroides</i>	'Akoko, Koko	Kawaiki ditch trail, Oahu	23 Jul 57	13 Aug 57	Br, Fl, L, St	S+, D+, Itr, Mtr, T+, P?	Str, Dtr, I+, M+, Ttr, Ptr
<i>E. clusiaeifolia</i>	'Akoko, Koko	Aiea trail, Oahu	6 Jan 57	1 May 57	F, L, St	S-, D-, I-, M-, T-, P-	
<i>E. Degeneri</i> var. <i>Degeneri</i>	'Akoko, Koko	Mokapu Point, Oahu	20 Jul 57	14 Aug 57	Fl, L, St	S-, D-, I-, M-, T-, P-	
<i>E. Hillebrandii</i> var. <i>waimanoana</i>	'Akoko, Koko	Kawaiki ditch trail, Oahu	7 Oct 56	10 Oct 57	Br, F	Str, D-, I-, M-, T+, P-	
GLEICHENIACEAE							
<i>Dicranopteris linearis</i>	Ulube, Unuhe	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	Fronds, R, Spores	S-, D-, I-, M-, T-, P-	S+, D+, I+, M+, T+, P+
GOODENIACEAE							
<i>Scaevola Gaudichaudiana</i>	Naupaka-kuahiwi	Aiea trail, Oahu	6 Jan 57	1 May 57	Fl, L, St	S+, D+, I+, M+, T+, P+	S+, D+, I+, M+, T+, P+
LABIATAE							
<i>Phyllostegia grandiflora</i> var. <i>grandiflora</i>	Kapana	Pohakea Pass, Oahu	26 Nov 56	4 May 57	F, L, St	S+, D+, I+, M-, T+, P-	Str, D+, I+, Mtr, T-, P-
LAURACEAE							
<i>Cassytha filiformis</i>	Kauna'oapehu	Pohakea Pass, Waianae, Oahu	26 Nov 56	1 Oct 57	L, St	S-, D-, I-, M-, T-, P-	S-, D+, I+, M-, T+, P-
LEGUMINOSAE							
<i>Acacia Koa</i>	Koa	Tantalus, Oahu	21 Dec 56	4 May 57	Br, F, L, St	S+, D+, I+, M+, T+, P+	S-, D+, I+, M-, T+, P-
<i>A. Koa</i>	Koa	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	B, R	S+, D+, I+, Mtr, T+, P-	
<i>Leucaena glauca</i> *	Koa-haole	UH campus, Oahu	4 Mar 57	20 Mar 57	Br, F, Fl, L, St	S+, D+, I+, M+, T+, P+	S+, D-, I-, M-, T-, P-

TABLE I—Continued

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	
						HCl	Prollius
LILIACEAE							
<i>Dianella sandwicensis</i>	'Uki'uki	Kawaiiki ditch trail, Oahu	23 Jul 57	11 Aug 57	F, L, R, St	Str, D-, Itr, Mtr, Ttr, Ptr	
<i>Smilax sandwicensis</i>	Hoi-kuahiwi	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	Str, Dtr, Itr, Mtr, Ttr, Ptr	Str, D+, Itr, Mtr, Ttr, Ptr
LOBELIACEAE							
<i>Clermontia Kakeana</i>	'Oha-wai, 'Oha	Manoa Cliff trail, Oahu	6 Aug 57	19 Aug 57	F, L, St	S+++, D+++ , I+++ , M+, T+++ , P+++	S+, Dtr, Itr, M-, Ttr, Ptr
<i>Gynera angustifolia</i>	'Oha-wai, 'Oha	Pupukea, Oahu	28 Oct 56	3 May 57	Br, F, Fl, L, St	S+++ , D+++ , I+++ , M+++ , T+++ , P+++	S+++ , D+++ , I+++ , M+++ , T+++ , P+++
LOGANIACEAE							
<i>Labordia tinifolia</i> var. <i>tinifolia</i>		Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	MF, L, St	Str, Dtr, Itr, M?, Ttr, P?	
LYCOPODIACEAE							
<i>Lycopodium cernuum</i>	Huluhulu-a-'iole	Aiea trail, Oahu	6 Jan 57	4 May 57	Br, L, St	Str, Dtr, Itr, M-, T+, P-	Str, Dtr, Itr, Mtr, T+, P-
<i>L. phyllanthum</i>	Wawae-'iole	Aiea trail, Oahu	6 Jan 57	1 Oct 57	L, Spores, St	S+++ , D+++ , I+, M+, T+++ , Ptr	
<i>Pilotum nudum</i>	Moa	Mokapu Point, Oahu	20 Jul 57	13 Aug 57	L, Spores, St	S+, D+, Itr, M-, T+, P-	
LYTHRACEAE							
<i>Cuphea carthagenensis</i> *	Tarweed	Kawaiiki ditch trail, Oahu	23 Jul 57	13 Aug 57	Fl, L, St	S+, D+, I+, Mtr, T+, P?	
MALVACEAE							
<i>Hibiscus Arnotianus</i>	Koki'o-ke'oke'o	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	L, St	S+, D-, I-, M-, T+, P-	
<i>Sida cordifolia</i> (Side fallax)	'Ilima	Mokapu Point, Oahu	20 Jul 57	14 Aug 57	Fl, L, St	Str, D-, I-, M-, Ttr, P-	
MYOPORACEAE							
<i>Myoporum sandwicense</i> var. <i>stellatum</i>	Naio, Bastard Sandalwood	Barbers Point, Oahu	16 Dec 56	1 May 57	Br, F, Fl, L, St	S+++ , D+++ , I+, M+, T+++ , P+++	S+++ , D+++ , I+++ , M+++ , T+++ , P+++

MYRSINACEAE <i>Myrsine Lesertiana</i>	Kolea	Kawaiiki ditch trail, Oahu	23 Jul 57	13 Aug 57	L, St	S+++ , D+++ , I+++ , M+++ , T+++ , P+++
MYRTACEAE <i>Eugenia Cumini</i> *	Java Plum	Waiahole trail, Oahu	2 Mar 57	22 Mar 57	B, L, St	S+ , D- , I+ , M- , T- , P-
<i>E. sandwicensis</i>	'Ohi'a-ha	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+ , D- , I- , M- , Ttr, P-
<i>Metrosideros collina</i> ssp. <i>polymorpha</i> , var. <i>glabrifolia</i>	'Ohi'a-lehua	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	Str, D+ , Itr, M- , T+ , Ptr
<i>M. macroopus</i>	'Ohi'a-lehua	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+++ , D+ , I+ , M- , T+++ , Ptr
<i>Puidium Cattelianum</i> *	Strawberry Guava, Waiawi-'ula 'ula	Kawaiiki ditch trail, Oahu	23 Jul 57	11 Aug 57	Br, F, L, St	Str, D- , Itr, M- , Ttr, P-
<i>P. Guajana</i> *	Guava, Kuawa	Waiahole trail, Oahu	2 Mar 57	19 Mar 57	IF, L, St	S- , D- , I- , M- , T- , P-
NYCTAGINACEAE <i>Boerhavia diffusa</i>	Alena	Mokapu Point, Oahu	20 Jul 57	13 Aug 57	F, L, St	S- , Dtr, Itr, M- , Ttr, P-
<i>Geodes umbellifera</i>		Kawaiiki ditch trail, Oahu	23 Jul 57	13 Aug 57	Br, L, St	S+++ , D+++ , I+++ , M+++ , T+++ , P+++
OLEACEAE <i>Osmanthus sandwicensis</i>	Olopuu	Aiea trail, Oahu	6 Jan 57	1 May 57	Br, F, L, St	S+ , D+ , I+ , M+ , T+ , P+
ORCHIDACEAE <i>Spathoglottis plicata</i> *	Philippine Ground Orchid	Kawaiiki ditch trail, Oahu	23 Jul 57	13 Aug 57	F, L, R, S	S+ , D+ , I+ , M- , T+ , Ptr
PALMACEAE <i>Pritchardia</i> sp.	Loulu	Summit, Castle trail, Oahu	— Jun 57	11 Aug 57	MS	S+ , D+ , I+ , Mtr, T+ , P?
PANDANACEAE <i>Freyinetia arborea</i>	'Ie'ie	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	L, St	S+ , D+ , I+ , M- , T+ , P-
<i>Pandanus odoratissimus</i>	Hala	Waiahole trail, Oahu	2 Mar 57	22 Mar 57	MF, L, R, St, Prop Roots	S- , D- , I- , M- , T- , P-
PASSIFLORACEAE <i>Passiflora edulis</i> *	Liliko'i, Passion Fruit	UH campus, Oahu	2 Mar 57	1 May 57	Br, L, St	S+++ , D+++ , I+++ , M+++ , T+++ , P+++
<i>P. edulis</i> cv. <i>flavicarpa</i> *	Yellow-fruited Liliko'i	Cultivated plant	— Jul 57	11 Aug 57	MF	S+++ , D+++ , I+++ , M+++ , T+++ , P+++
<i>P. suberosa</i> *	Huehue-haole	Tantalus, Oahu	21 Dec 56	1 Oct 57	F, L, St	S+ , Dtr, I- , M- , T+ , P-

TABLE I—Continued

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	
						HCl	Prollius
PIPERACEAE <i>Piper methysticum</i> *	'Awa	Waiahole trail, Oahu	2 Mar 57	22 Mar 57	L, R, St	S+, D+, I?, M+, T+, Ptr	S+, D+, I+, M+, T+, P+
PITTIOSPORACEAE <i>Pitiosporum glabrum</i> var. <i>glabrum</i>	Ho'awa	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	IF, MF, L, St	S+, D+, Itr, M-, T+, P-	S+, D+, Itr, M-, T+, P-
<i>P. sulcatum</i> var. <i>sulcatum</i>	Ho'awa	Aiea trail, Oahu	6 Jan 57	10 Oct 57	F, L, St	Str, Dtr, Itr, M-, T+, P-	Str, Dtr, Itr, M-, T+, P-
PLUMBAGINACEAE <i>Plumbago zeylanica</i>	'Ilie'e	Pohakea Pass, Waianae, Oahu	26 Nov 56	30 Sep 57	F, Fl, L, St	S-, D-, I-, M-, T-, P-	S-, D-, I-, M-, T-, P-
POLYPODIACEAE <i>Microlepia setosa</i>	Palapalai, Palai	Pohakea Pass, Oahu	26 Nov 56	4 May 57	R, Str, Fronds	S+, D+, I-, M-, T+, P-	S-, D-, I+, I+, M-, T-, P-
<i>Sadleria cyatheoides</i>	'Ama'u	Aiea trail, Oahu	6 Jan 57	4 May 57	R, Str, Fronds	S-, D-, I-, M-, T-, P-	S-, D-, I-, M-, T-, P-
<i>Sphenomeris chinensis</i>	Pala'a	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	Fronds, R, Spores	Str, D-, I-, M-, Itr, P-	Str, D-, I-, M-, T-, P-
RUBIACEAE <i>Bobea elatior</i>	'Ahakea	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+, D+, Itr, M-, T+, P-	S+, D+, I+, M+, T+, Ptr
<i>Cantium odoratum</i>	Walabe'e, alah'e	Aiea trail, Oahu	6 Jan 57	4 May 57	F, L, St	S+, D+, I-, M+, T+, P+	S+, D+, I+, M+, T+, P+
<i>Coprosma foliosa</i>	Pilo	Manoa Cliff trail, Oahu	6 Aug 57	19 Aug 57	L, St	S+, D+, I+, M-, T+, P?	S+, D+, I+, M-, T+, P+
<i>Gouardia terminalis</i>	Manono	Manoa Cliff trail, Oahu	6 Aug 57	21 Aug 57	MF, Fl, L, St	Str, Dtr, I-, M-, T+, P-	Str, Dtr, I-, M-, T+, P-
<i>Morinda citrifolia</i> *	Noni	Waiahole trail, Oahu	22 Feb 57	20 Mar 57	L, St	S+, D+, I+, M+, T+, P+	S+, D-, I-, M-, T+, P-
<i>Psychotria bexandra</i> var. <i>Rockii</i>			?	4 May 57	L, St	S+, Dtr, I-, M-, T+, P-	S+, Dtr, I-, M-, T+, P-
<i>Straussia kahuana</i>	Kopiko-kea	Pupukea- Kahuku, Oahu	2 Oct 57	4 Oct 57	F, L, R, St	S+, D+, I+, M+, T+, P+	S+, D+, I+, M+, T+, P+
<i>S. Mariniana</i>	Kopiko	Kawaiiki ditch trail, Oahu	23 Jul 57	14 Aug 57	Br, Fl, L, St	S-, D-, I-, M-, T-, P-	S-, D-, I-, M-, T-, P-

TABLE 2
SPECIES SHOWING POSITIVE TESTS WITH THE SIX REAGENTS

BINOMIAL	FAMILY	PLANT PART(S) TESTED
<i>Acacia Koa</i>	Leguminosae	Branchlet, Fruit
<i>Allamanda cathartica</i> var. <i>Hendersonii</i> *	Apocynaceae	Fruit, Leaves, Root, Stem
<i>Alyxia olivaeformis</i>	Apocynaceae	Branchlet, Fruit
<i>Canthium odoratum</i>	Rubiaceae	Fruit, Leaves, Stem
<i>Ceodes umbellifera</i>	Nyctaginaceae	Branchlet
<i>Charpentiera obovata</i>	Amaranthaceae	Branchlet
<i>C. ovata</i>	Amaranthaceae	Leaves, Stem
<i>Chenopodium oahuense</i>	Chenopodiaceae	Flowers, Leaves, Stem
<i>Clermontia Kakeana</i>	Lobeliaceae	Fruit, Leaves, Stem
<i>Cyanea angustifolia</i>	Lobeliaceae	Branchlet, Fruit, Flowers
<i>Dioscorea bulbifera</i>	Dioscoreaceae	Aerial bulblets
<i>Dubautia plantaginea</i>	Compositae	Fruit, Leaves, Stem
<i>Ipomoea alba</i>	Convolvulaceae	Fruit, Leaves, Stem
<i>Jacquemontia sandwicensis</i>	Convolvulaceae	Branchlet, Flowers
<i>Morinda citrifolia</i> *	Rubiaceae	Leaves, Stem
<i>Myoporum sandwicense</i> var. <i>stellatum</i>	Myoporaceae	Branchlet, Fruit, Flowers
<i>Myrsine Lessertiana</i>	Myrsinaceae	Leaves, Stem
<i>Ochrosia sandwicensis</i>	Apocynaceae	Bark, Root, Fruit
<i>Osmanthus sandwicensis</i>	Oleaceae	Branchlet, Fruit
<i>Passiflora edulis</i> *	Passifloraceae	Branchlet, Mature fruit
<i>Pelea Wawraeana</i> var. <i>tenuifolia</i>	Rutaceae	Leaves, Stem
<i>Piper methypticum</i> *	Piperaceae	Leaves, Root, Stem
<i>Planchonella (Sideroxylon) sandwicensis</i>	Sapotaceae	Flowers, Leaves, Stem, Root
<i>Rauvolfia Degeneri</i>	Apocynaceae	Bark
<i>R. maiensis</i>	Apocynaceae	Bark
<i>R. sandwicensis</i>	Apocynaceae	Bark
<i>Scaevola Gaudichaudiana</i>	Goodeniaceae	Flowers, Leaves, Stem
<i>Straussia kaduana</i>	Rubiaceae	Fruit, Leaves, Root, Stem
<i>Tacca Leontopetaloides</i> *	Taccaceae	Tuber
<i>Touchardia latifolia</i>	Urticaceae	Branchlet, Fruit

An asterisk (*) after the name denotes an introduced species.

molybdate was added. The resulting yellow precipitate was filtered, washed with water, acidified with conc. nitric acid, and dissolved in a hot 2 N solution of sodium carbonate. The solution was evaporated to dryness and ignited at dull red heat until all the ammonium salts had volatilized. The residue was moistened with conc. nitric acid and again ignited. The product, sodium phosphomolybdate, was dissolved in ten times its weight of a mixture of one volume of conc. nitric acid and nine volumes of water.

TESTING PROCEDURE. Approximately 0.2 ml. of the plant extract was treated with ca. 0.1 ml. of the reagent on a watch glass. The precipitates (if any) usually formed immediately and the results were evaluated after ten

minutes' standing. The precipitates were graded visually and estimated as trace, light, or heavy.

RESULTS AND DISCUSSION

Table 1 lists the results of the alkaloid tests which were carried out on 96 plant species, representing 77 genera and 49 families.

None of the test reagents was specific for alkaloids when used alone. However, when a species gave positive reactions with all six reagents, the presence of alkaloids was strongly suggested. Conversely, those plants giving consistently negative tests almost certainly did not contain alkaloids.

Included in the above table are species of nine genera which have never been tested for

alkaloids before. They are: *Charpentiera*, *Clermontia*, *Cyanea*, *Dubautia*, *Jacquemontia*, *Pelea*, *Straussia*, *Tacca*, and *Touchardia*. Those endemic to the Hawaiian Islands are: *Clermontia*, *Cyanea*, *Dubautia*, *Straussia*, and *Touchardia*. Pioneering work in these genera should afford fruitful rewards for workers interested in alkaloids.

SUMMARY

Preliminary investigations concerning the presence of alkaloids in 96 species of Hawaiian plants, representing 77 genera and 49 families, indicated that 30 species contained alkaloids. Thirty-two species gave negative tests while the remainder were listed as doubtful.

The testing procedure consisted of extracting various plant parts with hydrochloric acid and testing the extract separately with six test reagents. The acid extraction was supplemented in some cases by an ammonia-mixed organic solvent solution. The precipitates were graded visually on a trace, light, or heavy basis. Only those species which gave a light and/or heavy precipitate with all six test reagents were classified as containing alkaloids.

Among the 30 species which gave positive tests for alkaloids, 9 genera were represented for which no previous alkaloid information exists. These 9 genera, 5 of which are endemic to the Hawaiian Islands, should afford fruitful sources for future studies for alkaloids.

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News Note

EXECUTIVE COMMITTEE, 10th PACIFIC SCIENCE CONGRESS

The National Academy of Sciences-National Research Council and the Bishop Museum, at whose invitation the 10th Pacific Science Congress of the Pacific Science Association will meet in Hawaii in August-September 1961, have appointed the following to be members of the Executive Committee of the Congress:

President of the Congress: Dr. Laurence H.

Snyder, President of the University of Hawaii, Honolulu, Hawaii

Secretary-General: Harold J. Coolidge, Executive Director of the Pacific Science Board, N.A.S.-N.R.C., Washington, D.C.

Members

From the U. S. mainland

Knowles A. Ryerson, National Academy of Sciences representative on the Council of the Pacific Science Association and Dean of the College of Agriculture, University of California, Berkeley, California

Dr. G. P. Murdock, Professor of Anthropology, Yale University, New Haven, Connecticut

Dr. Harry Wexler, Director, Office of Scientific Services, U. S. Weather Bureau, Washington, D.C.

From Hawaii

Dr. Cyril E. Pemberton, Bishop Museum representative on the Council of the Pacific Science Association and Entomologist Emeritus of the Experiment Station of the Hawaiian Sugar Planters' Association, Honolulu, Hawaii

Dr. Robert W. Hiatt, Dean of the Graduate School and Director of Research, University of Hawaii, Honolulu, Hawaii

Dr. Alexander Spoehr, Director, Bernice P. Bishop Museum, Honolulu, Hawaii

The Executive Committee has overall responsibility for the organization and operation of the Congress. A preliminary schematic organization of the Congress program has been drawn up and President Snyder is appointing organizers for the program sections. The scientists selected to organize the program will be getting in touch with Standing Committees and with other scientists in the participating countries.

At the request of the Secretary-General all Congress enquiries should be addressed to him as follows:

Secretary-General

10th Pacific Science Congress

Bishop Museum, Honolulu 17, Hawaii

CHAIRMEN, STANDING COMMITTEES OF THE PACIFIC SCIENCE ASSOCIATION

The President of the Ninth Pacific Science Congress, Air Marshal Muni M. Vejjant-Rangstrisht, has now received confirmation of his appointments of Standing Committee Chairmen. The list of Chairmen is presented herewith:

Animal Improvement

Professor T. J. Robinson, Department of Animal Husbandry, The University of Sydney, Sydney, N.S.W., Australia

Anthropology and Social Sciences

Dr. Bernard P. Groslier, 4, rue Toricelli, Paris 17e, France

Botany

Dr. F. R. Fosberg, Pacific Vegetation Project, c/o National Research Council, 2101 Con-

stitution Avenue, Washington 25, D.C.,
U.S.A.

Chemistry in the Development of Natural Resources

Dean Tab Nilanidhi, Faculty of Science,
Chulalongkorn University, Bangkok,
Thailand

Conservation

Dr. Ian McTaggart Cowan, Department of
Zoology, University of British Columbia,
Vancouver 8, Canada

Crops and Crop Improvement

Dr. Iso Reksohadiprodjo, Djalan Widoro, 3,
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culture, Stock and Fisheries, Port Moresby,
Papua and New Guinea

Forestry

L. W. Bryan, Board of Agriculture and For-
estry, P.O. Box 1761, Hilo, Hawaii

Freshwater Sciences

Dr. Katsuzo Kuronuma, Chief, Freshwater
Fisheries Research Laboratory, Fisheries
Agency, Hino-Machi, Minamitama-Gun,
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Geography

Professor L. Dudley Stamp, c/o Mrs. A. N.
Clark, The Keep, Berkhamsted, Herts.,
England

Geology and Geophysics

Professor Gordon A. Macdonald, Institute of

Geophysics, University of Hawaii, Hono-
lulu 14, Hawaii

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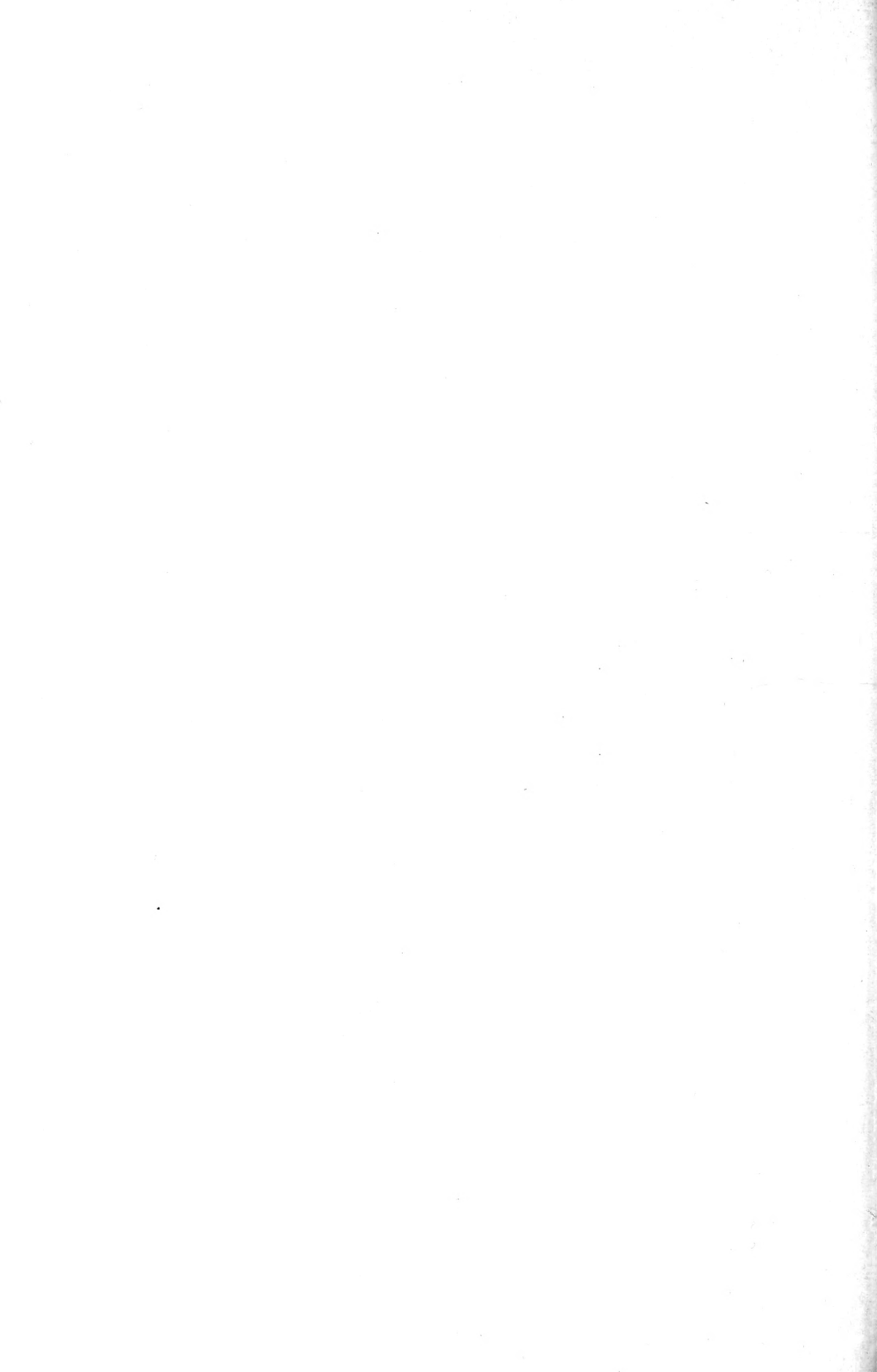
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A QUARTERLY DEVOTED TO THE BIOLOGICAL
AND PHYSICAL SCIENCES OF THE PACIFIC REGION



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Initial Discoveries of Fish Faunas on Seamounts and Offshore Banks in the Eastern Pacific¹

CARL L. HUBBS²

THE RECENT DISCOVERY in the Pacific Ocean of numerous submerged mountains (Hess, 1946; Menard and Dietz, 1951; Menard, 1955, and in press), including "banks" (rising to a depth of less than 100 fathoms) as well as the flat-topped "guyots" and other "seamounts" (with minimum depths greater than 100 fathoms), has posed intriguing questions regarding their faunas. Some of these questions are:

What species inhabit the individual banks and seamounts, and in what regularity and abundance?

How did these species become dispersed to and established on these structures?

What bearing may the determined constitution of these isolated faunas have on our ideas concerning past and present oceanic circulation and temperatures?

Do the banks and seamounts (as well as the islands) provide stepping stones for the transgression of narrow to broad oceanic areas, even the supposedly vast eastern Pacific barrier that separates the Indo-Pacific and American faunas (Ekman, 1953: 21, 72, 292)?

May some elements in the faunas of the deeper seamounts be relicts that have become adapted to increasing depths as the seamounts have subsided (or become flooded)? If so, the faunistic evidence may have some bearing on the historical interpretation of the seamounts.

To what degree has isolation on the banks and seamounts led to speciation?

Are either demersal or pelagic fishes (or other animals) sufficiently abundant and

available on or over these isolated rises to yield profitable fisheries?

What factors, physico-chemical or biotic, are responsible for the abundance of life on and over these rises? The first thought that comes to mind is that the elevations in the bottom contour induce disturbances in the deep currents, which no doubt have greater velocities than they were long thought to have, and that such disturbances induce upwelling and the enrichment of the upper waters.

Systematic explorations of the faunas on the isolated banks and seamounts (and oceanic islands) should yield rich returns, both scientifically and commercially. As yet only fragmentary information has been accumulated. Some such fragments of data, recently acquired, concerning the fish faunas on seamounts and banks from the Gulf of Alaska to far-off Chile, are presented here.

Embassichthys bathybius (Gilbert) on Pratt Seamount

On August 22, 1951, an adult "deepsea sole" 242 mm. in standard length surprisingly was caught in a rock dredge being hauled at a depth of 510 fathoms on the side slope of Pratt Seamount in the Gulf of Alaska, at Lat. 56° 20' N., Long. 142° 30' W., about 210 nautical miles offshore. It was obtained by Henry W. Menard and John D. Isaacs on the research ship "Horizon," on the Northern Holiday Expedition of the Scripps Institution of Oceanography (Dredge No. 5; Collection SIO 53-187).

This record constitutes a notable northward as well as seaward extension of the range of this deep-water pleuronectid. Long known

¹ Contributions from the Scripps Institution of Oceanography. Manuscript received April 10, 1958.

² University of California, La Jolla.

only from off southern California, recently it has been reported from off northern California (Hagerman, 1950) and from off Washington (Welander and Alverson, 1954: 42-43).

Unpublished records show that this commercially utilizable fish is not uncommon in deep waters off northern California and Washington. It is becoming of minor importance in the trawl fishery, as operations are being extended into deeper water. Its occurrence on at least one seamount suggests the possibility that the trawling grounds may eventually be extended far seaward, where depths are appropriate.

I have underway a distributional and variational study of this poorly-known flounder.

Sebastes ruberrimus Cramer and Other Fishes on Cobb Seamount

A rockfish caught on Cobb Seamount, about 280 nautical miles off Washington and about 240 miles southwest of Vancouver Island, at Lat. 46° 44' N., Long. 130° 47' W., was described by Welander and Alverson (1954: 37-40, figs. 1, 2) as representing a new species, *Sebastes bilineatus*. By examining this specimen (No. 10099, University of Washington Fish Collection) in detail on June 11, 1956, I verified the belief of Julius B. Phillips, W. I. Follett, and myself that it is a specimen of the large *S. ruberrimus*, in the striped, juvenile stage. The contrast between the dark ground color and the light stripes is unusually bold, but since color intensity varies so greatly in fishes and since all other characters observed fall within the observed range of variation of *S. ruberrimus*, it seems doubtful that the species is modified on Cobb Seamount. Slight differentiation, however, is a remote possibility. Data on the type of *S. bilineatus* will be included in a forthcoming contribution by Hubbs and Follett.

Thompson (1915: 121) observed that *S. ruberrimus* is "the most abundant of all species of the genus on the halibut banks," but in the same paper described what is now

thought to be a specimen of this species as *S. babcocki*, new species.

Welander and Alverson mentioned that the type of *S. bilineatus* was one of 30 fish specimens "caught by personnel of the U. W. oceanography vessel Brown Bear in the vicinity of Cobb Seamount on August 7, 1953." It is to be hoped that complete lists of species taken on or about each seamount will be published.

Perhaps fisheries may develop on the seamounts for rockfishes (*Sebastes* spp.), as well as for the halibut, *Hippoglossus stenolepis* Schmidt, and other flatfishes.

SHORE AND PELAGIC FISHES ON BANKS AND SEAMOUNTS OFF CENTRAL CALIFORNIA

A number of coastal and pelagic fishes of expectable species were recorded by Follett (1952) from several banks and seamounts off the central California coast, at no very great distance offshore. This is not to mean, however, that high interest and potential importance is not to be attached to such inshore rises.

TUNAS AND TUNA FORAGE FISHES FROM "STRANGER BANK" ("HURRICANE BANK")

In 1957, on an expedition from Scripps Institution of Oceanography, on the research ship "Stranger," Adrian F. Richards discovered, at Lat. 16° 52' N., Long. 117° 30' W., roughly 200 nautical miles southwest of Clarion Island, a shallow bank rising from oceanic depths to a depth of approximately 15 fathoms. This bank was assigned the tentative name Stranger Bank by the discoverer. Tuna fishermen of San Diego, who dub the structure "Hurricane Bank," from the heavy weather often encountered there, promptly began fishing there and in less than a year had taken from the newly found fishing ground well over 1,000 tons of yellowfin tuna, *Neothunnus macropterus* (Temminck and Schlegel), and smaller quantities of skipjack tuna, *Katsuwonus pelamis* (Linnaeus). At the time of writ-

ing it is evident that within the first full year the catch will definitely exceed 2,000 tons, with a value to the fishermen of more than one-half million dollars; and the relative proximity of the ground represents a great saving in expenses. Tuna fishermen have reported taking some rainbow runners, *Elegatis bipinnulatus* (Quoy and Gaimard), from this same bank.

During the Island Current Survey of May–June, 1958, personnel of the Inter-American Tropical Tuna Commission caught about the bank a number of young yellowfin tuna. On June 1 an adult male of the labrid *Bodianus diplotaenius* (Gill) was caught on the shoalest part of the bank (it was identified from a kodachrome). Many sharks, including some hammerheads, *Sphyrna* sp., were seen, to confirm the reports that sharks abound here. On June 5 one wahoo, *Acanthocybium solandri* Cuvier, was caught, and several mantas, presumably *Manta hamiltoni* (Newman), were seen.

Further information on other fishes that live over and about this bank comes from an initial examination of stomach contents of yellowfin tuna, collected there for the Inter-American Tropical Tuna Commission and now being analyzed by the staff of the Commission. Young to half-grown specimens of the spiny trunkfish, *Lactoria diaphana* (Bloch and Schneider), constitute a notably high proportion of the food. Some stomachs are filled with this bony creature, which elsewhere has been found to be eaten by this tuna. This trunkfish ranges very widely through tropical regions, and even, on occasions, as far northward as California. A sample (SIO 58-56) from the stomach of a tuna caught on this bank comprises 487 specimens of this trunkfish, 13 to 44 mm. in standard length. Another lot (SIO 58-57) comprises 7 specimens, of similar size. One tuna contained a large young triggerfish (SIO 58-54) of the common, wide-ranging, more or less pelagic species *Xanthichthys lineopunctatus* (Hollard); its standard length is 52 mm. Remains

of flying fish of undetermined species also occur in the tuna stomachs.

A thorough study of the fish fauna of Stranger Bank is much to be desired, especially in view of the thorough analysis of the Revillagigedo fish fauna being conducted by Boyd W. Walker and associates.

For information and material on the fishes and fisheries of this bank I am indebted to Bell M. Shimada and Franklin G. Alverson of the Inter-American Tropical Tuna Commission and to Wilbert M. Chapman of the American Tunaboat Association.

Pterygotrigla picta (Günther) on a Guyot far off Chile

On January 26, 1958, a triglid fish (gurnard or sea robin) of considerable zoogeographical interest was captured incidentally in a rock dredge being hauled at a depth of 129 fathoms on a guyot rising from an extensive ridge in the southeastern Pacific. It was preserved by Robert H. Parker on the research ship "Spencer F. Baird" of Scripps Institution of Oceanography, on the I. G. Y. Downwind Expedition (Station 73; SIO 58-42). This unnamed guyot is at Lat. 25° 44' S., Long. 85° 25' W., which is about 800 miles off the Chilean coast, about 300 miles westerly from Isla San Felix, and nearly 600 miles northwest of Isla Juan Fernández. It is in a region where seamounts appear to be numerous, and is on a submarine ridge that seems to extend westward at least to Easter Island (Fisher, 1958: 20–25, figs. 1, 8, 9).

Although the specimen is young (54 mm. in standard length) and was badly crushed posteriorly in the rock dredge, it seems identifiable as *Pterygotrigla picta* (Günther). This species was originally very briefly described, but magnificently figured, by Günther (1880: 24–25, pl. 13, fig. A), as *Trigla picta*, on the basis of a 10.5-inch specimen collected by the "Challenger" on Isla Juan Fernández, far off the coast of Chile. The species has been reported also from New Zealand and Australia (McCulloch, 1929: 393), but not from the

American mainland. This distributional pattern seems to be related to the bottom topography within the south temperate zone of the Pacific: there is a very deep trench off the Chilean coast, but from the vicinity of islas Juan Fernández and San Felix westward numerous submarine ridges and peaks rise to various heights below and above sea level. It may be predicted that the species will be found not only on the guyot nearly 600 miles northwest of Juan Fernández, but also on other rises between the offshore islands of Chile and New Zealand. It is not known whether seamounts intervene between Juan Fernández and San Felix, and it is now doubted that the long charted intervening ridge exists.

This young specimen differs in a number of respects from the characters indicated in the original description and figure of *Trigla picta*, but these differences seem attributable to age and individual variation. The dorsal spines number VIII instead of VII, but the eighth is short and very slender (and is perhaps concealed in the type); the number of dorsal soft rays (12) agrees. The anal rays are 11, not 12, but some variation is expected. (The principal caudal rays number $6 + 5 = 11$, and each pectoral has 15 rays, in the formula $i, 9, ii + 3$.) The nuchal spine is much longer, reaching to below the base of the third dorsal spine (probably as a function of youth), and is about as long as the humeral spine. (The pectoral fin, as in the type, reaches to about the seventh anal ray.) The preopercular spine (at the end of the cheek ridges) is double, rather than single, but the lower point is definitely the smaller, and it probably becomes obsolete in larger fish. The body is similarly marked with light-ringed blackish spots, but these spots (as expected) are fewer. On the head the spots are discernible, though faint, as though just developing. The fins, unlike those on the type, are unspotted: in the spinous dorsal the membranes are sooty outward; the second dorsal has a submarginal dark band; the pectoral is very dark, except

for a light border; the other fins are almost wholly clear. In coloration the young specimen corresponds better with the figure given by Mann (1954: 309) for the "pez mariposa de Juan Fernández," which he designated *Chelidonichthys pictus*.

Trigla picta has been referred, properly I think, to the genus *Pterygotrigla* Waite (1899: 108), which was based on the Australian species *Trigla polyommata* Richardson. Although quite different in coloration, *P. picta* and *P. polyommata* seem very similar in structure.

The genus *Pterygotrigla* has been attributed to Japan (Matsubara and Hiyama, 1932: 8-14, figs. 2-5), but the Japanese species referred to the genus differ trenchantly from *P. picta* and *P. polyommata* in lacking vomerine teeth. They are also said to have a "distinct anal spine" (a hardened soft-ray?), which does not seem to be true of the Southern Hemisphere species. Though the two groups agree in many characters it seems advisable to put them in separate genera. The name *Otobime* Jordan and Starks (1907) is available for the common Japanese species *hemisticta* (the type species), and probably for *Pterygotrigla ryukyuensis* Matsubara and Hiyama.

Otobime differs further from *Pterygotrigla* in the small size of the dorsal bucklers. The distinction in the first anal ray may not be valid, for a young specimen of *Otobime hemisticta* has this ray paired, articulated, and flexible.

It seems clear from the original account that *Trigla guttata*, which was described without comparisons by Philippi (1896: 375-376) from Juan Fernández, is a synonym of *Pterygotrigla picta* (Günther)—as was assumed by McCulloch (1929: 393). But the gurnard from Islas Juan Fernández that was figured and discussed by Mann (1954: 309) as *Trigla punctata* Philippi obviously belongs in a very different species. From the figure it seems clearly referable to *Chelidonichthys*, as defined by Matsubara and Hiyama (1932: 4). It even seems probable that the specimen may be referred to *C. kumu* (Lesson and Garnot), an

important species that is accorded a range from New Zealand and Australia to Japan (see Matsubara and Hiyama, 1932: 5-7, fig. 1). Like *Pterygotrigla*, *Chelidonichthys* is unknown in Chile. Its occurrence on Juan Fernández parallels that of *Pterygotrigla picta*, and it may be predicted that *Chelidonichthys* will be found on seamounts, banks, or islands between Juan Fernández and New Zealand.

Both *Pterygotrigla* and *Chelidonichthys* belong to a distributional category that may be classified as antitropical Indo-Pacific, and contrast sharply with the American triglids (*Prionotus* and the derived *Bellator*). Comparison of a specimen of *P. picta* from Isla Juan Fernández (an adult 340 mm. in standard length collected by the Mellon Expedition in Bahía Cumberland on February 28, 1936) with specimens of *Chelidonichthys kumu* from Japan discloses many differences. The row of keeled scales along the entire dorsal base is replaced by greatly enlarged flat bucklers along the base of the spinous dorsal only. *P. picta* differs further from *C. kumu* in a feature of the lateral line, which ends simply, immediately beyond the caudal base, instead of being forked and continued as two or three lines across the caudal fin. The head is much larger, and the body is much more contracted at the base of the caudal fin, which is sharply forked rather than merely emarginate. The orbital rim is spineless, but the opercular, nuchal, and humeral spines are greatly enlarged. The nape, in advance of the greatly enlarged buckler surrounding the first dorsal spine, is scaleless rather than scaly. The teeth are almost shagreenlike; those of the lower jaw are deflected outward over the anterior edge of the lower lip. The vomerine teeth are in an oval rather than a broadly V-shaped patch. Most of these differences show in the figures reproduced by McCulloch (1922: 119, pl. 39).

NEED FOR FURTHER STUDIES

These brief notes tend to show that great scientific as well as commercial importance

may be attached to a study of the faunas of the many banks and seamounts that rise toward the surface from the depths of the Pacific Ocean. Many and perhaps most of these structures seem capped and surrounded by productive water. The spectacular take of tuna on the Stranger, or Hurricane, Bank has been mentioned. Milner B. Schaefer, director of research for the Inter-American Tropical Tuna Commission, has assured me that good catches have been made about other banks and even about seamounts that nowhere closely approach the surface. Henry W. Menard of the Institute of Marine Resources, University of California, leading student of seamounts, tells me that he has obtained strong field indications, from echograms, that large objects (presumably fish or giant squid) form a halo around and far above many seamounts between California and Hawaii. It seems highly probable, as is stated in the introduction, that the submarine mountains, even those that are isolated and deep, disturb the currents sufficiently to induce extensive upwelling.

The benthic faunas of the banks and seamounts do not give promise of such commercial potential, but may prove of greater scientific interest, particularly in respect to zoogeography and speciation.

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Ecology and Distribution of Some Pelagic Hyperiidea (Crustacea, Amphipoda) from New Zealand Waters

B. M. BARY¹

THE MARINE pelagic Amphipoda recorded from New Zealand have been discussed systematically (Stephensen, 1927; Barnard, 1930, 1932; Hurley, 1955), but few data are available on their distribution and ecology. The situation in Australia (Barnard, 1931; Dakin and Colefax, 1933, 1940) and South Africa (Stebbing, 1910; Barnard, 1916, 1925, 1940) is similar. However, in antarctic latitudes some features of the ecology of amphipods have been fairly extensively treated (Mackintosh, 1934, 1937; Hardy and Gunther, 1935).

The data presented herein are of collections made from the survey-frigate H.M.N.Z.S. "Lachlan," in southern New Zealand waters, during the summer of 1951. The hyperiids from these collections have been identified by D. E. Hurley, who generously undertook this taxonomic study (Hurley, 1955).

Fourteen species were present in the collections. Seven of these were new records for New Zealand. Five species, namely, *Paratthemisto* (*Euthemisto*) *gaudichaudii* (Guer.), *P. australis* (Stebbing), *P. gracilipes* (Norman), *Cylopus magellanicus* Dana, and *C. macropis* Bovallius, were present in sufficient numbers to permit discussing some features of their ecology, especially their relationships to the water masses in the area about southern New Zealand. The remaining nine species were of rare occurrence, although their biological

and environmental associations provoke discussion.

ACKNOWLEDGMENTS

The writer gratefully acknowledges Dr. D. E. Hurley's identification of the amphipod material, useful discussions of data, and reading of typescripts and proofs.

MATERIAL AND METHODS

Details of the areas from which collections were made, the gear and the methods, are discussed elsewhere (Bary, 1956, 1959). The areas sampled extended between Wellington and Dunedin (one cruise in January, a second in March, 1951), between Dunedin and Foveaux Strait (during January through March), and between Wellington and Auckland and Campbell islands, about 400 miles south of New Zealand (one cruise, November, 1951). (See Figs. 5, 6.) Procedure and gear were standardized: tows were of 3 minutes at 1½ to 2 knots, within the surface metre of water, using a net of graded silks, 50 cm. in diameter. Of the 80 samples, those of Stations 74-85 were collected whilst the ship was at anchor overnight in a tidal stream in western Foveaux Strait (Bary, 1956). Although the temperature was taken at each of these, salinity was determined only for Station 79. Therefore, only this station is shown in the various figures. All of the rare species collected at Stations 74-85 are shown as being captured at Station 79 in Figures 2, 5a. Of the common species, only those captured at Station 79 are illus-

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trated. All samples have been quantitatively analysed.

The method of the temperature-salinity-plankton (T-S-P) diagram (Bary, 1959) is used here to elucidate the distributions of species. Occurrences of species are plotted in the intercepts of the temperatures and salinities of the stations at which they were captured. Species are thus related to the hydrological conditions as indicated by these properties. The water-envelope (Figs. 1-4) surrounds the intercepts of all the temperatures and salinities of the surface waters in the sampled areas, but Figure 1 shows only those for plankton stations. The hydrology of the area and the relationships of these waters are illustrated and discussed by Bary (1959).

T-S-P diagrams of the five commonly occurring amphipods are shown in Figures 3 and 4. The geographical distributions of these species in relation to temperatures (Figs. 5, 6) are discussed and interpreted in the light of information derived from the T-S-P diagrams. The stations have been subdivided into several series, and each of these is as near as possible a synoptic series and a geographic unit. The geographical distribution of the subantarctic species and the coastal-subtropical species are charted for each series. Rare species are charted according to the water properties with which they are associated in the T-S-P diagram (Fig. 2). Thus, *Vibilia stebbingi* (?), at Station 210, is shown to be in water of subantarctic origin in the T-S-P diagram; therefore, the appropriate geographical chart is that which concerns other subantarctic species (Fig. 5g). As well, the rare species are listed in Table 1 and appreciations are made of their distributions as recorded by other investigators, and as indicated by the relationships exhibited in the T-S-P diagrams. In the charts they are shown together at Station 79 among the subtropical species.

DISTRIBUTION

Indicator groups of species were selected previously (Bary, 1959) for coastal water (one

group), for water originating in the subtropical region (one group), and for the subantarctic region (two groups, a Southern Group for cold water, and a Northern Group for that cold water which has undergone a temperature increase in its progress northward). The cohesion of each of these groups in the T-S-P diagrams can only be interpreted as being due to a correlation between the distribution of the individual species composing the group and the properties of the water body which they inhabit and of which they are indicators. The area of chief concentration of each indicator group of species is shown in Figure 2 by lining-in; there are, however, no species of the Northern Group among the Amphipoda. The stippled arrows indicate the routes (within the diagram) along which oceanic species are believed to be penetrating towards coastal waters. These routes closely coincide with the direction of water movements as deduced from the corresponding T-S diagram of the surface waters (Fig. 1).

The cold-water Amphipoda are represented solely by species of the Southern Subantarctic Group (Fig. 3). Large numbers of *Parathemisto* (*Euthemisto*) *gaudichaudii* were captured; there were fewer specimens of *Cylopus magellanicus*, and *C. macropis* was rare. Both the numbers of these oceanic species, and the frequency of their occurrences decreased in coastal waters, probably as a result of their being transferred into relatively adverse conditions. However, the greater number of the stations in coastal waters were occupied in daylight (Fig. 1) which may contribute towards the taking of fewer specimens (this feature is discussed by Bary, 1959).

The occurrences of two Coastal species, *Parathemisto gracilipes* and *P. australis*, and of the subtropical species, *Hyperoche mediterranea* Senna, are shown in Figure 4. *Hyperoche mediterranea* is restricted to a narrow range of temperature in the warmest waters (except for Station 100) whilst *P. gracilipes* and *P. australis* occur commonly over much the same salinities, but over a wider range of temperatures.

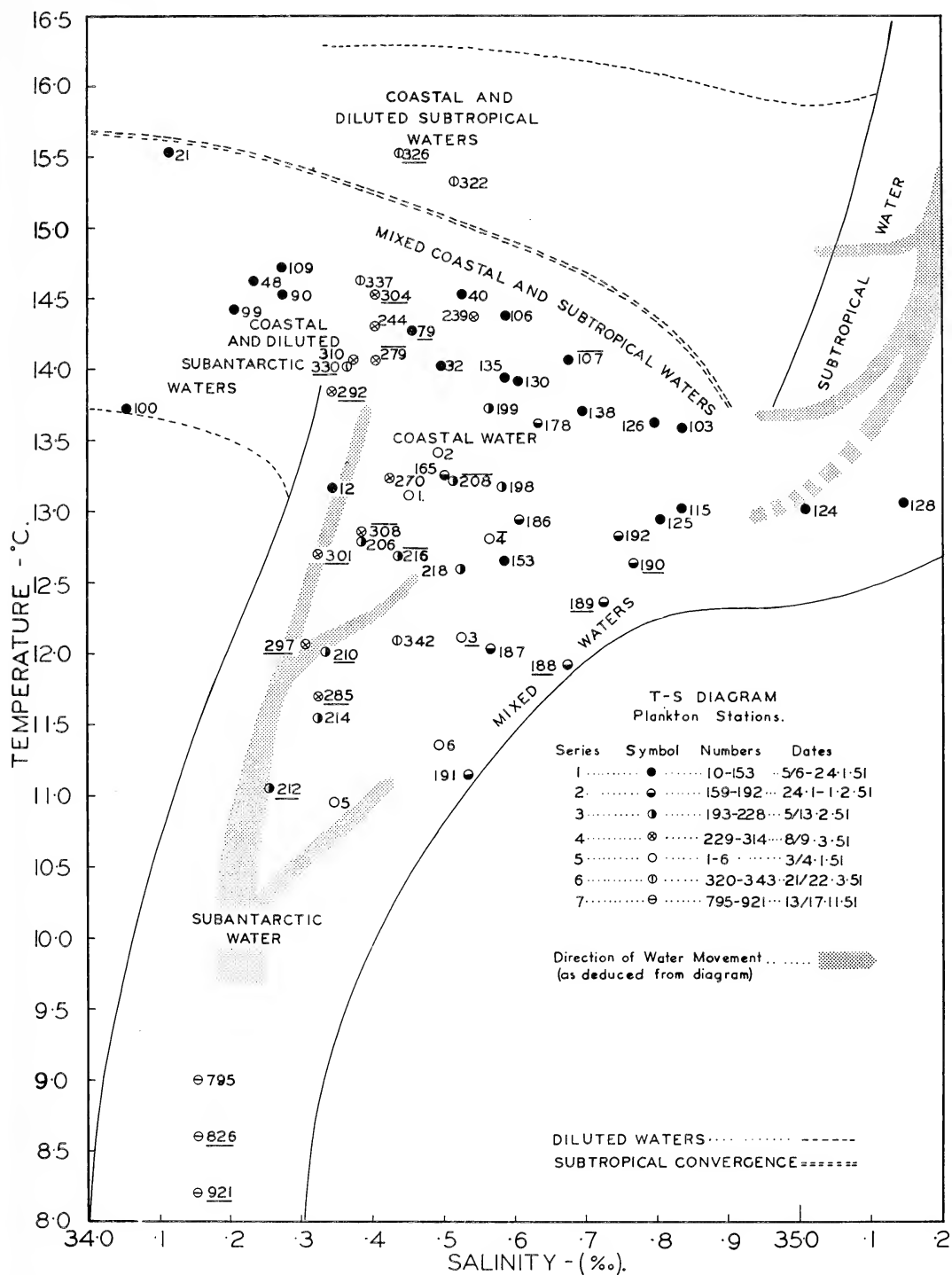


FIG. 1. Temperature-salinity (T-S) diagram of surface waters about eastern and southern South Island, New Zealand, extending southwards to Auckland and Campbell Islands. Plankton stations for which temperatures and salinities were obtained are entered. Numbers underlined (e.g., 212) represent night stations; numbers overlined represent stations between dawn and sunrise or sunset and dark. Stations without lines were occupied in daylight.

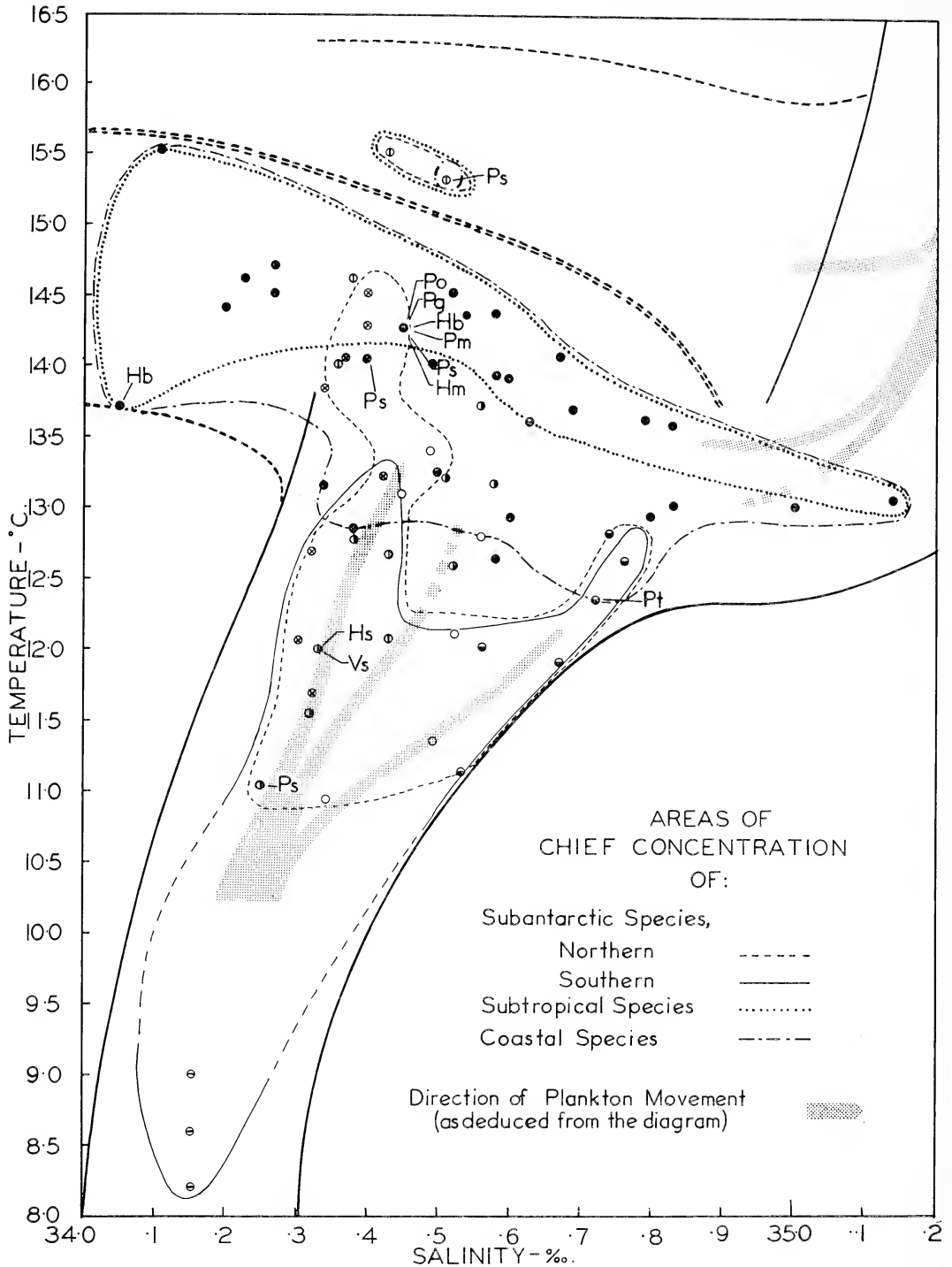


FIG. 2. Generalised T-S-P diagram showing areas of chief concentration of indicator groups of species for waters of subtropical and subantarctic origins and for coastal waters. Species captured rarely are shown by their initial letters adjacent to the station at which they were captured (see text for Station 79). *Po* = *Platyscelis ovoides*. *Pg* = *Paralycaea gracilis*. *Hb* = *Hyperia bengalensis*. *Pm* = *Primno macropa*. *Ps* = *Phronima sedentaria*. *Hm* = *Hyperoche medusarum*. *Pt* = *Parascelis typhoides* (?). *Hs* = *Hyperia spinigera*. *Vs* = *Vibilia stebbingi* (?).

The species discussed normally inhabit waters of a restricted and specified range of properties. However, the subantarctic species *Parathemisto gaudichaudii* and *Cylopus* spp. and the Coastal species *P. australis* and *P. gracilipes* occur together at Stations 308, 292, 330, 310, 279, and again at Station 189 (Figs. 1, 2); again, the subtropical species *Hyperoche mediterranea* and the coastal species *P. australis* and *P. gracilipes* occur at Station 79. These collections of amphipods of mixed origin are present along with other species belonging to one or more of the several indicator groups of species. This is interpreted as evidence that the waters in which the species are habitually present are mixing together.

The water movements in the area have been deduced from the combined evidence of distributions of salinities, temperatures, and the zooplanktonic indicator species. They are discussed in detail elsewhere (Bary, 1959), but the isotherms of Figures 5 and 6 serve as a basis to recapitulate the main features. Briefly, there appears to be a moderately strong influence from water of subtropical origin which extends from the west into Foveaux Strait and can be traced around the coast to Dunedin and beyond. It is probable that some water of subantarctic origin, mixed with the subtropical water, also enters the Strait from the west. Water of subantarctic origin periodically penetrates in smaller or larger intrusions into the waters in the Strait and coastal areas. These several waters mix to form one of intermediate properties which is designated herein as "coastal water" (Fig. 1). It is believed probable that only water of subantarctic origin is present at Stations 826 and 921 of Series 7, and possibly also at Station 725 (Figs. 1, 6c). Data from stations of Series 5 and 6 (Fig. 6), together with those from a surface thermograph trace made two weeks later, on a course parallel to and seaward of the stations of Series 6, indicate the location of the subtropical convergence. It was not crossed by "Lachlan" in January when it was probably to the north of Station 1, but it was

present a little northward of Station 330 in March (Series 6).

With the species of Amphipoda related to their respective waters by the T-S-P diagrams, their presence or absence at a station becomes significant in that there is an indication of the waters present. The subtropical species *Hyperoche mediterranea* is confined to that portion of Foveaux Strait likely to be most directly influenced by water of subtropical origin (Fig. 5a). The coastal species *Parathemisto australis* and *P. gracilipes* occur along with *H. mediterranea*, but in all series they occur over a larger area, and a wider range of temperatures. From Figure 5a to d, it is clear that neither subtropical nor coastal species penetrate into areas where the influence of water of subantarctic origin is strong, e.g., Stations 210 to 218 (Fig. 5c, g), or 285, 297 (Fig. 5d, b). On the other hand they are found, together with subantarctic species, at those stations in the mixed waters immediately northeast of Stewart Island (Fig. 5a, e) and more especially at Stations 187, 189 (Fig. 5b, f), 208 (Fig. 5c, g), 279, 292, 308, 310 (Fig. 5d, b), and again at Station 330 (Fig. 6d, e). In the T-S diagram (Fig. 1) these stations (except 187, 189) are seen to extend as a group between water of subantarctic origin and coastal water. In the T-S-P diagrams Figures 2, 3 the occurrence of the subantarctic species of plankton at all of these stations emphasises a certain affinity between them; it would seem that they are directly within the influence of water of subantarctic origin. This is confirmed by the geographic charts, which suggest that although some of the stations are located in inshore waters each, in fact, is located in the vicinity of tongues of colder water penetrating shorewards. This is especially so for Stations 279 and 292, less so for Station 208. Stations 308 and 310 appear to be in waters that are more generally mixed, but into which water of subantarctic origin appears to be intruding, particularly about Station 297 (Fig. 5d, b). Stations 187 and 189 (Fig. 5b, f) are also located near intruding

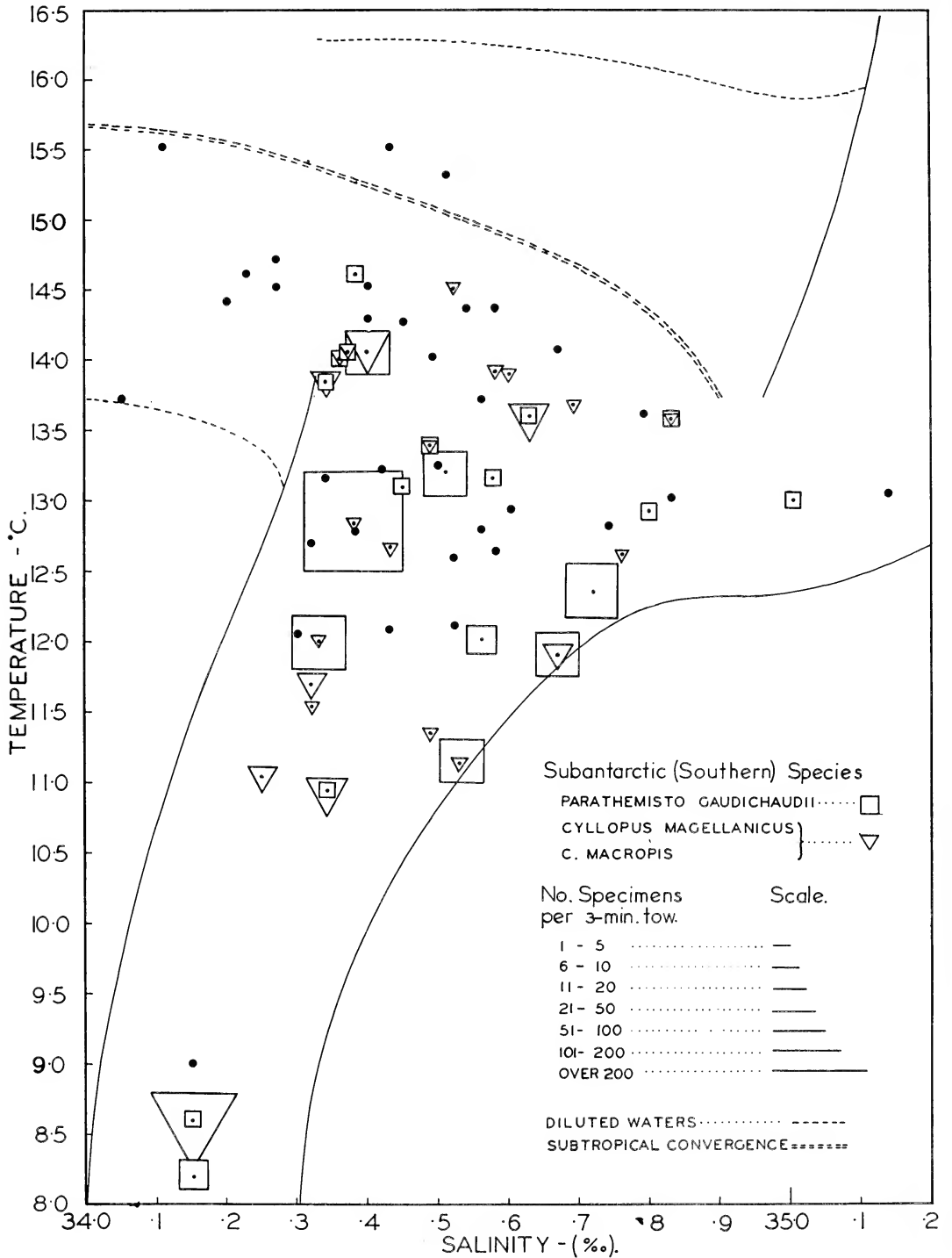


FIG. 3. Temperature-salinity-plankton (T-S-P) diagram of the species of Amphipoda associated with water of subantarctic origin.

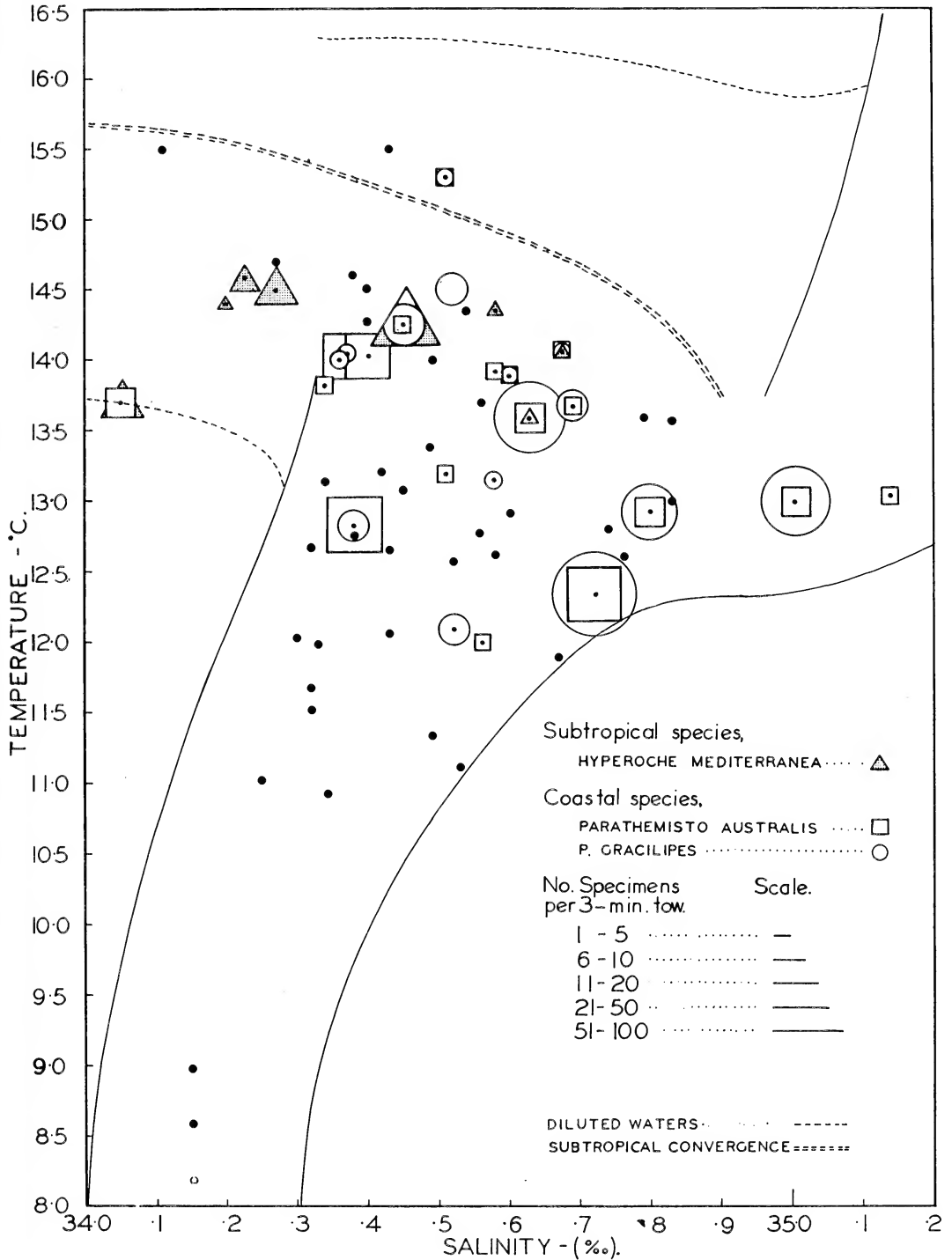


FIG. 4. T-S-P diagram of the species of Amphipoda associated with water of subtropical origin, and with coastal waters.

subantarctic water, and again the mixture of species results. At these stations there is a slightly stronger influence of coastal water than in the previous examples, as shown by higher salinities (Fig. 1). The absence of any subtropical species at 187 and 189 suggests little influence from water of this source.

The isotherms for January (Series 5, Fig. 6a, b) indicate that water of subantarctic origin extends at least to Cook Strait. One or both of the subantarctic species *Parathemisto gaudichaudii* and *Cylopus magellanicus* are present at four of the six stations. They are absent from Stations 3 and 4. This, together with salinities which are a little higher than in neighbouring subantarctic water (Fig. 1), indicates that those stations are being influenced by coastal water, probably from south of Banks Peninsula. Although this water does not exclude subantarctic species, it supplies a reason as to why *Parathemisto gracilipes* occurs at Station 3 (and also why other species of the Coastal Group were present at both Stations 3 and 4). In Figure 6d, e, the subtropical convergence transects the series. Subantarctic species are present at Stations 337 and 330; *P. gracilipes* is also present at Station 330, and both *P. gracilipes* and *P. australis* at 322. Station 322, north of the convergence, is in mixed subtropical-coastal waters (Figs. 1, 2) and the occurrence there of a coastal species is consistent. Species from all groups are to be expected at Station 330. It is shown by the mixture of zooplankton to be situated in mixing waters in the T-S-P diagram (Fig. 2), and this is borne out by its geographical location near or within the mixing area between waters originating in the subtropical and subantarctic masses (Fig. 6d, e).

Perhaps the most important feature illustrated by Figure 6 is that the two subantarctic species, few in individuals though they are, are present only in water believed to have originated in the subantarctic. They act as indicators and demonstrate the northward extent of subantarctic water, as well as demarcate the approximate position of the subtropical

convergence in March, 1951.

It perhaps should be emphasised at this point that in the southeast coastal area of New Zealand, where mixed waters of diverse origins predominate, it would be most difficult to disentangle the sources of the waters and the species from charts of distributions alone. Interpretations would be largely deductive and subjective. The T-S-P diagram demonstrates in a clear and effective manner, the source of both the waters and the species in the area. At the same time it provides a means of utilising occurrences of species to follow the trends of water movements. Thus the occurrences of species of plankton at certain localities, and of the means by which they arrived at their point of capture, can be explained with a fair degree of certainty.

Rare species are symbolised in Figures 2, 5, and 6 by their initial letters. Occurrences of one or a few species, on one or two occasions, are often insignificant in distributional studies. In the context of the T-S-P diagram (Fig. 2), however, their occurrences may assist in the interpretation of conditions; conversely, the conditions in which they occur may assist in interpreting other features concerning the species, e.g., see a later discussion of *Parathemisto* spp.

The cold-water species *Hyperia spinigera* is demonstrated as being captured in water of subantarctic origin (Station 210, Figs. 2, 5g)—water in which the species is normally resident. *Hyperoche medusarum* Kroyer, another cold-water species, occurs at Station 79 (Figs. 2, 5a). This might be regarded as a stray specimen, but the presence of small numbers of other species of the Subantarctic groups, e.g., Copepoda, suggests an intrusion of water of subantarctic origin towards this station. Two species present at Station 79 are of subtropical origin, namely *Platyscelus ovoides* (Claus) and *Paralycaea gracilis* Claus. These, and probably also *Hyperia bengalensis*, are regarded as entering, along with water of subtropical origin, into Foveaux Strait from the west. As would be expected, undoubted cos-

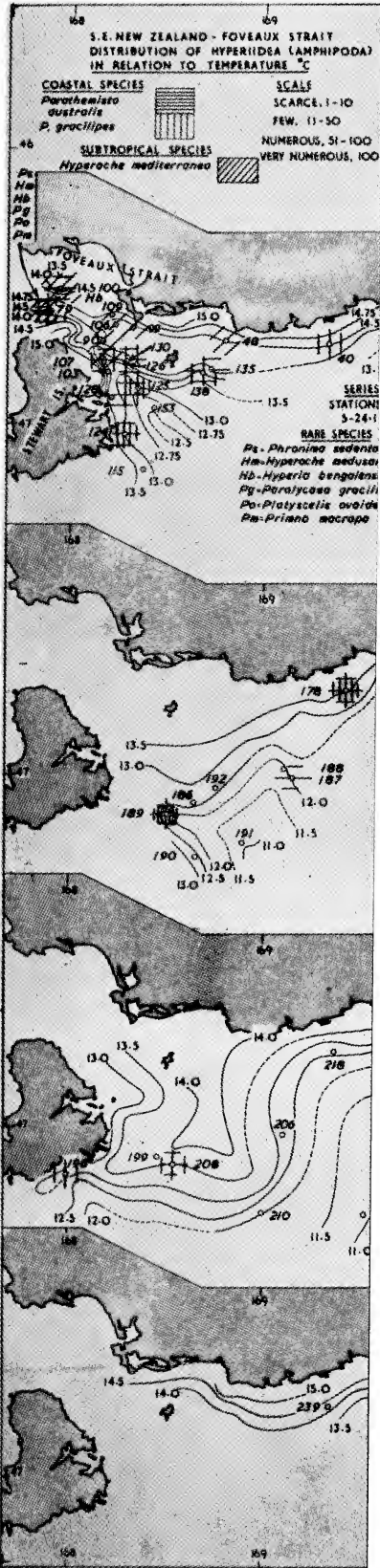


FIG. 5. Charts of distributions of Amph separately from Subantarctic species (e-b)

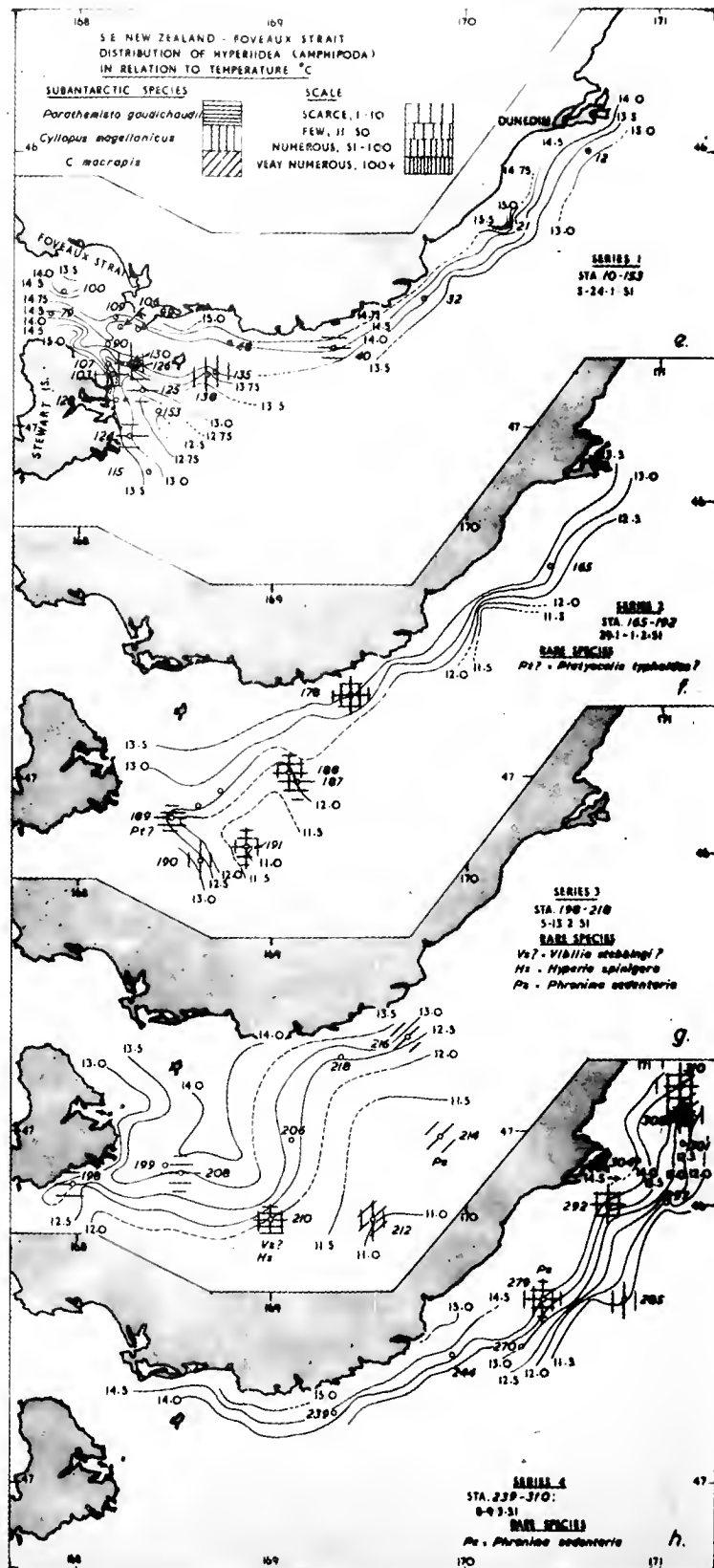
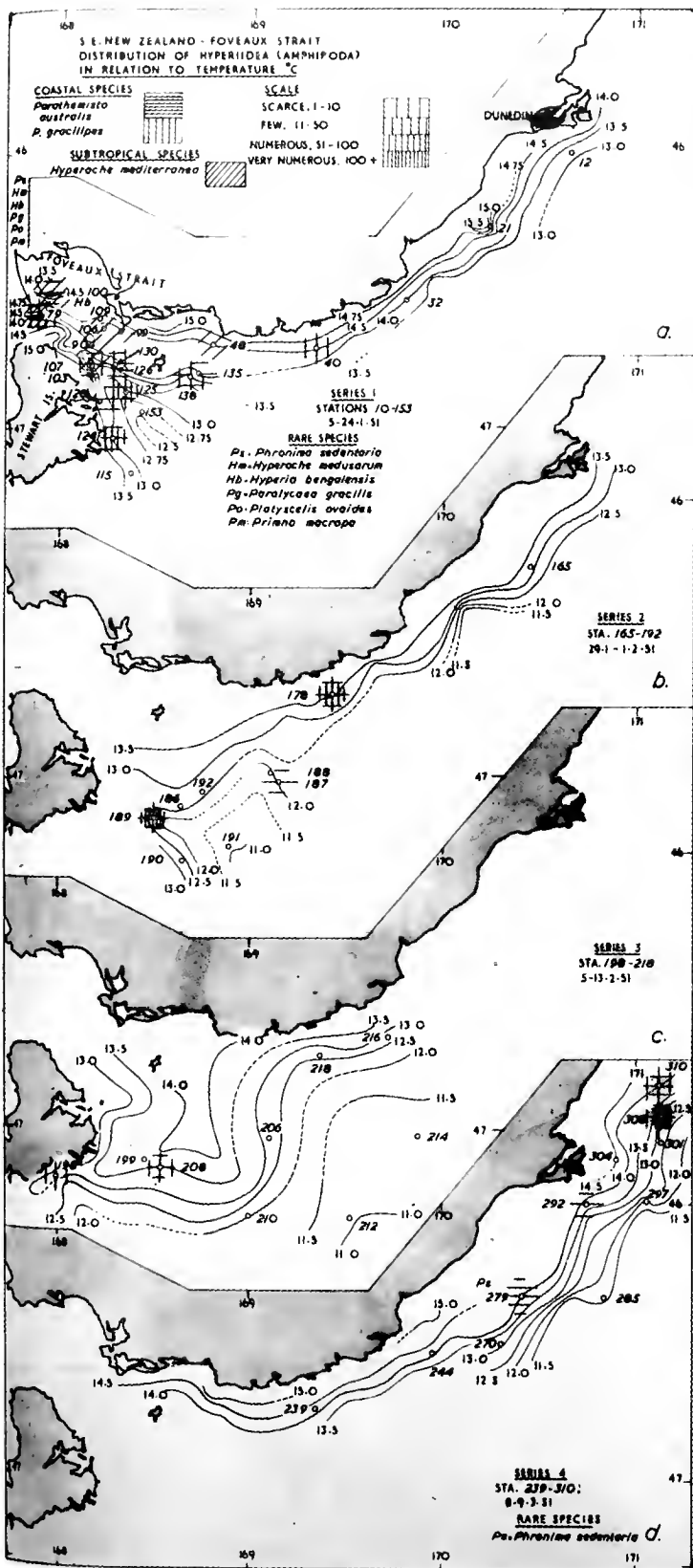


Fig. 5. Charts of distributions of Amphipoda relevant to temperature distribution about Foveaux Strait. Coastal and Subtropical species (a-d) are illustrated separately from Subantarctic species (e-h) for each series of stations. For a discussion of the rare species, see text.

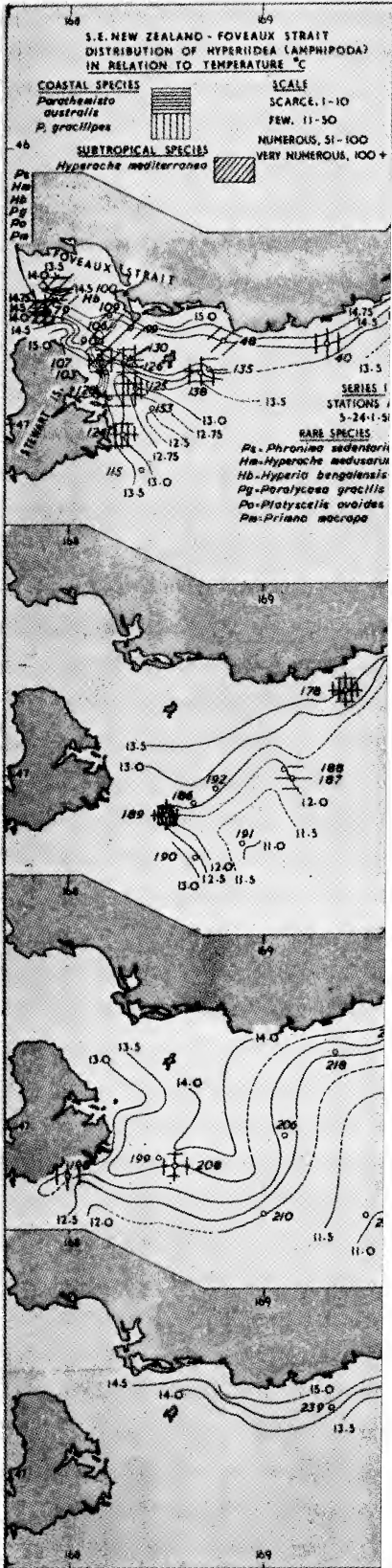


FIG. 5. Charts of distributions of Amphipoda separately from Subantarctic species (e-h)

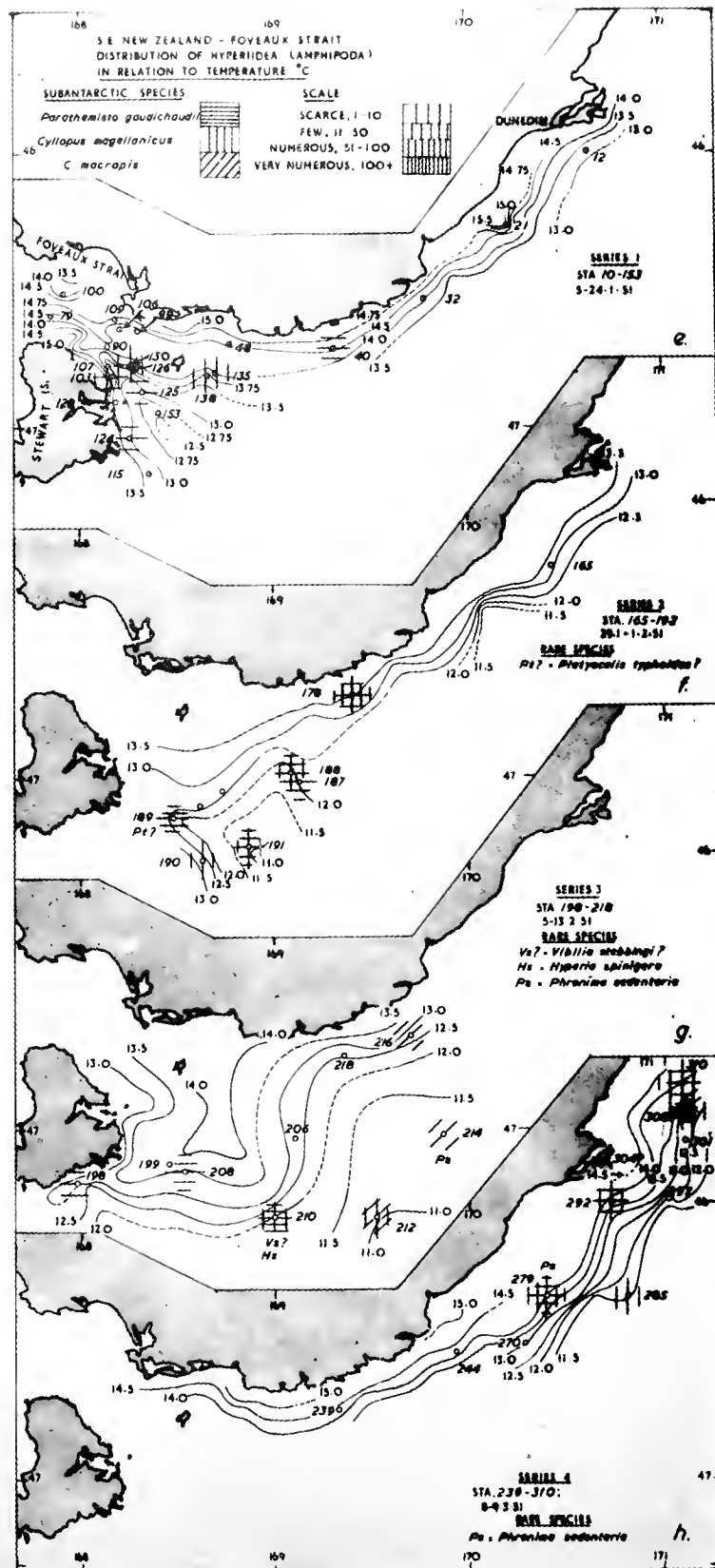
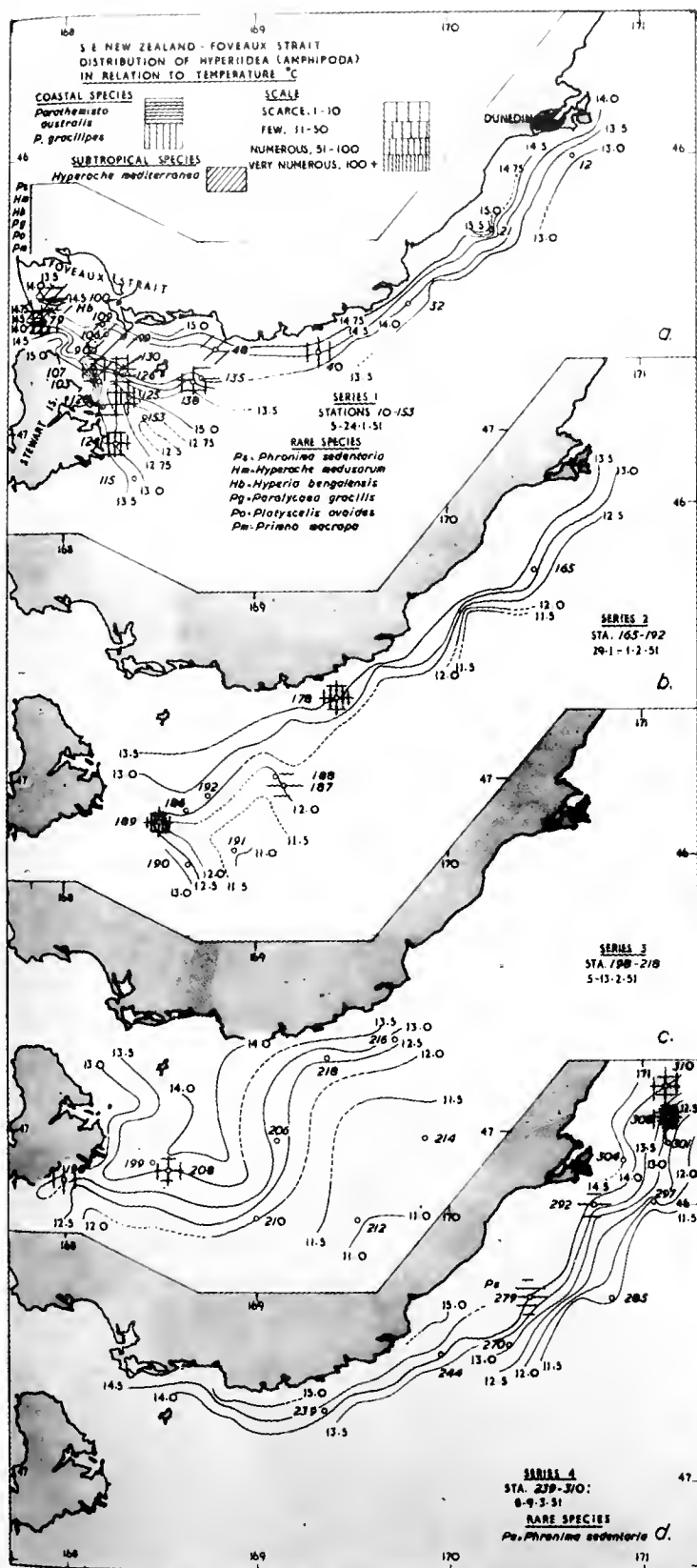


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mopolites may occur at stations located in a variety of waters. Thus, *Phronima sedentaria* (Forskal) is present in water of subtropical origin north of the subtropical convergence (Station 326, Figs. 2, 6*d*), in mixed water (Station 79, Fig. 5*a*), and in water predominantly of subantarctic origin (Stations 214, Fig. 5*g*), or being influenced by this water (Station 279, Fig. 5*b*). *Hyperia bengalensis* (Giles) was present in mixed or diluted coastal waters (Stations 79, 100), and *Primno macropa* Guer., another cosmopolitan species, also occurred at Station 79 (Figs. 2, 5*a*). Thus, on the whole, these species are shown to have been captured in conditions suitable for them. Conversely, their occurrences in conditions consistent with those previously recorded for them adds to the value of interpretations based on the more commonly occurring species.

Two of the New Zealand species listed in Table 1 are regarded as being doubtfully identified (Hurley, 1955). The identification of one, and possibly also of the other species, is not upheld when their relationships to the water masses, demonstrated in the T-S-P diagram, are compared with their previously recorded distributions. *Vibilia stebbingi* (?) Behn and Wolt, is present in water of subantarctic origin (Station 210, Figs. 2, 5*g*) which is out of character with the tropical-subtropical range usually ascribed to this species. *Parascelis typhoides* (?) Claus, another tropical-subtropical species was captured at Station 189 (Figs. 2, 5*f*), believed to be located in a mixture of coastal and subantarctic waters; the absence of any others of the selected Subtropical Group of species indicates little influence at this point from water of subtropical origin. Thus this occurrence of *P. typhoides* (?) may also be anomalous, suggesting again that misidentification is possible.

A comparison of the average numbers of a species captured in coastal and in offshore waters may indicate the degree to which the species penetrate from one water into the

other. When numbers captured per haul over a specified range of depth are plotted against depth of water, the commoner amphipod species illustrate that this applies. (See Fig. 7; deeper water in the area of sampling is indicative of an increase of distance offshore and proximity to oceanic water.)

Both *P. gaudichaudii* and *Cylopus magellanicus* (Fig. 8, unbroken line) show decided increases in the numbers captured from shallow (coastal) to deep water. A fair degree of tolerance to coastal waters is suggested for *P. gaudichaudii* by the almost steady increase in numbers as samples proceed offshore. On the other hand, the sudden decrease in water shallower than 50 fathoms (91.5 m.) shown by *C. magellanicus* is indicative of intolerance to conditions in the coastal water. *P. gracilipes* and *P. australis* (Fig. 7) increase in numbers to a peak at 50 fathoms (91.5 m.), and decrease in the deeper, offshore water. This suggests that neither species is tolerant of conditions in this water (see later). These facts confirm the relationships of the species to water masses already obtained from the T-S-P diagrams (Figs. 2, 3, 4).

The collections of this study were made during a period of three months. During the latter half of this a larger proportion of stations were over deeper water, either directly influenced by, or believed to be situated in water of subantarctic origin. It seemed possible, therefore, that variations in the catches of a species, relative to depth of water, might be reflected in the numbers captured at different times in the three months. So that direct comparisons might be made, the average number of specimens per haul for each month are included in the figures of changes of the catch with depth (Fig. 7 dashed line). *Cylopus magellanicus* shows an overall decrease in numbers during January through March which is opposed to the increase with depth. Numbers of *P. gaudichaudii* on the other hand, increase with each monthly catch, although less so for March than for January and February. Even so, the number collected

TABLE 1
RARELY CAPTURED SPECIES AND THEIR PREVIOUSLY RECORDED DISTRIBUTION IN RELATION TO THAT SHOWN BY THE T-S-P DIAGRAM

SPECIES	SYMBOLS IN FIGURES	STATIONS COLLECTED	NUMBER OF SPECIMENS	DISTRIBUTION		AS FROM T-S-P	AGREEMENT
				Recorded in literature	Summary*		
1. <i>Vibilia stebbingi</i> ?	Vs	210	1	Mediterranean; 35°N.-30°S. Atlantic; E. Pacific; N.Z.	ST-T	SA	Poor (possibly misidentified)
2. <i>Hyperia bengalensis</i>	Hb	83 100	14 4	40°N.-45°S. Atlantic; Mediterranean; Arabian Sea; Cape Howe and N.S.W., Australia; Bermuda	ST-COS	Mixed ST-C-SA	Satisfactory
3. <i>Hyperia spinigera</i>	Hs	210	1	North Norway; Labrador current; W. Ireland; S. England; E. mid- Atlantic; S. Georgia; Friday Harbour; N.Z.	Arctic- Subarctic; A-SA	SA	Very good
4. <i>Hyperoche medusarum</i>	Hm	75	1	55°-77°N. Atlantic; N. Alaska; S. Georgia; at 1500-3000 m., 19°- 35°S. Atlantic; N.Z.	Arctic- Subarctic	Mixed ST-C-SA	Fair
5. <i>Phronima sedentaria</i>	Ps	82 214 279	1 1 3	Mediterranean; 60°N.-36°S. Atlantic; Indo-Pacific; N.Z.	COS	82 Mixed ST-C-SA 214 { SA 279 }	Very good
6. <i>Primno macropa</i>	Pm	326 74	1 1	Mediterranean; 30°N.-66°S. Atlantic; Indian; N. Pacific; 58°-66°S. Pacific	COS	326 ST Mixed ST-C-SA	Good
7. <i>Paralycaea gracilis</i>	Pg	75 83	1 1	Mediterranean; 53°N., 47°N., and Trop. Atlantic; 39°S., 140°E., Pacific; N.Z.	T-ST	Mixed ST-C-SA	Satisfactory
8. <i>Parascelis typhoides</i> ?	Pt	189	1	N.-S. Atlantic; Mediterranean, Red Sea	T-ST	Mixed SA-C	Poor (possibly misidentified)
9. <i>Platyscelis onoides</i>	Po	75	3	N.-S. Atlantic; Indian Ocean and G. of Aden; Mediterranean	T-ST	Mixed ST-C-SA	Fair

* T—Tropical; ST—Subtropical; SA—Subantarctic; A—Antarctic; COS—Cosmopolitan; C—Coastal.

per haul over 100 fathoms (182.9 m.) of water increases slightly. Captures of both *P. australis* and *P. gracilipes* increase to February and decrease to March. The T-S-P diagram demonstrates, however, that the two species are resident in coastal water, and it is probable therefore that the February-March (seasonal) decrease is not more than a contributing factor to the lower number of specimens captured from the deeper water. Thus, for the most part there appears to be a considerable degree of independence between the numbers of a species captured per haul per month and the numbers captured relative to depth of water. A similar condition is also suggested by the averages of all the common amphipods (Fig. 7). The average catch increases to 100 fathoms in a similar manner to that for January and February. However, the catch from water deeper than 100 fathoms continues to increase, although at a lesser rate, while the catch for March drops sharply.

DIURNAL VARIATION

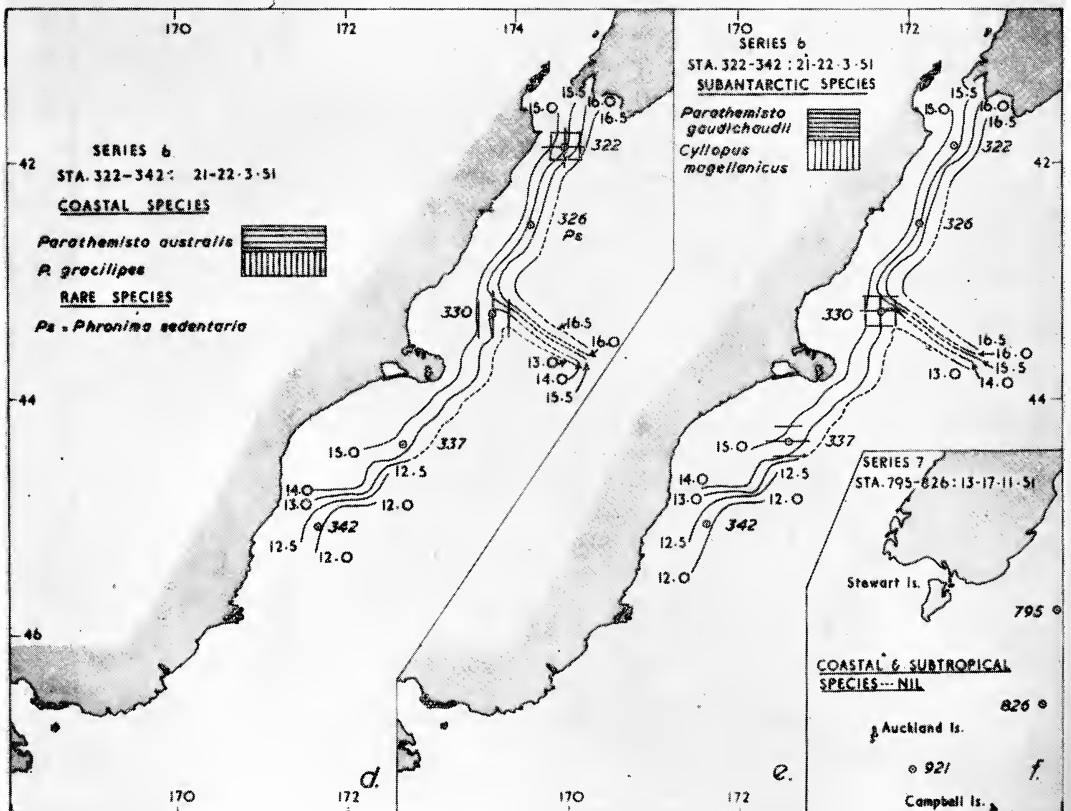
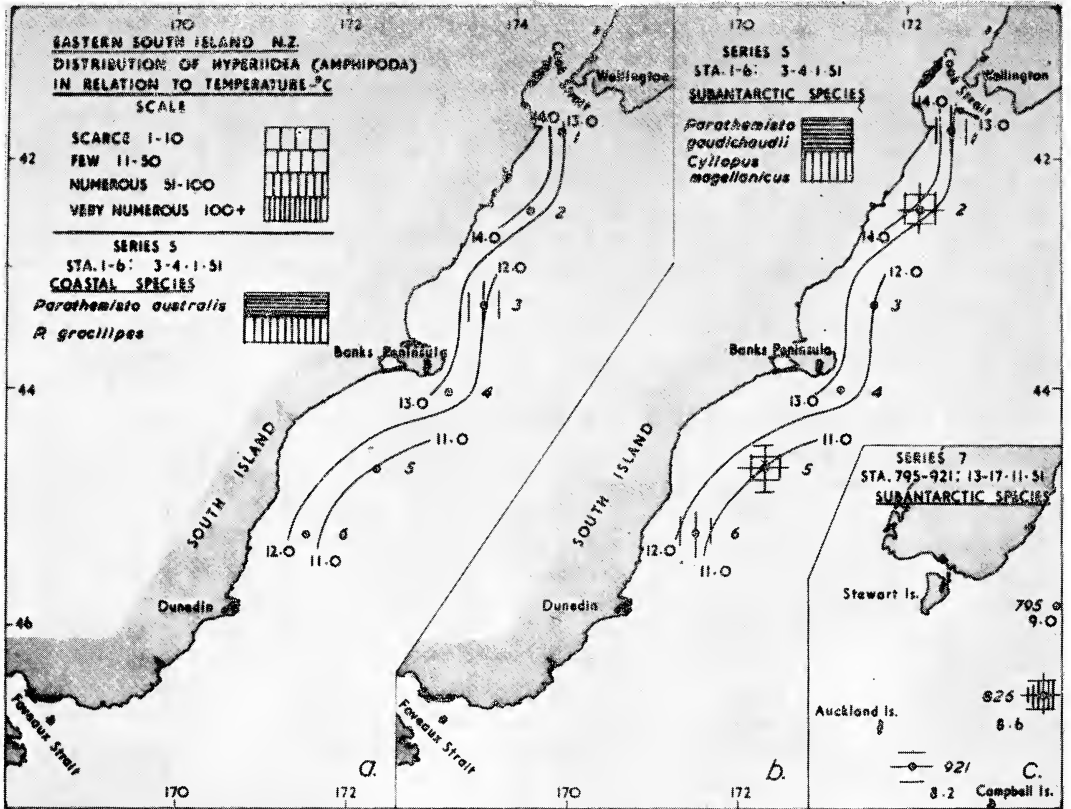
Vertical migration undoubtedly occurs among species of Amphipoda (e.g., Stephensen, 1925; Hardy and Gunther, 1935; Bousfield, 1951). However, other factors than light intensity would appear to be operative in the control of vertical distribution. Bousfield suggests quality and quantity of food, age of specimens and predation, and implies that the results of vertical migration may be modified by these. There may be vertical migration in connection with propagation as well (Stephensen). Stephensen also discusses the point that a number of species occur singly, or in groups of a few specimens. He considers that this applies to almost all deep-sea species, and also to some surface species. As well, there appears to be an inherent tendency for some species to shoal (Hardy and Gunther, 1935).

These several factors, some of which appear to be interrelated, almost inevitably would result in anomalous occurrences in terms of a normal diurnal rhythm. With species tending to appear somewhat irregularly

at the surface, patchiness in their occurrences would result. Hardy and Gunther (1935) discuss such patchiness among amphipod species and the effects this has on their distribution patterns, with particular reference to the area about South Georgia.

The data on the species in the present study demonstrate that vertical migration takes place and that patchiness is frequently met. The former is reflected in diurnal variation of numbers at the surface, and the latter in the great variation in the numbers captured from hour to hour (Figs. 8, 9), or station to station, of all the common species (Figs. 5, 6). The average haul for each hour is derived from the average of one to five stations. In contrast the average number of tows per hour is low (almost three per hour), which precludes the present data from being fully representative of the patterns of diurnal variation in New Zealand waters.

However, the numbers of the five commonly captured species, and of the juveniles of *Parathemisto* spp., increased at night. *Parathemisto gaudichaudii* and juveniles of *Parathemisto* spp. exhibited pre- and post-midnight increases in numbers; although such is more or less typical of the diurnal behaviour of zooplankton (Cushing, 1951), the post-midnight rise occurs between 0100–0200 hours, which in southern New Zealand is several hours too early to be considered a predawn rise. The other species increase to a single peak during darkness either prior to (*Hyperoche mediterranea*), or subsequent to midnight (*Cylopus magellanicus*, *Parathemisto australis*, *P. gracilipes* and *Parathemisto* juv.). A large catch of several species, made at Station 189 at 0125 hours, is responsible for the peak of numbers taken between 0100 and 0200 hours for *P. gaudichaudii*, *P. australis*, *P. gracilipes*, and *Parathemisto* juveniles. A total of four stations were occupied between 0100 and 0200 hours, but only at Station 189 were any of these species captured. This may be a result of patchiness in distribution. On the other hand, Station 189 was in mixed coastal-subantarctic



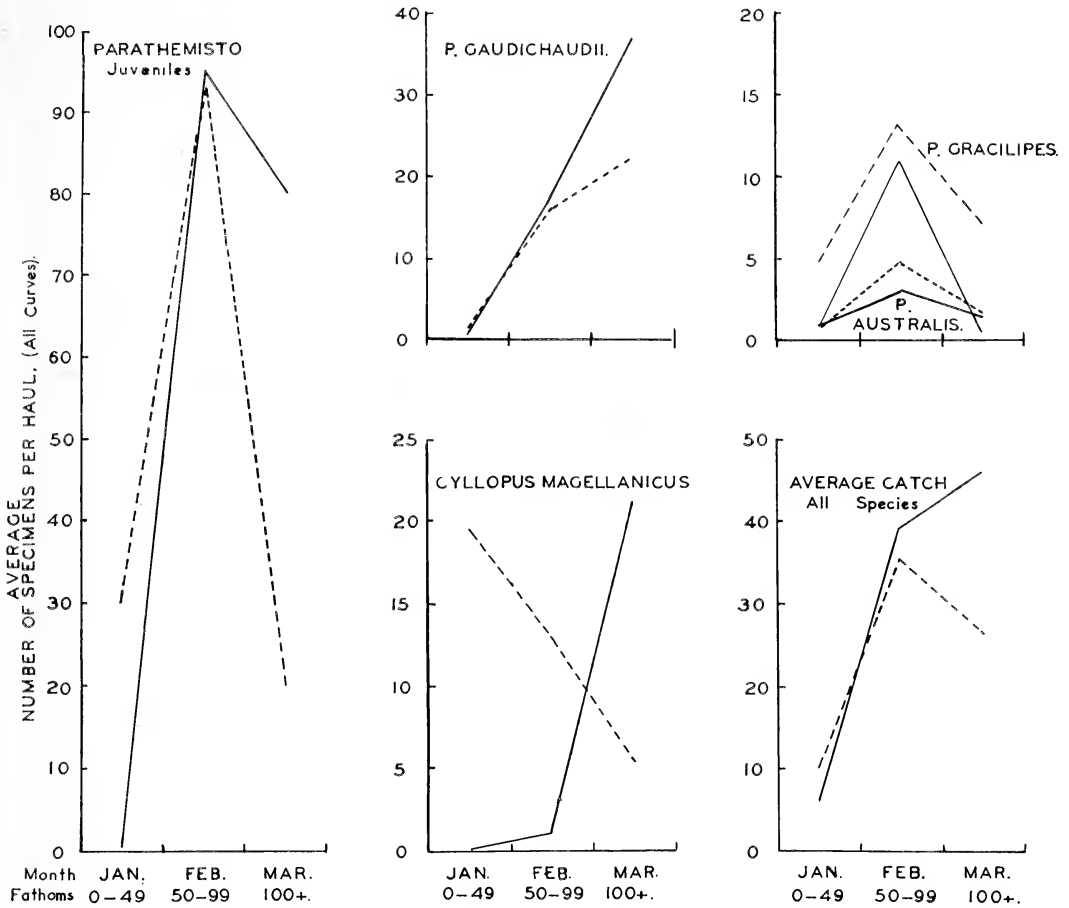


FIG. 7. The average number of the commonly occurring Amphipoda per haul per month for January, February, and March, plotted together with the average number of species per haul over each of the ranges of depth 0-49, 50-99 and 100+ fathoms (0-89.6, 91.4-181.1, and 182.9+ m.).

waters and perhaps the several species were dependent on the particular hydrological conditions. That these examples of diurnal variation are so weighted by a single haul indicates the need for a large number of samples when dealing with species exhibiting such variable distributions in time.

Several quite considerable hauls made in daylight (Figs. 8, 9) emphasise what appears to be a certain independence of controlling conditions (e.g., light intensity) in the vertical movements of the several species. Daylight

hauls were scattered over a range of conditions (see Fig. 1) and thus it is unlikely that too frequent sampling in particularly favourable conditions is weighting the curves. *Parathemisto gracilipes* and *P. australis* (Fig. 8) were most consistently present in daylight, the one or the other being captured at most times. *P. gaudichaudii*, *Parathemisto juveniles*, *Cylopus magellanicus*, and *Hyperoche mediterranea* were usually taken in very small numbers during daylight (Fig. 8). It seems probable from the 2-hour averages of all spe-

FIG. 6. Charts of distributions of Amphipoda relevant to temperature for the east coast of South Island. Coastal species (a-c) are shown separately from Subantarctic species (d-f) for stations of Series 5 and 6.

cies (Fig. 9) that species may be present, in moderate numbers, up to midmorning and from midafternoon on. However, all species, except *P. gracilipes* and a few *P. australis*, were absent or rarely captured in hauls between these times.

The common species of amphipod, by their irregular, spasmodic occurrences, suggest that in New Zealand waters, as elsewhere, distribution is affected by patchiness, and that a degree of independence of known controlling factors in the vertical movements of species is probable. Interpretations of distributions of species may thus be conditioned by the presence or absence of specimens as a result of (undetected) irregularities in their vertical movements.

PARATHEMISTO SPECIES

Hurley (1955) analyses the complex taxonomy of *P. gaudichaudii*, *P. australis*, and *P. gracilipes*. He points out (p. 161) that "although the three groups of *Parathemisto* here recorded from New Zealand can be separated quite distinctly by the pectination of the uropods, the general facies and by ecological preferences and habits, it is still possible that they do not warrant specific status. . . ." He briefly discusses the ecological data available to him from preliminary studies, and their relationships to the systematic positions of the species. As a result of the more detailed treatment possible in the present study, Hurley's general statement can now be amplified and modified.

In the preliminary studies it appeared that the habitats of *P. australis* and *P. gracilipes*, although overlapping, were separable respectively into shallow inshore waters and waters of intermediate depth. However, the T-S-P diagram (Fig. 4) shows that they occur at similar temperatures and salinities frequently at the same stations, in the warm coastal and mixed waters. In contrast, *P. gaudichaudii* inhabits colder water originating in the subantarctic, although it is able to penetrate into the inshore waters. Thus, for the area in ques-

tion, there appear to be environmental preferences between *P. gaudichaudii* on the one hand and *P. gracilipes* and *P. australis* on the other, but not between *P. gracilipes* and *P. australis*, which facts are well demonstrated in the T-S-P diagrams (Figs. 3, 4).

The variations in the diurnal patterns of the three species provide further evidence toward distinguishing between *P. gaudichaudii* and *P. australis*-*P. gracilipes*. *P. gaudichaudii* is rarely taken at the surface during daylight, but *P. gracilipes* and *P. australis* may be common (Figs. 8, 9). There is a double peak of numbers for *P. gaudichaudii* during darkness; both *P. australis* and *P. gracilipes* occur in large numbers at one and the same time. Further, the curve of diurnal variation for *P. gracilipes* closely parallels that for *P. australis*, indicating similar reactions to changing conditions (Fig. 9). Other similarities between *P. gracilipes* and *P. australis* are apparent in their relations to depth of water, and in the increases and decreases in numbers during January through March (Fig. 7). *P. gaudichaudii* differs considerably on these two points.

Ecologically, it would appear that *Parathemisto gaudichaudii* is separable as a distinct species from *P. australis* and *P. gracilipes*. However, an ecological distinction between *P. australis* and *P. gracilipes* in the New Zealand area cannot be substantiated because of their closely parallel diurnal behaviour and similar distribution. These points are probably not of sufficient moment to make *P. gracilipes* and *P. australis* conspecific, especially as Hurley states the two forms are readily separable by their general facies. Their previous distributional records, too, indicate that the former is an oceanic, and the latter a coastal species. Although such markedly different distributions should be reflected in their relationships to water masses in T-S-P diagram, this is not so. Thus the ecology of *P. gracilipes* and *P. australis* does little to assist in clarifying their systematic positions. On balance, it seems, however, that some taxo-

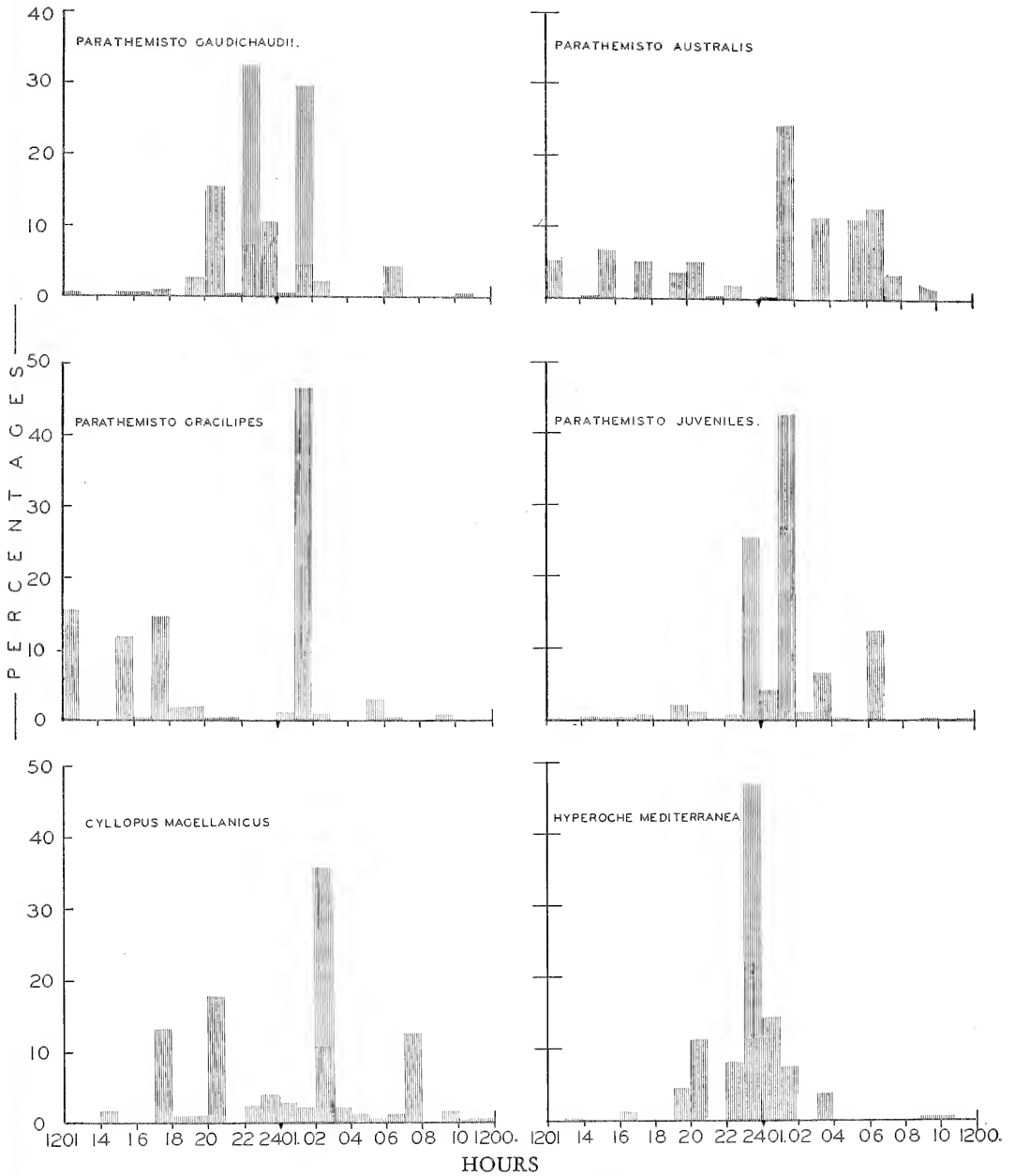


FIG. 8. The diurnal variation at the surface as shown by the hourly catches of commonly occurring species expressed as a percentage of the total catch of the species.

nomic distinction between them is desirable, but preferably at an infraspecific level.

AMPHIPODS IN THE ECONOMY OF THE AREA

An assessment of the position of species of Amphipoda in the productive economy of

southern New Zealand waters was not aimed at, although the common species would seem to be important. Species are frequently captured and may occur in large numbers, even in the 3-minute tow, e.g., 729 *P. gaudichaudii* collected from 22 stations; 408 *P. gracilipes*

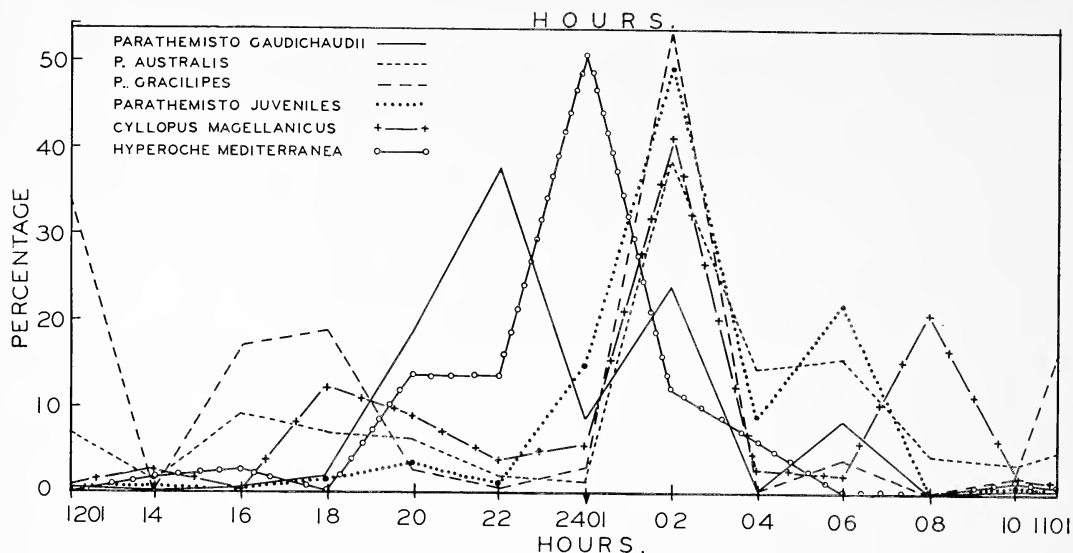


FIG. 9. The diurnal variation as shown by 2-hour averages of the data in Figure 8.

from 18 stations; 3,500 *Parathemisto* juveniles from 32 stations. The numbers of juveniles captured decrease rapidly between February and March (Fig. 7) but, even so, they were present in fairly high numbers throughout the summer. They ranged in size between specimens just released from the brood pouch to about 6.5 mm. long (at which length they usually can be assigned to sex and species), and because of their numbers are probably important in food cycles.

Barnard (1930) noted an increase in the sizes of the adults of Amphipoda at higher latitudes. In the present material, specimens of *Cyllopus magellanicus*, captured in the warmed waters (12–13°C.) of subantarctic origin off the New Zealand coast, averaged 7 to 8 mm. long and only occasionally exceeded 9 mm.; those from Station 826 (Fig. 6), in colder water (8.6°C.), averaged 9 to 10 mm. and were often 11 mm. and longer. If numbers of a species were maintained in the colder waters, such an increase in size would be reflected in an increased bulk of material available as food. Thus the size-increase in southern waters may well be related to production, the more so if it is a widespread phenomenon among those dominant species of the zooplankton.

Except for juvenile stages, the numbers of the species of amphipods captured do not reach those of some euphausiids or copepods in the area, but their large size and frequent occurrence in both oceanic and coastal waters (together with the fact that oceanic species may extend into coastal waters), suggest that species are important in productivity throughout the area. This is in part borne out by the quantities of these and other species of amphipod which are often present in the stomach contents of birds (e.g., Dawbin, 1954), and by personal observations of *Puffinus griseus* (flocks of which reach many thousands of birds) and of fish stomachs.

DISCUSSION AND SUMMARY

Of the 14 species of hyperiid Amphipoda collected by the "Lachlan" between Wellington and Auckland-Campbell islands, five are sufficiently common to be of value in studies of distribution. The occurrences of these and the remaining nine species are of interest when considered in relation to the water properties from which they were taken. In general, a strong affinity to the subantarctic, and to a lesser extent the antarctic faunas, is indicated in the frequent occurrences of species typical of southern waters, viz., *Parathe-*

misto gaudichaudii and *Cylopus magellanicus* (and also *C. macropis*). Two species, *Hyperia spinigera* and *Hyperoche medusarum*, were rarely captured, but may be considered as inhabitants of cold waters. In the New Zealand area the first occurred in water of subantarctic origin, the second in mixed water, probably being influenced by subantarctic water. The influence of subtropical water is apparent in the moderate numbers of *Hyperoche mediterranea*, a warm-water species captured in western Foveaux Strait. Additional evidence of this influence accrues from the rare occurrences of other warm-water species, *Platyscelis ovoides*, *Paralycaea gracilis*, and possibly also *Hyperia bengalensis*. The cosmopolitan species *Phronima sedentaria* and *Primno macropa* were in low numbers, but were present in mixed subtropical-coastal waters and also in water of subantarctic origin.

There is reasonably close agreement between the distributions of species relative to water properties in the area, as shown by the T-S-P diagrams, and their distributions as recorded previously. It is rare in these earlier accounts for temperatures and/or salinities to be included, the relationships of which are important to the interpretation of species' distributions; nor are the interrelationships of species necessarily discussed. Data relevant to these features are necessary in discussion of vertical distribution where waters of diverse origins may be more or less stratified, and in horizontal distribution where waters of different properties may be mixing. It appears of small value to record the presence of species without also obtaining hydrological data by means of which ecological and distributional relationships may be assessed. With these data collected, the T-S-P diagram offers a means of precisely summarising it and, at the same time, demonstrating some of these relationships. The diagrams also emphasise the need to include, at least, data on temperatures and salinities in any discussion of distribution.

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Aluminum in Some Hawaiian Plants¹

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THE RECENT INTEREST in Hawaiian gibbsitic soils (Sherman, 1957; Tamura, Jackson, and Sherman, 1955) as a potential commercial source of aluminum has stimulated concurrent interest in the plants of these latosols.

The major and closely related questions that arise concern (1) the role of plant species or plant communities as indicators of aluminum, (2) the ecological significance of plant accumulators of aluminum, and (3) the role of aluminum in plant metabolism and its relation to plant tolerance and toxicity. It is the purpose of this paper to discuss data on a selection of Hawaiian plants with emphasis on the latter two questions. The floristics and ecology of study sites on gibbsitic soils will be considered later.

REVIEW OF LITERATURE

Much of the early development of information concerning aluminum in plants was stimulated by the interest in plant materials as mordants for the dye industry. Aluminum is one of the most abundant elements in the soil and is almost universally present in plants but varies widely in amount. Robinson and Edington (1945) define an "accumulator" plant as one which takes up "the particular element in quantities very far above, sometimes many thousands of times above, the average for 'normal' plants." If the mean Al⁺⁺⁺ content of herbaceous vegetation is taken to be about 0.02 per cent of the dry matter (Hutchinson, 1943) or 200 p.p.m., the criterion of 1000 p.p.m. or 0.1 per cent used by Webb (1954) in a semiquantitative test

would seem to be adequate to qualify a plant as an aluminum accumulator. Many workers have reported aluminum contents of non-accumulator plants, corn for example (Meyer and Anderson, 1952), that equal this level. Several studies have attested to the variability of aluminum content within individual plants, usually with higher concentrations in roots and stems than in leaves and variability within a species when grown on different substrates (Webb, 1954). The extensive work of Webb and of Chenery (1948, 1948a, 1951) on local and world-wide floras has resulted in compilation of lists of aluminum accumulators. The highest content of aluminum found in plant tissue is reported for *Symplocos spicata* (Webb, 1954), 7.1 per cent, and for a *Carpinus* species, 8.5 per cent (Howard and Proctor, 1957). Massive deposits of almost pure aluminum succinate have been found in the heartwood cavity of *Cardwellia sublimis* (Webb, 1953) and *Orites excelsa*. Costin (1954) stated *Poa caespitosa* to have an aluminum content of 7.8–10.4 per cent and showed that it produced a material richer in sesquioxides than the parent rock from which the soils of the region were derived.

Chenery (1951) challenges the emphasis of some Russian workers on the role of aluminum accumulators in podzolization and offers other explanation for the observed soil aluminum distribution. Howard and Proctor (1957) studied the floristics of the bauxitic soils of Jamaica and found few of the families of accumulator species in Jamaica and fewer still on the bauxitic soils. They used neither tissue nor soil analyses but reported no species they could call indicators of aluminum and, on the contrary, concluded that factors other than the aluminum content of the soil controlled the success or failure of plants on Jamaican bauxite.

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Aluminum is thought to function in plant maturation and seed setting (Hutchinson, 1943) and in water uptake. The work relating aluminum to the blue pigments in plants (Chenery, 1948), especially in *Hydrangea*, is well known. The element has been thought to exercise a strong influence in plant competition in pastures (Shorland, 1934). Aluminum accumulation is thought to be a primitive phylogenetic character in plants (Webb, 1954) because it is generally confined to the Archichlamydeae and the primitive sections of Metachlamydeae. High aluminum concentrations are rarely found in monocotyledons (Chenery, 1949) and Webb records no positive Gramineae of 16 species tested. In the pteridophytes, accumulators are again confined to more primitive families and *Lycopodium* has been extensively studied to relate aluminum content and alkaloid molecular weight. Hutchinson (1943) considered the evidence in *Lycopodium* to suggest "that the capacity to accumulate the element has been developed more than once in the genus."

Although some workers have reported a requirement for the element in trace amounts (Hutchinson, 1945) by some plants, and stimulation from aluminum, especially of the ferns (Yoshii, 1939), it is not usually considered to be one of the essential nutrients. The more frequently reported condition is that of aluminum toxicity (Gilbert and Pember, 1935; McLean and Gilbert, 1926; Rees and Sidrak, 1956). This effect is usually related to soils below pH 5.5 (Chenery, 1951; Nagata, 1954) and is frequently correlated with high concentrations of manganese and free oxides or soluble aluminum compounds in leached podzolic and latosolic soils (Ellis and Truog, 1955; Perkins *et al.*, 1955). Magistad (1925) reported toxicity on an alkaline soil from a soluble aluminate and demonstrated the insolubility of aluminum in circumneutral soils, nutrient solutions, and water.

The free hydrated oxides of iron and aluminum have been shown to be more effective

in fixing phosphorus added to Hawaiian soils than are the crystal lattice clays of either the 2:1 or 1:1 types (Chu and Sherman, 1952). Free aluminum oxides do occur in montmorillonite clays (Ellis and Truog, 1955) however, and do account for most of the phosphorus fixation in soils of this type. Nagata (1954) has shown this effect to be more pronounced on calcicolous plants and Saeki and Okamoto (1954), studying the pure aluminum-phosphorus system, showed complete fixation to occur only when the P/Al ratio was less than unity and that iron and aluminum systems showed an almost identical trend. Perkins *et al.* (1955) attributed phosphate-fixing soluble aluminum to decomposition products of clay minerals.

Wright and Donahue (1953) definitely show aluminum to interfere with the phosphorus metabolism by precipitation on the root surfaces although Wallihan (1948) concludes that aluminum does not interfere with the activity of phosphorus in the tops of ladino clover plants. Rees and Sidrak (1956) found aluminum induced phosphorus deficiency in barley but not in spinach or *Atriplex*.

Hou and Merkle (1950) reported little correlation between pH and aluminum content even though accumulator plants are usually calcifugous and have a greater content of either aluminum or manganese than "acid-indifferent" plants.

METHODS

Collection Procedure

Samples of a selection of plants from three of the Hawaiian Islands were collected during the winter of 1957-58 (October-March). The principal areas of collection were those soil series currently under investigation as potential sources of alumina (gibbsite). About 500 grams of fresh plant material were collected of mature leaf, frond, or shoot unless otherwise specified. Special attention was given to some of the species known to be accumulators of aluminum and in many cases the same species were collected in areas of nonaluminous soils.

The species sampled were about equally divided among Pteridophyta, Dicotyledoneae, and Gramineae, the emphasis on grasses resulting from the present use of these areas mainly for grazing. The plants were identified by J. C. Moomaw and E. Y. Hosaka.

Analytical Procedure

Chenery's colorimetric analysis of aluminum using thioglycollic acid as inhibitor for iron (Chenery, 1948b) was followed with a few modifications.

The plant samples were prepared for analysis of aluminum according to the method described by Piper (1944). Two grams of oven-dried plant material were dry-ashed in a Vycor crucible. The ash was put into solution with dilute hydrochloric acid and the silica was separated and destroyed with hydrofluoric acid.

A suitable aliquot of the plant digest was first pipetted into a 100 ml. beaker and diluted to about a 20 ml. volume. To prevent the interference of Fe^{+++} , 2 ml. of 1:100 thioglycollic acid was added to the diluted solution to reduce the Fe^{+++} to Fe^{++} . Next, 10 ml. of the aluminum mixed reagent was added. The pH of this entire mixture was adjusted to 4.2 with NH_4OH using the Beckman pH meter. Although Chenery's mixed reagent is buffered at pH 4.0, the extreme acidity of the plant digest overcomes the buffering capacity and makes this pH adjustment necessary. The intensity of the color of the aluminum lake is highly sensitive to pH changes; therefore, in order to have reproducible results, it was necessary to have the pH of the plant sample and the standards equal.

The adjusted solution was transferred to 50 ml. volumetric flasks and heated in a boiling water bath for 12.5 minutes. The flasks were removed and allowed to stand for 10 minutes, then they were immersed in a cold water bath to be cooled to room temperature. The cooled solution was diluted to mark and mixed. The transmittancy of the solution was

read on the Klett-Summerson photoelectric colorimeter using a green filter.

RESULTS AND DISCUSSION

Of the 45 determinations reported in Table 1, 18 exceed the Chenery criterion of 1000 p.p.m., thus designating 13 of the 23 species as aluminum accumulators for one or more of the determinations. Three of the 13 are well known from the literature as accumulators: *Lycopodium cernuum*, the club moss or wawae'iole; the staghorn fern, *Gleichenia linearis*; and *Melastoma malabathricum*. The magnitude of the aluminum content of *Lycopodium* species is in good agreement with the 0.71 per cent found in the extensive review of Hutchinson (1943) and others. Staghorn is considered by some to be a fair indicator plant for bauxitic soils and was given special attention in being collected from seven different stations. It shows a high aluminum content from all collections falling in the relatively narrow range of from 3500 to 6300 p.p.m. High aluminum contents from nonaluminous soil areas, such as the Naalehu pahoe-hoe lava and the Honokaa soil (Table 2), are taken as evidence that it may be an obligate accumulator. *Melastoma* shows a very high content of aluminum, especially in the older tissue; this is a condition frequently mentioned in the literature, although Webb indicates some variability in *M. polyanthum* in New Zealand.

The highest aluminum content was found in *Polypodium phymatodes* on the Haiku series site considered most highly gibbsitic. Webb (1945) found all species in *Polypodium* examined by him to be negative but it is not known whether *P. phymatodes* was one of these. *Stenoloma chinensis*, another of the Polypodiaceae, shows evidence of a strong accumulation tendency, although it becomes a rather low-level accumulator on the Kukaiau soil series.

Pityrogramma and *Nephrolepis* (Boston fern), also in the Polypodiaceae, have a mixed record and indicate a facultative accumulation tendency. Two tree ferns, *Sadleria cyatheoides*

TABLE 1
ALUMINUM (AJ+++)
CONTENT OF SOME HAWAIIAN PLANT MATERIALS IN PARTS PER MILLION OF DRY MATTER
(All determinations are means of duplicates unless agreement was not closer than 10 per cent, when additional samples were run.)

Soil Series	MAUI			KAUAI			HAWAII			
	Camp. Maui	Haiku		Haiku (beyond gulch)	Kapaa		Pahoehoe lava	Kukaiiau	Honokaa	Lithosol
		Halehaku	Haiku		Bauxite Reclamation Site	Wailua Game Reserve				
Pteridophyta										
<i>Cibotium chamissoi</i>		3490	5670	6300		5875	4650	5725	210 4825	
<i>Gleichenia linearis</i>			8950			3850				
<i>Lycopodium cernuum</i>		350	6660	150				570		
<i>Nephrolepis exaltata</i>		204	3525	16,000						
<i>Pityrogramma calomelanos</i>										
<i>Polypodium phymatoides</i>						210				
<i>Sadleria cyathoides</i>		1795	6100	1550		1200		1200		
<i>Stenoloma chinensis</i>										
Spermatophyta										
Monocotyledons—Gramineae										
<i>Digitaria decumbens</i>	64		780							
<i>Paspalum conjugatum</i>			1400			2525 (young shoots)			115	
<i>Paspalum orbiculare</i>										
<i>Setaria geniculata</i>			1540							
<i>Sporobolus capensis</i>			5475							
Monocotyledons—Orchidaceae										
<i>Spathoglottis plicata</i>			3550							
Dicotyledons										
<i>Cassia leschanaliliana</i>			660			1600				59 60
<i>Macadamia ternifolia</i> (var. 246)										
<i>Macadamia ternifolia</i> (var. 333)										
<i>Melastoma malabatricum</i>						5500 (terminal shoots) 70 (terminal shoots)		10,300		
<i>Metrosideros collina</i> subsp. <i>polymorpha</i>			247			250			250 110	
<i>Psidium guajava</i>										
<i>Rhodomyrtus tomentosa</i>										
<i>Solanum nodiflorum</i>		3850	680							
<i>Stachytarpheta cayannensis</i>										
<i>Styphelia tameiameia</i>				880						

in the Polypodiaceae and *Cibotium chamissoi*, contained very low levels of aluminum where they were encountered.

Among the monocotyledons, the common, naturalized, wild orchid, *Spathoglottis plicata* was found to have a sufficiently high aluminum content in the leaves (3550 p.p.m.) to be classed as an accumulator but the single determination is considered insufficient for a firm decision. This is the first known positive report for orchids.

The three positive finds for the grasses are thought to be especially interesting because of their involvement in the phosphorus metabolism of herbivores and because of negative reports for 16 species by Webb (1945), and for the family in general by Hutchinson (1943). Costin (1954) is the only known source of a positive graminaceous determination. All three of the species of grasses with high aluminum are common in the native pastures on the acid soils of the high rainfall areas in Hawaii. Yellow foxtail (*Setaria geniculata*) was relatively low (1540 p.p.m.) for a single determination, but rattle grass (*Sporobolus capensis*) contained more than 5000 p.p.m. in the Haiku area. Rice grass (*Paspalum orbiculare*) qualified as an accumulator in all three of the collection locations and shows a tendency toward increased aluminum content with age as well as a wide range (1400–5970 p.p.m.). It should be pointed out that the accumulation of aluminum in a forage grass may account in part for the observed phosphate deficiency symptoms of cattle grazing in these areas since it has been shown (Hutchinson, 1943) that ingestion of aluminum lowers phosphorus levels in blood, bone, and urine of several other animals. Hilo grass (*Paspalum conjugatum*) and fountain grass (*Pennisetum ruppelii*) were low in aluminum where they were collected and the introduced pangola grass (*Digitaria decumbens*) was very low.

The dicotyledons of interest, other than *Melastoma*, are the dark-blue-fruited nightshade, or popolo, *Solanum nodiflorum*, which

TABLE 2
ALUMINUM CONTENT, DOMINANT SOIL MINERAL,
AND CLASSIFICATION OF HAWAIIAN SOILS FROM WHICH
PLANT SAMPLES WERE TAKEN

SOIL SERIES	GREAT SOIL GROUP	DOMINANT SOIL MINERAL	ALUMINUM CONTENT (% Al ₂ O ₃)
Haiku	Humic ferruginous latosol	Free oxides	25–40
Kapaa	Aluminous ferruginous latosol	Free oxides	40–60
Kukaiau	Humic latosol	Free oxides, amorphous minerals	20–35
Honokaa	Hydrol humic latosol	Free oxides, amorphous minerals	15–30

was high (3850 p.p.m.) in aluminum, and Japanese tea (*Cassia leschenaultiana*), which was positive on Maui but not on Kauai. The widespread and remarkably adaptable ohia lehua (*Metrosideros collina* subsp. *polymorpha*) was very low, as was the closely related Macadamia nut (a member of the Proteaceae). These two plants and pangola grass show such low levels of aluminum that a metabolic device for excluding aluminum seems probable. *Rhodomyrtus* contains a slightly low level but guava (*Psidium guajava*) maintains a consistently "average" value even on soils varying widely in aluminum content (Table 2). Although a more intensive sampling program may reveal more members of these categories as well as more samples of an intermediate nature, it seems reasonable to classify the plants sampled—all calcifugous species growing on soils of low pH, and highly leached root zones—into the following categories:

1. Plants that exclude aluminum to some degree
2. Plants that take up aluminum
 - Facultative accumulators
 - Obligate accumulators
3. Plants indifferent to aluminum in the substrate

Supporting physiological evidence is needed

but it can be inferred from reports in the literature that the exclusion or accumulation of aluminum is closely related to the phosphorus metabolism of a particular species, and that presumably the phosphorus balance in the plant can be maintained either by restricting the intake of aluminum which precipitates phosphorus, or by precipitating aluminum in the leaf or other tissue in a form that will not interfere with the phosphorus metabolism.

SUMMARY

The aluminum content of selected Hawaiian plants was determined using the "aluminon" method. The plants were obtained largely from highly leached latosol soils of low pH known to have a high aluminum content. Aluminum content of some species classed as accumulators of aluminum agree closely with literature sources. High levels of aluminum are reported for the first time from some common grasses (*Sporobolus capensis* and *Paspalum orbiculare*) and from an orchid (*Spathoglottis plicata*). Thirteen of 23 species qualified as accumulators (>1000 p.p.m.) and others had unusually low aluminum levels. A classification scheme to include "aluminum-excluders" is proposed and the relationship to phosphorus metabolism is discussed, including the possible influence of plant aluminum on phosphorus levels of grazing herbivores.

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Tagging of Skipjack in Hawaiian Waters

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THE FISHING of the Hawaiian skipjack (*Katsuwonus pelamis*) though relatively small if compared with the major fisheries of the United States, is the most important commercial fishery in the Hawaiian Islands and the only American fishery exploiting mid-ocean stocks of skipjack. Annual landings average about 11,000,000 pounds with a value to the fishermen of about one and a half million dollars.

The Pacific Oceanic Fishery Investigations (POFI), of the U. S. Fish and Wildlife Service, is engaged in a skipjack tagging program which, it is hoped, will provide information that will increase the effectiveness of the local fishery. Tagging offers a direct means of increasing our knowledge of the growth rates, general migrations, and inter-island movement of the fish. In this report we will describe the type of tags used and the results of our initial studies during the years 1954 to 1956.

A major difficulty in early tuna tagging investigations (Rounsefell and Kask, 1945; Wilson, 1953) was the lack of a suitable tag. Alverson and Chenoweth (1951) contributed to the development of a better tag by their water tunnel experiment to determine the effect of flowing water on various tags attached to frozen albacore (*Germo alalunga*). Following this work, the California Department of Fish and Game developed a tubular plastic tag (Wilson, 1953) and used it extensively for tagging albacore, yellowfin (*Neothunnus macropterus*), and skipjack tuna (Ganssle and Clemens, 1953; Blunt, 1954);

this tag is often called the type G or spaghetti tag.

Prior to announcement of the successful California tag, POFI experimented with several other types, both at sea and in ponds. These tests involved internal tags and external tags of the hook and streamer type. Experiments conducted in 1950 and 1952 were either inconclusive or unpromising, so the California tag (Fig. 1) was adopted for use in Hawaiian waters from 1954 to 1956.

APPLICATION OF THE TAGS

The type G tag was applied in the manner described by Wilson (1953), with certain modifications. Skipjack were caught by live-bait fishing methods as described by June (1951), with 3 or 4 men in the racks. A skipjack was hooked, swung up, caught by the fisherman, passed to a man designated as "holder," the tag was attached, and the fish was returned to the water. With an experienced crew a skipjack could be tagged and returned to the water in about 20 seconds.

Because it is difficult to handle skipjack without injuring them, various methods including canvas cradles, padded boxes, and electronarcosis were used in attempts to calm the fish. None of these was successful. Since it was deemed necessary to return skipjack to the water as rapidly as possible and since our efforts to quiet the fish were unsuccessful, no attempt was made to measure individual fish. Instead an estimate of the size of skipjack tagged was obtained by measuring fish which were caught and not tagged. Brock (1954) has shown that skipjack school by size, so it was believed that a reliable estimate of the size of tagged fish was obtained in this manner.

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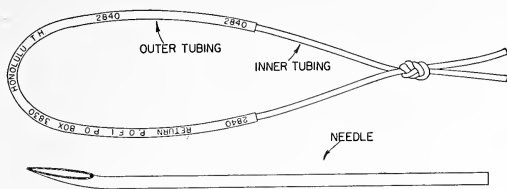


FIG. 1. California type G tag and tagging needle. Legend is on inner tubing only; serial numbers on inner and outer tubing.

Most of the skipjack tagged as described above sounded immediately upon release. On a few occasions they were seen to lead fish from the accompanying school away from the stern of the vessel. While some tagged fish left the school when released, there were indications that others remained in the same school from which they were caught. In one instance a fish released with a white type G tag was observed accompanying the vessel with part of the school for 4½ hours.

RELEASES

Between May, 1954, and July, 1956, 1,961 skipjack were tagged with the California type G tag and released in Hawaiian waters (Fig. 2).²

Most of the releases were within the area of the Hawaiian skipjack fishery; a few were released outside this area. This release pattern was followed in order to (1) establish the rate of recovery within the fishery, (2) study the movements of skipjack within the fishery, and (3) ascertain the direction from which skipjack approach Hawaiian waters.

It should be pointed out that the tagged fish were smaller than the usual size (18–22 pounds) composing the season's commercial landings. Eighty-five per cent were 10 pounds or smaller, 14 per cent between 11 and 20 pounds, and only 1 per cent larger than 21 pounds. The small percentage of releases in

² In addition, 20 skipjack were tagged with white type G tags and released in the vicinity of the Line Islands, and 12 with blue type G tags northeast of Midway Island.

the larger size categories is due partly to the difficulty in handling these fish, and partly to the general scarcity of large fish when most of our tagging was done.

PUBLICITY PROGRAM

Publicity is an important part of most tagging programs, because one way to maximize the returns is to minimize the loss of tags recovered but not noticed by persons unaware of the program. We conducted personal interviews with skipjack fishermen on all islands and distributed posters to major fishing companies, fishing supply centers, and ports throughout the Hawaiian Islands. Fishermen were also informed of our tagging activities through radio broadcasts, transmitted by POFI vessels during their cruises in Hawaiian waters, and through informal letters. Also, wardens of the Hawaiian Division of Fish and Game stationed on the various islands were furnished photographs of tagged skipjack, together with standard recovery information forms. Because of the distinctive appearance of the tag, the publicity program, and the extensive handling of individual fish (when caught, during stowage and unloading of catch, and during butchering at the cannery), the possibility of loss of tags through nonrecognition of tagged fish was considered negligible.

Rewards for the return of tags were not part of the recovery program. Instead we purchased the tagged fish at a price slightly above the market value. A letter giving pertinent information was also sent to the person, or persons, involved in the recovery.

RECOVERIES

Of the 1,961 skipjack tagged and released, 9 were recovered by the commercial pole-and-line fishery and 3 from the stomachs of large longline-caught tunas between July, 1955, and February, 1956. The areas of release and recapture for these 12 skipjack are shown in Figure 3 and listed in Table 1. The low rate of recovery, 0.6 per cent, may be attributed in

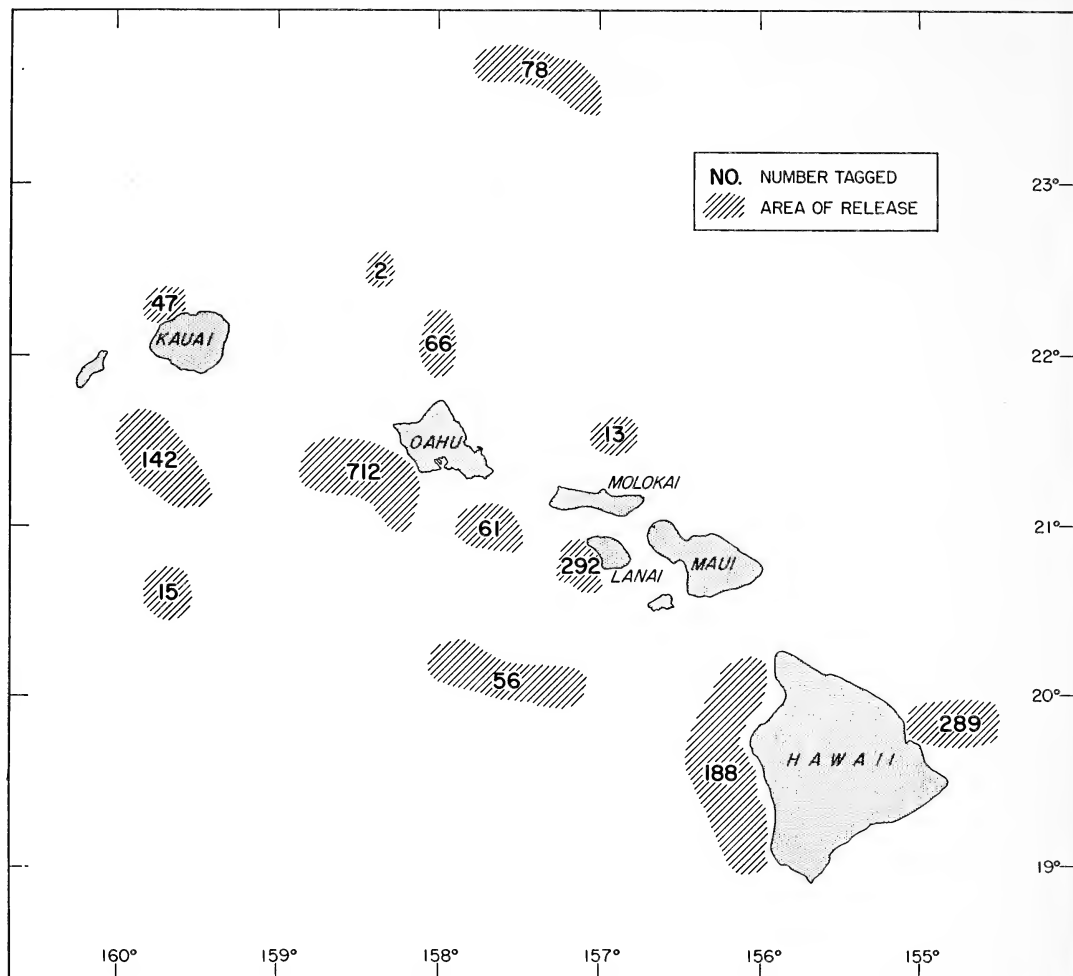


FIG. 2. Skipjack releases in Hawaiian waters, May 1954-July 1956.

part to a combination of the following factors: (1) the initial tagging mortality resulting from handling in the tagging process may have been high; (2) mortality caused by predation of large tunas and spearfishes may have been excessive; and (3) certain groups of tagged skipjack may have moved out of the area covered by the fishery.

Condition of Tags and Fish: The condition of the tag and of the skipjack was noted for each of the 9 pole-and-line caught recoveries. One fish, recaptured after only 6 days at liberty, showed quick recuperation. The tag wound

appeared raw and enlarged but there were no signs of infection. Another skipjack, retaken 12 days after tagging, had new skin forming around the edges of the tag wound.

Most of the recovered fish showed a slight chafing of the anterodorsal margin of the caudal fin, caused by the free ends of the tag striking the fin. This could be prevented by trimming the ends of the tag after the knot was tied.

One skipjack recaptured 252 days after release bore only the outer jacket portion of the tag. This protruded from the right side of the fish. The wound on the left side had

TABLE 1
POFI SKIPJACK RECOVERIES WITH WHITE CALIFORNIA TYPE G TAG

ORDER OF RECOVERY	WEIGHT RANGE OF SCHOOL AT RELEASE	DATE TAGGED	DATE RECOVERED	DAYS OUT	DISTANCE TRAVELED	WEIGHT AT RECOVERY	REMARKS
	Lbs.				Miles	Lbs.	
1	5-10	6/1/55	7/12/55	41	0	3-4	Recaptured from one school
2	6-8	6/8/55	7/12/55	34	0	3-4	
3	3-5	7/20/55	7/26/55	6	40	4	
4	5-8	7/18/55	7/30/55	12	0	6	Found in stomach of longline-caught 189-lb. yellowfin
5	3-6	8/22/55	8/24/55	2	6	3½	
6	3-5	7/20/55	8/28/55	39	17	4	Tag only found in stomach of longline-caught 190-lb. yellowfin
7	4	8/17/55	8/17- 8/26/55	0-9	0(?)	-	
8	3-5	8/25/55	8/25- 9/1/55	0-7	0	4	Found in stomach of longline-caught 209-lb. big-eye
9	4-5	8/8/55	8/29/55	21	14	3	Recaptured from same school
10	4-5	8/8/55	8/29/55	21	14	3	
11	4-5	8/8/55	10/29/55	82	9	4½	
12	5½-9½	5/25/55	2/1/56	252	30	14	

healed completely and was marked only by a black spot on the skin (Fig. 4). Adhesion between the flesh and the plastic held the tag in place.

Movement: All of the skipjack recovered were small (3 to 10 lbs.) when tagged. They showed surprisingly little movement, all of them being recaptured within 40 miles of the point of release (Fig. 3 and Table 1). There was no inter-island movement of tagged fish. The probability of recovery of tagged skipjack in offshore waters (beyond 50 miles from land) is low because very little fishing is done in this area. However, each of the main Hawaiian islands has fisheries within 20 miles of shore, so this lack of evidence of inter-island movement cannot be attributed to the distribution of fishing effort.

Two of 39 fish (Table 1, recoveries 9 and 10) released in one group were recaptured 3 weeks later from a single school, indicating that a school of skipjack retains its identity as a unit for some time. Recoveries 3 and 6 tagged on the same day and from the same school, may provide an example of the use-

fulness of this hypothesis. This school may have traveled 63 miles between July 20 and August 28, 1955; 40 miles to where No. 3 was retaken, and 23 miles back to where No. 6 was retaken. Similarly, the group in which recoveries 9, 10, and 11 were released may have traveled a minimum of 37 miles between August 8 and October 29, 1955. These are straight-line distances, and in all likelihood a much greater distance was covered during this period.

Growth: Information concerning the rate of growth of skipjack was gained from a tagged fish which weighed 14 pounds when recovered after 252 days (8.4 months) at liberty. Based on the average weight of fish (7 pounds) and the size range of fish (5.5 to 9.5 pounds) in the school at the time of release, a comparison may be made with the growth rates obtained by Brock (1954) in his length frequency studies. If this tagged fish was at the lower end of the size range (i.e., 5.5 pounds) when tagged, it grew at the rate of about 1.0 pound per month. This closely approximates Brock's estimate of 1.2 pounds

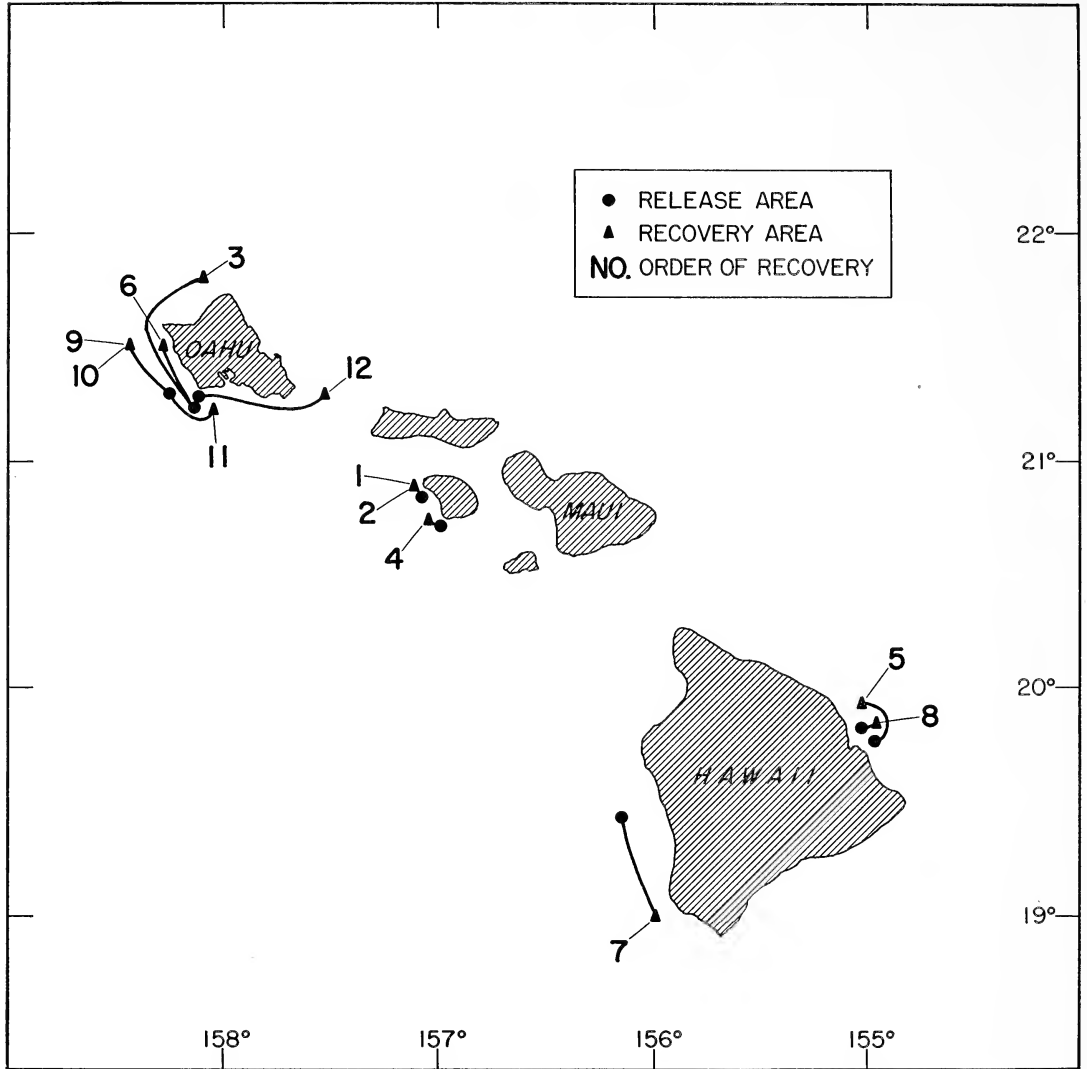


FIG. 3. Skipjack recoveries in Hawaiian waters, July 1955–February 1956.

per month for skipjack of this size (from his fig. 2). If the fish was of average size (i.e., 7 pounds) at the time of release, then a growth of 0.8 pound per month is indicated, which is slightly more than one-half the growth of 1.4 pounds per month shown by Brock. Finally, if the fish was at the upper limit of the size range (i.e., 9.5 pounds), it grew at the rate of 0.5 pound per month, or one-third the rate of growth of 1.5 pounds per month indicated by Brock.

Predation: There was evidence that some

loss of tagged skipjack resulted from predation. Two tagged skipjack and one tag were recovered through incidental examination of stomachs of large tuna caught by longline near the island of Hawaii (recoveries 5, 7, 8 in Table 1). All three skipjack weighed about 4 pounds and were recovered within a few days of release. They were the only recoveries of skipjack released in that area.

In order to determine the incidence of skipjack, tagged or untagged, in the stomachs of larger fish, a sampling program at the

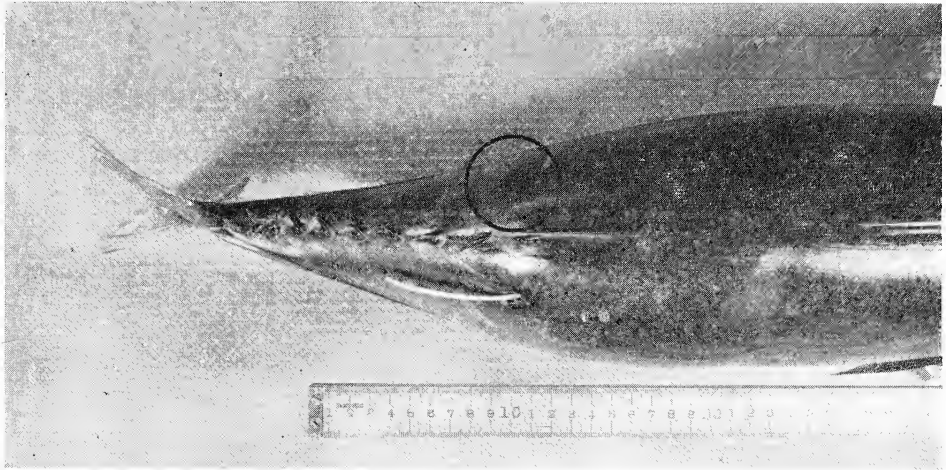


FIG. 4. Tagged skipjack recovered 252 days after release with only the jacket portion of the tag still in place. Dorsal view showing healed wound (dark area in circle) on the left side. Photograph by E. D. Stroup.

Honolulu auction markets was carried out between October, 1955, and June, 1956. During this interval, which included periods when skipjack were being tagged and released within the fishery, stomachs were examined from 538 bigeye (*Parathunnus sibi*), 103 yellowfin, 128 striped marlin (*Makaira audax*), and 74 black marlin (*Makaira ampla*) taken in the Hawaiian longline fishery. Twenty-eight of these stomachs (3.3 per cent) contained a total of 30 skipjack, none of which was tagged. Furthermore, only 9 of the 30 skipjack were as large as those being tagged, i.e., 2 pounds or larger, and the rest were estimated to be 1 pound or less. Only one large skipjack was taken from the stomach of a tuna; the others were from black and striped marlins. Unfortunately, there are no comparable data concerning the number of untagged skipjack from stomachs at the time the three tagged fish were found, but on the basis of subsequent sampling it seems that there was a higher rate of predation on tagged than on untagged fish.

SUMMARY

A tagging project was inaugurated to study migrations and to supplement our knowledge

of growth of skipjack in Hawaiian waters.

During the period 1954–1956, California type G tags were attached to 1,961 skipjack released in Hawaiian waters. The majority of these fish weighed less than 10 pounds.

Only 12 or 0.6 percent of these fish were later recovered. This low recovery rate may be attributed to tagging mortality, predation, and movement out of the fishery.

The longest interval between release and recovery, by pole-and-line fishing, was 252 days and the shortest interval was 6 days.

Net movement was limited to 40 miles or less and no inter-island travel was shown.

The tag wounds on recovered skipjack were enlarged but well healed after 12 days. When used on smaller fish, the free ends of the tag caused chafing of the anterodorsal margin of the caudal fin.

One skipjack weighing 14 pounds at recovery grew at an estimated rate of 0.8 pound per month over an 8½-month period.

Predation by large tunas and spearfishes may be greater on tagged than on untagged skipjack. This conclusion is based on the recovery of three tagged skipjack from the stomachs of large tuna.

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The Synonymy of the Viviparous Polychaete *Neanthes lighti* Hartman (1938) with *Nereis limnicola* Johnson (1903)

RALPH I. SMITH¹

Nereis limnicola was described by Johnson (1903) from the fresh-water Lake Merced in San Francisco, California. Since that time no reports of its occurrence have been published. Hartman (1938) noted that the boundaries and bed of the lake have been "altered by dredging and roadbuilding operations, and that what was once the type locality of *Nereis limnicola* now lies many feet below a road bed." In 1938 Hartman described *Neanthes lighti* from small estuaries on the coast of Marin and Sonoma counties to the north of San Francisco, and from pools described as fresh along the Russian River. In this paper Hartman mentions *N. limnicola*, but does not discuss the possibility of the two forms being synonymous. Later she has stated (Light *et al.*, 1954: 88) that *N. lighti* "may prove to be *Nereis limnicola* . . ." In 1941, *N. lighti* was found to be viviparous by Dr. Marian Pettibone (reported by Hartman, 1944: 252), and an account of its embryology has been given by Smith (1950). Since viviparity and the ability to live in fresh water are rare among polychaetes, and since *N. lighti* seems to offer excellent experimental material, it is important that its identity be clearly established.

In recent years, reports of the existence of fresh-water nereids in Lake Merced have reached us, and search revealed them. A viviparous nereid answering the descriptions of *N. limnicola* and *N. lighti* has been found in abundance in a sandy beach on the northern shore of the northern part of what was originally the single lake. The type locality

described by Johnson ("the outlet of a 'slough' on the eastern shore of the southern arm of the lake") has indeed been filled for a roadbed, as Hartman stated, and yielded no specimens, although further search at lower water levels may reveal them; the present substrate is not especially favorable.

The finding of this material makes possible a comparison of *N. limnicola* and *N. lighti*. Johnson's description (1903) fits both species well, except that he did not notice viviparity in *N. limnicola*. Hartman's description (1938) also fits both, except that she did not observe in *N. lighti* a feature remarked upon by Johnson (1903: 210), namely, the presence in posterior neuropodia of a "stout, falcate type of setae . . . in which the appendage is firmly ankylosed to the shaft, the whole forming one continuous piece." As for the first discrepancy, it is clear that the Lake Merced population is viviparous, precisely in the fashion described in the Salinas River population of *N. lighti* by Smith (1950), and subsequently observed in populations from other localities along the coast as far north as the Canadian border. As for the second discrepancy, in 1951 the writer examined, in the U. S. National Museum, two specimens of *N. limnicola*, Cat. no. 5166, collected in Lake Merced on Oct. 29, 1895, by H. P. Johnson, and labeled as "type specimens." At that time I also inspected the type lot of *Neanthes lighti* Hartman, USNM Cat. no. 20537. The fused setae as described by Johnson are present in both groups of specimens, as they are in all *N. lighti* of the writer's collections, and the parapodia of both lots answer Johnson's de-

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scription; there is not the marked reduction of the median lobe in posterior parapodia mentioned by Hartman. Hence there is no reason to doubt that the two are identical, and that the viviparous nereid commonly called *Neantbes lighti* should be known as a synonym of *Nereis limnicola* Johnson (1903).

Since the viviparity of *N. limnicola* is the consequence of hermaphroditism making possible internal self-fertilization (Smith, 1950), *N. limnicola* must be regarded as an entity reproductively isolated from certain nonviviparous but morphologically very similar species. A more extended discussion of the implications of this contention is to appear elsewhere (Smith, 1958).

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On a New Species of *Caligus* (Copepoda Parasitica) from the Coast of California

SUEO M. SHIINO¹

AMONG THE MATERIAL of parasitic copepods which Dr. W. L. Klawe of the Inter-American Tropical Tuna Commission collected from fishes in the eastern Pacific and sent to the author for identification, there was an interesting specimen representing a new species of the genus *Caligus*. The specimen, consisting of a single female, was obtained off the coast of California. It has been preserved together with the host, *Engraulis mordax*, to whose body it was firmly clinging. The present note contains the description of this parasite.

The author wishes to express his thanks to Dr. Klawe for providing the present material, and takes a great pleasure in associating the name of the species with the naturalist.

Caligus klawei sp. nov.

Figs. 1-3

A female found on a specimen of *Engraulis mordax* 7.9 cm. long, taken off Coronado Hotel, San Diego, California, late in May, 1956. It was clinging to the side of the host above the pectoral fin. The anterior region of the body is lapped by a fleshy fold which is an abnormal outgrowth of host skin caused by the presence of the parasite.

Body flattened, length excluding rami 5.46 mm., carapace excluding marginal rim 2.39 mm. \times 1.71 mm., fourth thoracic segment 0.21 mm. \times 0.61 mm., length of exposed region of same 0.07 mm., genital segment 2.47 mm. long on midline, 2.89 mm. long in lateral region, 2.25 mm. wide, abdomen 0.56 mm. \times 0.61 mm. Color whitish in formalin, without pigment.

Carapace elongate oval, about three quarters as wide as long, somewhat more strongly

convex above than in ordinary case, with lateral regions turning downward. Two sides very widely curved and fringed by relatively narrow rim. Frontal plates two thirds the width of carapace, only slightly arched on margin and provided with a lunule close to each lateral end. Median lobe half as wide as the carapace at its base, and about as long as it is wide. It is roughly trapezoid in shape, with well-rounded corners, and extends considerably beyond the lateral lobes. Sinuses between adjoining lobes are shallow and narrow, opening backward. The transverse dorsal rib is placed at about the center of the carapace, and arches forward to make, together with the incurved posterior halves of the longitudinal ribs, a continuous semicircle. Anterior halves of the latter extend diagonally outward, separating narrower lateral areas from the broader central area, in the center of which the eyes are located. Fourth thoracic segment is covered by carapace in front and by genital segment in the rear, showing merely a very short central region in dorsal aspect. Genital segment is a huge quadrangular segment which is produced backward on either side of abdomen into a pair of oval lobes. Anterior end is contracted into a short neck, but expanded just behind this abruptly to form gracefully round shoulders which continue back to slightly arched lateral margins. Segment as long as carapace on the midline, but one fifth longer on the lateral region; width across middle of segment is one and one third that of carapace. Abdomen is about a quarter of preceding segment in length, beyond whose lateral lobes it extends only a little. It is one-segmented, as long as wide, and has slightly undulated sides and V-shaped caudal margin.

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FIG. 1. *Engraulis mordax* infected by *Caligus klawei* sp. nov. $\times 2.5$.

First antennae two-jointed as usual. Apical joint ends in several delicate hairs and two thicker spines, and bears a solitary hair at about the center of its side. Basal joint triangular and fringed by three or four rows of stout pinnate spines on frontal margin. Lunules semicircular, truncate on front side. Second antennae three-jointed. Terminal joint sharp, strongly curved and carrying two tiny spinules, one at the base and the other a short distance distally. Basal joint armed with a pointed, spurlike posterior process. Mouth tube has broad apex, enclosing slender mandibles well dentate on their curved apical blade. First maxillae small in size, apex hook-like, base oblong and furnished on the surface with two delicate hairs, each arising from a papilla. A similar hair present on the sternum behind the maxilla. Second maxillae broad at base, slender toward tip and directed straight backward; exopodite made up of one longer and two shorter spines. First maxillipeds slender; terminal joint longer than basal joint, ending in two unequal claws with finely pectinate, narrow rims and carrying a narrowly triangular accessory lamina a short distance behind. Second maxillipeds cheliform, moderately stout. Their palm fusiform, about thrice as long as wide and with a very slight bulge at about the center of inner margin. Finger straight in its basal half, but terminating in a strongly curved, sharp claw which

acts against the bulge of the palm. Claw bears two short spines at its base. Sternal furca V-shaped, branches uniform in breadth, blunt at tip and without marginal rim.

First swimming legs provided with triangular rudiment of endopodite. Protopodite of second legs indistinctly divided into two joints. Two rami of third legs widely separated from each other by a crescentic dilatation of basal apron; exopodite two-jointed, whereas endopodite is practically one-jointed, owing to almost complete reduction of basal joint. Fourth legs uniramous, having protopodite longer than two-jointed exopodite. Arrangement of spines and setae present in each of four pairs of legs is shown in Table 1.

Of the apical spines on the first legs, the middle two are deeply forked into parallel, unequal branches; the external branch is shorter and has fine pectination on the sides. The outermost of them is bifid to a very slight extent, and the innermost is simple and more than once the length of the others. Plumose spines borne on the third joint of first legs, on the exopodite of second legs, and on the first endopodite joint of the latter are rimmed on one side for some distance from the base by hairs which are shorter but stiffer than those fringing the opposite side and other regions. The similar spine on the protopodite of second legs is dilated at the base into a semicircle, where it bears stiff hairs

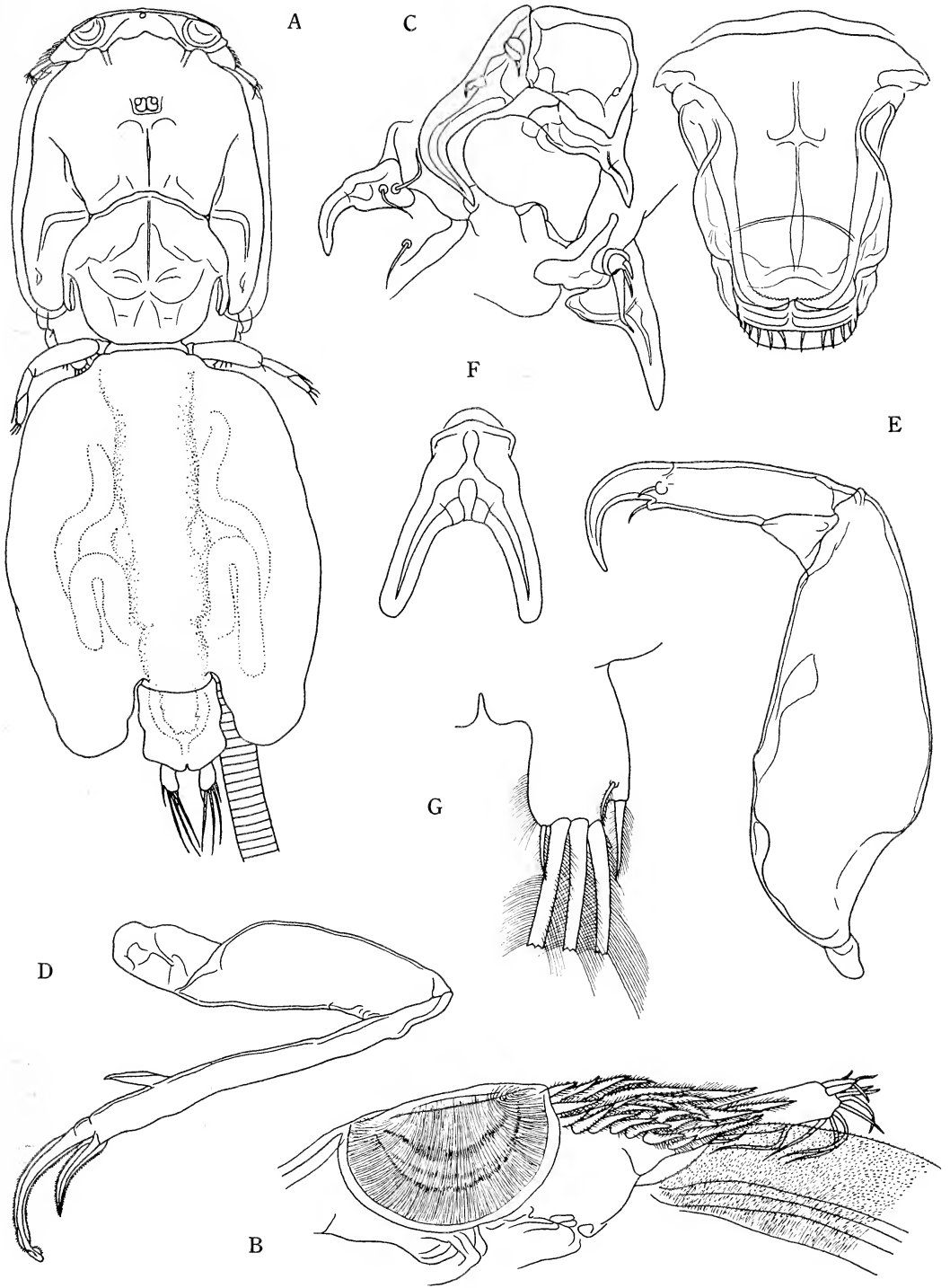


FIG. 2. *Caligus klawei* sp. nov. A, female, dorsal aspect; B, first antenna with lunule; C, second antenna, mouth tube and first and second maxillae in situ; D, first maxilliped; E, second maxilliped; F, sternal furca; G, uropod. A $\times 19$, B-G $\times 100$.

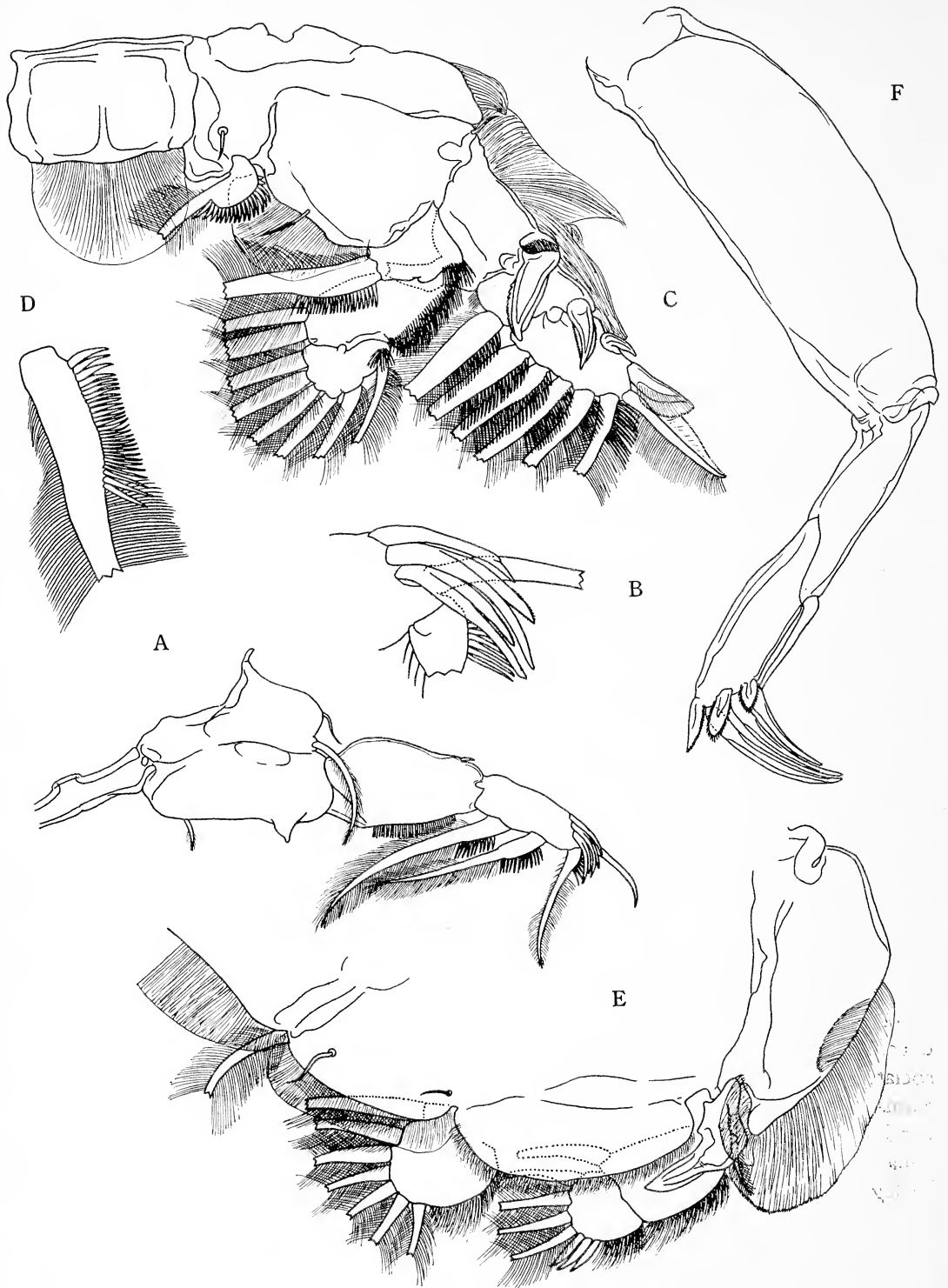


FIG. 3. *Caligus klawei* sp. nov. A, first swimming leg; B, apex of same; C, second leg; D, one of the spines on the exopodite of same; E, third leg; F, fourth leg. A, C, E, F $\times 100$; B $\times 340$; D $\times 170$.

TABLE 1
ARMATURE PRESENT ON SWIMMING LEGS

LEG	BORDER	STERNAL PLATE	PROTOPODITE		EXOPODITE			ENDOPODITE		
			I	II	I	II	III	I	II	III
I	outer inner		1s, 1p 1p		1rh c	3H, 1H 3P				
II	outer inner	f	1s, 1P	f, 1s f, 1s	f, 1H c, 1P	1H c, 1P	2H, 1Q 5P	c 1P	CC c, 1P	c 6P
III	outer inner	f	f, 1p 1P, f, 2s, c		1H', c c, 1P	c, 3h 4P		1P	c 6P	
IV	outer inner				1H	3H				

Abbreviations: c, row of hairs; CC, area covered with spinules; f, membranous flange; H, stouter simple spine; h, feeble simple spine; H', hooklike spine; P, stouter plumose spine; ph, feeble plumose spine; Q, spine rimmed with hairs on one side, with membrane on the other; rh, tiny spine; s, solitary hair. Roman numerals represent the ordinals of legs or of joints and Arabic numerals denote the number of spines, or of other armature present on each of them.

the same as those on the spines just named. External spine on the first two exopodite joints of the same legs acuminate toward the tip and has pectinate rims along two opposite borders; that of the first joint accompanies a basal lamina with parallel striation on its surface. The basalmost of external spines on the third joint of the same exopodite is much reduced in size, without rim; the middle spine has a broad striated membrane on the inner side, and the terminal one bears an inner row of hairs besides the outer membrane. Basal hook on the exopodite of third legs ends in a straight apex which is narrowed to a point resembling an arrowhead. Terminal spines on the fourth legs are equal in length except the outermost, which is slightly shorter; all of them are doubly edged with a narrow rim and associated at the base with a fusiform lamina, circumscribed with pectination. Spine on the second joint is simple and devoid of basal lamina. Genital segment lacks any trace of fifth legs. Caudal rami are small in size and terminate in three plumose spines, which are attended outside with two similar, but much shorter, spines and inside with another short one. Inner margin of the rami is fringed by a short row of hairs. Egg strings are longer than

the body and packed with uniserial, flattened eggs.

REMARKS

The new species is characterized, above all, by the enormous size of its genital segment, which surpasses the carapace in length and width. In the genus *Caligus*, there are a number of species which present certain resemblances to the new species in the outline of this segment, in its size relative to that of the carapace, and in the possession of a small one-segmented abdomen. To facilitate distinction of *klawei* from such species some of the characters are summed up in Table 2.

As may be seen from this table, no species has a genital segment so strongly expanded as that of *klawei*. It is, however, close to *polycanthi*, *glandifer*, *fistulariae*, and *macarovi* in the outline of this segment. The first of these has the second maxillipeds stouter than in *klawei*, the second has the same limbs feeble, and the others are longer in the abdomen, which in them extends considerably beyond the foregoing segment.

The specimen will be preserved in the museum of the Prefectural University of Mie.

TABLE 2
COMPARISON OF *Caligus klawei* WITH ALLIED SPECIES

	G.L/C.L	G.W/C.W	FOURTH LEG	
			Number of joints of exopodite	Number of spines
<i>alalongae</i> Kröyer (after Kirtisinghe) ¹	1.00	0.66	3	0), 1, 1, 3
<i>alatus</i> Heegaard	0.70	0.77	2	0), 1, 3
<i>bicycletus</i> Heegaard	0.92	1.00	3	0), 1, 1, 3
<i>fistulariae</i> Yamaguti	0.86	0.82	2	0), 1, 3
<i>glandifer</i> Shiino	0.81	0.68	2	1), 1, (1) 3
<i>macarovi</i> Gussev ²	0.77	0.87	2	1), 1, 3
<i>minimus</i> Otto (after Brian)	1.00	0.73	2	1), 1, 3
<i>polycanthe</i> Gnanamuthu	0.66	0.77	2	0), 1, 3
<i>zei</i> Norman and Scott	0.71	0.76	2	1), 1, (1) 3
<i>klawei</i> sp. nov.	1.21	1.31	2	0), 1, 3

C.L = length of carapace; C.W = width of same; G.L = length of genital segment; G.W = width of same. Proportion of genital segment and carapace is taken from the drawings given by the original authors unless otherwise indicated. Numerals shown in the rightmost column represent from the left to the right the number of spines on each of joints from basal to apical in due order. They denote, when put in parentheses, the spine borne on the outer border of joint, otherwise the terminal spines. Presence or absence of spine on the protopodite is indicated by 1) or 0).

¹Kirtisinghe's *alalongae* does not seem conspecific with Kröyer's.

²*C. fulvipurpureus* Shiino is a synonym of *macarovi*.

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Intraspecific Variation in the Purple Secretion of the California Sea Hare, *Aplysia californica* Cooper

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THE SEA HARE is probably best known because of the red to purple fluid secreted from the margin of its mantle. There is only a superficial resemblance between this secretion and that of the genus *Murex*, which is the source of the anciently famous dye, "Tyrian" or "Royal Purple." *Aplysia* purple, however, found no practical use, probably because of one important deficiency—it turns a dirty brown upon exposure to air and sunlight.

Our knowledge of the nature and composition of aplysia purple has been increased periodically since DeNegri (1876) presented a series of beautifully colored spectra. The most significant of the early papers is that of MacMunn (1899), who attempted an analysis but concluded that there was no reason to believe that aplysia purple was composed of more than a single component. Durrien and Turchini (1925) published a minor observation which, unfortunately, was recognized as the oldest literature on the subject by some later authors. Schreiber (1932) presented the results of an extensive study of aplysia purple. He divided the purple into two components, one of which he showed to be a substance similar to urobilin and the other its precursor substance, which is also pigmented but very unstable. Fontaine and Raffy (1936) made suggestions as to the possible source of the

pigment molecules from the food of the sea hare. Lederer and Hutterer (1942) used chromatographic columns to separate the two components found in the pigment. Fox (1953) summarized the work of the three last-mentioned authors. Christomanos (1955) presented a summary of biochemical studies on the purple of a questionable species he specified as *A. depilans*. He also reported isolating a green band on his powdered sugar column from the purple of the *Aplysia* which he refers to as *A. depilans*. He was unable to obtain sufficient concentrations to produce a spectrum.

The present writer noticed that there was a gross color difference between young animals and adults of the west coast sea hare, *Aplysia californica* Cooper, the younger producing a bluer, the older a more reddish secretion. Experiments to test the cause of this phenomenon led to more basic studies of the composition and instability of aplysia purple.

MATERIALS AND METHODS

To obtain aplysia purple uncontaminated by salt water, specimens of *Aplysia californica* Cooper at Lunada Bay, Palos Verdes, California, were caught and the mantle area was rinsed with distilled water. This usually caused sufficient irritation to stimulate flow of the secretion but not enough to cause the opaline gland to discharge its contaminating viscous protein material. The aplysia purple was caught in small vials, to each of which a

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drop of hydrochloric acid was added to prevent degeneration. The material was returned to the laboratory where it was refrigerated or frozen for long-term storage. Spectrophotometric curves and chromatographic separations were made using 10 per cent hydrochloric acid as diluent. Spectrophotometric curves were run on a Beckman Model DU spectrophotometer.

The writer used two methods of analysis. Chromatographic columns were prepared, using corn starch packed in a column two feet deep, in four-foot sections of soft glass tubing ($\frac{3}{8}$ in., outside diam.). A very small piece of glass wool at each end of the column held the corn starch in place.

The tube was placed in a stopper which in turn fitted into a suction flask. Approximately one half cc. of aplysia purple was placed in the top of this column. As soon as the substance had penetrated the column, the top of the tube was filled with 10 per cent hydrochloric acid and suction was applied to the base of the column. About 8 hours later, when pigment had reached the bottom, the tube was removed and cut into sections corresponding with the color components. The starch was removed and the color components were eluted with dilute hydrochloric acid. Instead of cutting up the column, suction can be continued and each fraction can be caught as it drips from the bottom of the column. This method is very slow, requiring several days for one complete separation.

It was found that quicker determinations, especially where it was unnecessary to collect the fractions, could be made by paper chromatography. Several alterations in the methods were used, depending upon the nature and purpose of the particular investigation being carried on. Square sections of Whatman No. 1 filter paper measuring 18×18 cm. were spotted or lined with aplysia purple at a point $1\frac{1}{2}$ cm. from the margin which would become the base. The liquid was applied with either a fine pipette or with an Esterbrook No. 2 drawlet pen. Each paper was then

folded twice parallel to the line of travel of the components, after which the folds were relaxed enough so that the papers would stand without any two parts of the paper being in mutual contact. The papers were stood in petri dishes containing about $\frac{1}{2}$ cm. of dilute hydrochloric acid and each paper and its petri dish was then covered with a bell jar. Separations made by this method were complete in one hour. Great care was necessary, however, in making the original spot or line. Thin lines and small spots produced the best results, especially where the distance of upward migration was limited. Strips 3 feet long were used with large initial wide lines of pigment. These resulted in excellent separations but required from 8 to 12 hours. The papers were dried and stored until the time of elution. Lining rather than spotting simplified the separation and subsequent elution. The papers were cut into strips parallel with the original pigment line so that each strip contained only one color component. Elution was then made by "siphoning" dilute hydrochloric acid lengthwise through the strips thus formed.

EXPERIMENTAL DATA

To determine the spectrophotometric differences between the purple secretion of young specimens whose purple appears bluish and that of adult specimens which is of a reddish hue, studies were made upon diluted aplysia purple. The most striking differences, as shown in Figure 1, were: (1) the differences in relative height of the two peaks, and (2) the variation of $15 m\mu$ in the location of the broad peak in the high 500 region.

The components of the purple of *A. californica* were separated in quantity by column chromatography. Though no blue region was distinct as a separate band on the starch column, the collected fraction from the extreme trailing region of the lavender zone gave high concentrations showing a deep blue gross color, which produced a different absorption curve than that of the earlier lavender collec-

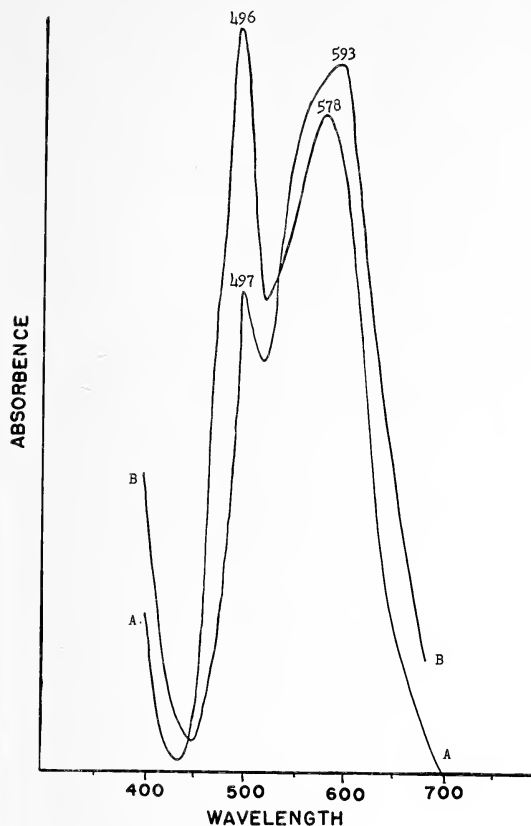


FIG. 1. The spectral curves of the aplysia purple taken from (A) a *Plocamium*-feeding adult, and (B) a young specimen showing no signs of feeding on *Plocamium*. The pigment was diluted in 10 per cent hydrochloric acid.

tions. The absorption spectrum (Fig. 2) showed a far sharper peak but a much less acute slope toward the red end of the spectrum than was noted earlier in the lavender collections. This suggested that it constituted a separate component. Paper chromatography was then tried as a means of separation, and by this it was possible to prove the existence of a third component of the aplysia ink of *A. californica*. On the dried paper a rhodonite pink component (Ridgway, 1912) left a wide band in the center of the paper. The second, a deep lavender, lagged behind at one-quarter the distance above the starting line. Scarcely clearing the initial line was a calamine blue area. Elution produced weak concentrations

of the pigments, but these were adequate to produce curves on the Beckman Model DU spectrophotometer. However, these papers were dried and stored before elution, and this treatment gave opportunity for oxidative changes (Fig. 2).

DISCUSSION AND CONCLUSIONS

Though a component was isolated which gave a virtually pure curve at 496 m μ (Fig. 3), the writer has never succeeded in isolating a fractional component with a peak in the high 500 region which did not also have a weak peak at 499.5 m μ (not 496). As this material having two peaks (which will be shown to be composed of more than one, separable, but similar components) stands under refrigeration over a period of time, the relative heights of the two peaks change. The D band peak decreases and the F band peak increases in height, with a gradual shift of the F band from 499.5 to 497 and finally to 496 m μ , eventually giving approximately the same spectrum and gross color as the original aplysia purple from which it was separated (Fig. 3).

Aplysia purple is believed to be a bilin (Fox, 1953), a linear chain of pyrrole molecules connected by $-\text{CH}=\text{}$ or $-\text{CH}_2-$ linkages, as it gives a positive Gmelin reaction. Brode (1955), by using commercial dyes, showed that the spectrophotometric effect of these linkages is insulating for $-\text{CH}_2-$ and coupling for the $-\text{CH}=\text{}$ configuration. In *Aplysia* the pyrrole molecules of the bilins seem to be joined by the insulating linkages when in the blue state, which thus inhibits the normal F band absorption characteristic of the chain of pyrrole molecules absorbing together. In time, these insulating linkages gradually change to coupling linkages, perhaps due to enzymatic activity or other causes as yet unknown. As Brode (1955) puts it, "If the linkage is changed to a conjugating (=coupling) connection . . . there is a marked change in the spectrum with the production of a single resonance structure involving both

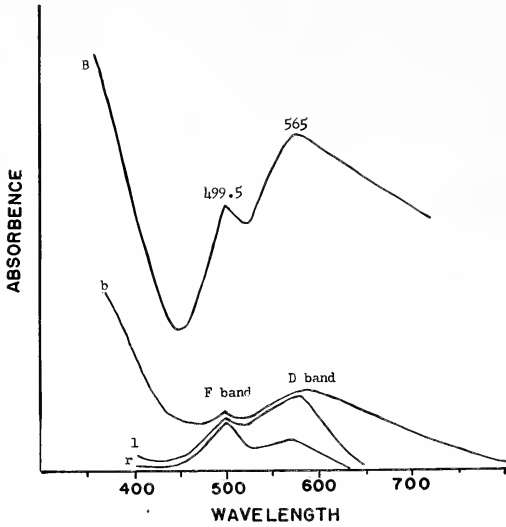


FIG. 2. Curve B shows the extreme trailing blue portion of the column chromatogram. The paper chromatographic curves are indicated by small letters. The curves of the rhodanite pink (r), the lavender (l), and the calamine blue (b) regions were read from weak solutions produced by eluting dried papers.

chromophores as a single coplaner chromophore." The curves he used as examples compare markedly with the curves of aplysia purple.

The writer has not yet found a satisfactory explanation for the instability of the D band absorption peak, which seems quite sporadic in its variation but doubtless follows well-defined laws.

Schreiber's work (1932) on the Mediterranean purple-producing *Aplysia* indicated that the peak in the F band (at approximately 500 mμ) represents the absorption by a substance similar to urobilin, and that the other peak in the high 500 region (Schreiber's broad unstable D band) represented the precursor of this substance. The above data confirm his theory.

It seems that the fast-growing young do not possess as much of the red finished product as do the adult specimens and hence secrete a larger percentage of the blue precursor substance. No basic differences other than that of relative quantity of the substance and its precursor are indicated by the spectrophotometric studies.

The condition of the individual animal is indicated as being highly influential in this respect as well. Well-fed adult specimens seem to have an excess of purple which is secreted at the slightest provocation, and often with no provocation at all.

The vertebrate bilins are derived from the breakdown of the tetrapyrrole molecules of hemoglobin. However, in plants tetrapyrrole molecules are the basis of chlorophyll. The quantities of aplysia purple produced would indicate a plentiful source such as chlorophyll, which is consumed in quantity by these algae eaters.

The bilichromes of the red algae may well be an additional rich source of the purple, as suggested by Fontaine and Raffy (1936). This is supported by the fact that adult animals feeding largely on *Plocamium pacificum*, which has a low chlorophyll but a high phycobilin content, usually produce a much greater quantity of pigment and with less provocation than those subsisting on other algae.

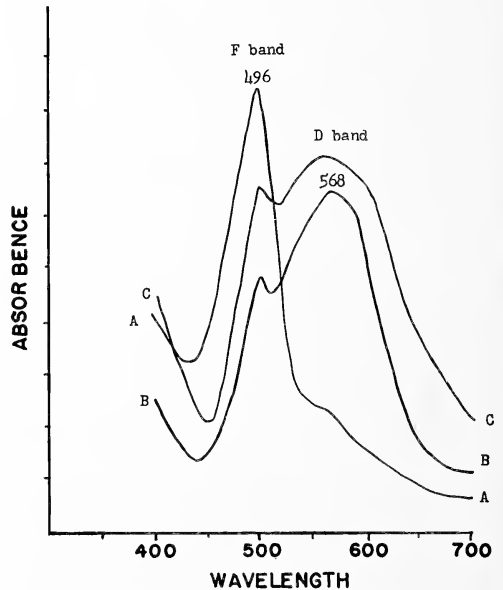


FIG. 3. The absorption spectra of the red (A), and composite lavender and blue (B) regions from the column separations. After the solution giving curve B had been in the refrigerator for two weeks it had changed its gross color and produced the curve marked C.

However, these other algae can not be the only source as the writer has kept small *A. californica* until they have approximately tripled in size while feeding them on parsley and celery tops, which contain none of the phycobilins, and he has found that they could still produce the purple secretion, though in reduced quantity.

Lederer and Hutterer (1942) followed current practice in naming the two components which they isolated from the purple of *A. punctata*. To the redder of the two components, which is the "urobilin" of Schreiber (1932), they gave the name *aplysiorhodin*; and to the bluer component, or the "urobilinogen" of Schreiber, they gave the name of *aplysi violin*. For convenience of identification the writer gives the name *aplysi azurin* to the additional blue component he has isolated from the secretions of *A. californica*.

Spectrophotometrically, this new blue component is responsible for the sharp rise in absorption below 425–450 m μ , as noted in all spectral curves produced by solutions from which it had not been removed. The rise was absent from the spectra of the other two components in the paper separations (Fig. 3).

Actually, in view of Schreiber's work (1932) *aplysi violin* would be the precursor of *aplysiorhodin*. It is not yet evident what the role of *aplysi azurin* may be.

SUMMARY

From the foregoing discussion of *aplysia* purple the writer proposes: (1) that there are two apparent absorption peaks in the spectrum of *aplysia* purple from *Aplysia californica* when hydrochloric acid is used as the solvent; (2) that the relative height of these two peaks indicates the proportion of precursor to finished product in the purple from an individual specimen; (3) that the gross color varies widely from animal to animal; (4) that col-

umn chromatography as used here is superior for large scale separations but poor for qualitative separation; (5) that paper chromatography is more sensitive and is superior for quick qualitative isolation of components into individual zones; and (6) that the purple of *A. californica* contains a third component, *aplysi azurin*, in addition to the major components, *aplysiorhodin* and *aplysi violin*.

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Spiders from Some Pacific Islands, III The Kingdom of Tonga

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THE KINGDOM OF TONGA consists of some 200 islands occupying an area in the south-west Pacific bounded by latitudes 15°S. and 23°31'S., and by longitudes 173°W. and 177°W. The islands fall into three groups, Vava'u in the north, Ha'apai in the centre, and Tongatabu in the south, the overall length being about 175 miles. All the islands are small; Tongatabu Island, 25 by 10 miles, is much the largest, and the total area is about 385 square miles. Most of them are elevated coral reefs and so are very low and flat. The highest point of Tongatabu Island is only 60 feet above the sea. A few are volcanic islands, and one of these reaches a height of 3,380 feet. During the year the maximum temperature varies between about 75°F. and 85°F., and there is a rainfall of about 80 inches. Hurricanes occasionally occur. The principal adjacent island groups are Fiji to the west and Samoa to the north, each 200 or 300 miles from Tonga.

Spiders have been described previously from Tonga by Koch (1872), Berland (1934), and Marples (1955). Apparently, no spiders have been collected on the high islands. The present collection consists of 34 species, and brings the total now recorded from 31 to 49 species. Of the spider fauna of adjacent island groups that of Samoa with 128 species is the best known. Sixty-six are recorded from Fiji, and, though unpublished records bring the total to 92, there are very many more to be found. The present list for Tonga is also doubtless far from complete, but a few com-

parisons can be made.

No Uloboridae are known (not even *U. geniculatus*, which is commonly found in houses), as compared with three in Fiji and six in Samoa. There are five species of Thomisids, against one in Samoa and one in Fiji, *D. praetexta* occurring in all three. The three Epeirid genera *Gasteracantha*, *Argiope*, and *Nephila* occur in Fiji and the islands to the west. *Gasteracantha* is not known in Tonga, but one species of *Argiope* is recorded from Tongatabu; this is the most eastern record for the genus in the southwest Pacific. Five species of *Nephila* are present, and the genus occurs also in Niue, some 200 miles to the east of Tonga, and doubtfully in Samoa. Of the 49 species recorded from Tonga 32 occur also in Fiji, and 32, not all the same species, occur also in Samoa.

I am indebted to my wife and son for collections of 14 species from each of the islands, Tongatabu and Vava'u. The greater part of the collection was made on various islands by Dr. N. L. H. Krauss, and I am grateful to him for the opportunity of examining it. The specimens will be deposited in the Bernice P. Bishop Museum in Honolulu.

In the descriptions the measurements were made with an eyepiece micrometer and are given in millimetres. The leg indices are derived by dividing the length of each leg by the length of the carapace, and the tibial indices, which give a measure of the stoutness of the legs, by dividing the combined lengths of the patella and tibia by the proximal breadth of the patella. The eye measurements are given in direct scale readings, so they indicate proportions only.

¹ Department of Zoology, University of Otago, Dunedin, New Zealand. Manuscript received July 14, 1958.

LIST OF THE SPECIES RECORDED
FROM TONGA

(T = Tongatabu, H = Ha'apai, V = Vava'u)

DICTYNIDAE

Dictyna bifasciata. V.

OONOPIDAE

Gamasomorpha loricata ? V.

SCYTODIDAE

Scytodes marmorata. T,V.*S. striatipes*. T,H,V.

PHOLCIDAE

Pholcus ancoralis. T,V.*Physocyclus globosus*. T.*Smeringopus elongatus*. T.

CLUBIONIDAE

Chiracanthium diversum. T,V.*C. furax*. T,H,V.*C. longimanum*. T.*Clubiona alveolata*. T,V.

SPARASSIDAE

Heteropoda venatoria. T,V.

THOMISIDAE

Diaea praetexta. T,H,V.*D. septempunctata*. T.*D. tongatabuensis*. T.*Hedana subtilis*. T.*H. pallida*. T.

SALTICIDAE

Ascyltus pterygodes. T,H,V.*Bavia aericeps*. T,V.*Erasmia nigrovittata*. T,V.*Hasarius insularis*. T.*H. albocircumdatatus* ? T.*Menemerus bivittatus*. T.*Mollicia microphthalma*. T,H,V.*Plexippus payculli*. V.*Thorellia ensifera*. T,V.*Trite longipalpis*. T.*Vitia albipalpis*. T.

LYCOSIDAE

Lycosa tongatabuensis. T.

THERIDIIDAE

Conopistha samoensis. T.*C. unimaculata*. T.*Rhombphaea cometes*. T,V.*Theridion adamsoni*. T.*T. albostriatum*. T,V.*T. aleipata*. T,V.

TETRAGNATHIDAE

Leucauge tuberculata. T,H,V.*Tetragnatha macilenta*. T,H,V.*T. panopea*. T.*T. keyserlingi*. T.

EPEIRIDAE

Cyclosa litoralis. V.*Cyrtophora moluccensis*. T,V.*Argiope plana*. T.*Epeira plebeja*. T,H.*E. tbeisi*. T,V.*Nephila flagellans*. T.*N. durvilla*. T.*N. prolixa*. T.*N. vitiana*. T.*N. tetragnathoides*. T.

DICTYNIDAE

Dictyna bifasciata L. Koch

4 Vava'u. New record, previously recorded from Samoa.

OONOPIDAE

Gamasomorpha loricata L. Koch

1 Female. Neiafu, Vava'u. The female is not specifically identifiable but those found throughout the Pacific are taken to be of this species. It is recorded from widespread localities, this being the first from Tonga.

SCYTODIDAE

Scytodes marmorata L. Koch

3 Female, 1 male. Neiafu, Vava'u. This has

been previously recorded from Tongatabu and is widespread in the Pacific.

Scytodes striatipes L. Koch

1 Female and 1 imm. Neiafu, Vava'u. 1 Female, 1 male. Ohonua, Eua Island, Ha'apai. Previously recorded from Tongatabu and widespread in the Pacific.

PHOLCIDAE

Pholcus ancoralis L. Koch

1 Female and 3 imm., 2 male and 1 imm. Nuku'alofa, Tongatabu. 1 Male. Neiafu, Vava'u. First records from Tonga, widespread in the Pacific.

Physocyclus globosus Taczanowski

1 Male. Nuku'alofa, Tongatabu. 2 imm. possibly this species. Vava'u. First records from Tonga, widespread in the Pacific.

Smeringopus elongatus Vinson

2 Female. Nuku'alofa, Tongatabu, whence it has been recorded. With the exception of a record from the Marquesas this species is known from the islands in the western and central regions of the south Pacific.

CLUBIONIDAE

Chiracanthium furax L. Koch

5 Female, 2 male. Nuku'alofa, Tongatabu. 1 Female, 2 male. Neiafu, Vava'u. 1 Female, 2 male. Ohonua, Eua Island, Ha'apai. Berland (1929), who described the male of *C. furax*, states that it differs from that of *C. longimanum* in having a hooked central apophysis on the palp, a condition found in all the present specimens. These two species are very similar and it seems highly likely that they are synonymous, in which case *C. longimanum* has page precedence. A difference mentioned by Koch (1872) is a dark streak on the carapace of *C. furax*, which is absent in the present specimens. *C. furax* is recorded

from Samoa and Fiji, *C. longimanum* from these islands and also from Tonga, New Hebrides, and Australia. Two males, one from Tongatabu and one from Vava'u, resemble the others in palps and chelicerae but are considerably smaller, having a carapace length about 4.5 mm. instead of 7.5 mm.

Chiracanthium diversum L. Koch

1 Female, 2 males. Nuku'alofa, Tongatabu. 1 Male. Neiafu, Vava'u. One male from Tongatabu is somewhat larger and has three teeth on the promargin of the groove, as has the female. The female has not previously been described.

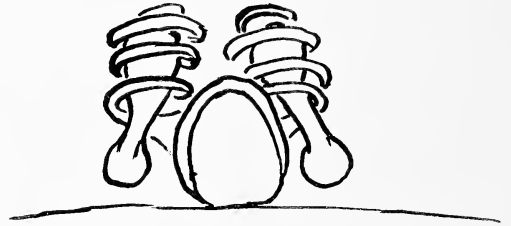


FIG. 1. *Chiracanthium diversum*. Epigynum.

FEMALE. Length 7.36 mm. Pale yellowish brown.

Carapace: Length 3.60 mm., breadth 2.40 mm. Low and smooth truncated in front.

Eyes: Eight. From above both rows slightly recurved, the anterior eyes project anteriorly beyond the carapace. Clypeus very low, about the diameter of AME. Breadth of eyegroup 1.60 mm. Ratio of eyes and of their distances apart: AM, 80; AL, 85; PM, 77; PL, 80; AM-AM, 160; AM-AL, 236; AM-PM, 115; PM-PM, 186; PM-PL, 268; L-L, 46.

Chelicerae: Large and projecting forwards, boss present, groove oblique. Three teeth on the promargin, the middle the largest. Three teeth on the retromargin, the most dorsal the largest. The dorsal promarginal tooth opposite to the ventral retromarginal one.

Maxillae: Much longer than the lip. Semicircular anteriorly, concave laterally.

Lip: Free. Longer than broad, concave anteriorly.

Sternum: Length 1.73 mm., breadth 1.37 mm. Convex. Lateral margins notched for the bases of the last three legs, anterior margin slightly concave.

Palp: Long and slender. Minute claw.

<i>Legs:</i>	I	II	IV	III	Palp
	4.1	3.2	3.2	2.2	1.3

	FEMUR	PATELLA AND TIBIA	META- TARSUS	TARSUS	TOTAL
Palp.....	1.69	1.55	1.34	4.59
I.....	4.18	5.26	4.14	1.17	14.76
II.....	3.42	4.00	3.13	0.95	11.51
III.....	2.34	2.81	2.20	0.76	8.11
IV.....	3.38	4.00	3.31	0.95	11.64
Tibial Index I	10.2				
Tibial Index IV	8.2				

Claws: Two, pectinated about 12. Tenent hairs in dense tufts on the feet and extending along the ventral surface of each tarsus and metatarsus, and sparsely on tibiae I and II.

Spines: I. One pair at the proximal end of the tibia. II. None. III. One retrolateral-distal on the tibia; 2 median and 4 distal on the metatarsus. IV. One retrolateral-distal on the tibia; 1 ventral-proximal, 2 median and 4 distal on the metatarsus.

Abdomen: Length 4.33 mm., breadth 2.48 mm. Epigynum as in figure.

Clubiona alveolata L. Koch

1 Female. Nuku'alofa, Tongatabu. 1 Male. Neiafu, Vava'u. Several immature specimens which may belong to this species, which is widespread in the Pacific but not previously recorded from Tonga.

SPARASSIDAE

Heteropoda venatoria (Linn.)

1 Female. Tongatabu. 1 Female, 2 males. Vava'u.

THOMISIDAE

Diaea praetexta L. Koch

4 Females. Nuku'alofa, Tongatabu. 17 Fe-

males, 4 males. Vava'u. 1 Female. Ononua, Ha'apai. This species was described from Samoa, where it is very variable in colour, being frequently without the dark markings. The very similar *D. septempunctata* was described by Koch from Tonga. The present specimens are pale, or sometimes with three pairs of small spots, but their reproductive organs resemble those of specimens from Samoa and they seem to belong to this species.

SALTICIDAE

Asclytus pterygodes (L. Koch)

3 Females, 3 males, 14 imm. Tongatabu. 1 Male, 2 imm. Eua Island, Ha'apai. 7 Females, 5 males, 24 imm. Vava'u. Widespread species, not previously recorded from Vava'u.

Bavia aericeps Simon

1 Male, 3 imm. Tongatabu. 1 imm. Vava'u. First records for the Tonga group. A widespread species.

Erasmia nigrovittata Keyserling

1 Female. Vava'u. This species was described from a single female from Tonga. Keyserling does not mention the cheliceral teeth, but Berland (1934) places the species amongst the Fissidentati. Petrunkevitch (1928) lists it as a synonym of *Iona* Peckham, one of the unidentate species. The present specimen agrees well with Keyserling's description, and has four distinct teeth on each of the margins of the cheliceral groove.

Menemerus bivittatus Dufour

1 Female. Nuku'alofa, Tongatabu.

Mollicia microphthalma L. Koch

1 Female, 2 imm. Tongatabu. 1 Female. Panga, Ha'apai. 1 Male. Holonga, Vava'u. A widespread species, first records for the Tonga group.

Plexippus payculli Auduin

1 Female. Vava'u. A widespread species, first record for Tonga.

Thorellia ensifera Thorell

9 Females, 3 males. Tongatabu. 2 Females, 1 male. Vava'u. Widespread in the central and eastern regions of the Pacific as far west as Fiji. First record for Tongatabu.

Vitia albipalpis Marples

1 Male. Nuku'alofa, Tongatabu. Described from Fiji, first record for Tonga.

THERIDIIDAE

Conopistha samoensis L. Koch

2 Females. Tongatabu. Widespread species.

Conopistha unimaculata Marples

1 Female. Tongatabu. Previously recorded from Samoa and Niue, as well as Tonga.

Rhomphaea cometes L. Koch

1 Male. Tongatabu. 1 Male. Falevau Island, Vava'u. New records for Tonga. Known also from Fiji, Samoa, and Tahiti.

Theridion adamsoni Berland

1 Male, imm. Tongatabu. Probably belonging to this species, previously known from Tahiti, Austral Islands, and Samoa.

Theridion albostriatum L. Koch

1 Male. Vava'u. Widespread species, previously recorded from Tongatabu.

Theridion aleipata Marples

2 Females. Tongatabu. 3 Females. Vava'u. New record for Tonga, previously known from Samoa and Aitutaki.

TETRAGNATHIDAE

Leucauge tuberculata Keyserling

2 Females. Tongatabu. 2 Females. Vava'u. 1 Female. Eua Island, Ha'apai. Widespread in the central and eastern parts of the Pacific. Previously recorded from Tongatabu.

Tetragnatha macilenta L. Koch

2 Females and 2 imm. Tongatabu. 1 Female, 1 male. Ohonua, Ha'apai. 3 Females and 2 imm. 2 Males. Vava'u. Widespread species not previously recorded from Tonga.

Tetragnatha panopea L. Koch

1 Male. Tongatabu. Widespread species, first record from Tonga.

EPEIRIDAE

Cyclosa litoralis (L. Koch)

1 Female. Vava'u. The specimen is smaller than ones from Samoa and the epigynum is slightly different, but it seems likely to be this species. It is widespread and occurs in both Fiji and Samoa. This is the first record of a *Cyclosa* from Tonga.

Cyrtophora moluccensis Doleschall

13 Females. Tongatabu. 6 Females. Vava'u. A very widespread species.

Epeira theisi Walckenaer

2 Females. Tongatabu. 7 Females, 2 males. Vava'u. Very widespread species, new record for Vava'u.

Epeira plebeja L. Koch

1 Female, 1 male imm. Eua Island, Ha'apai. 1 Male imm. Tongatabu. This female has a mottled brownish abdomen whose shape and pattern do not resemble those of *E. theisi*, though the epigynum is similar. According to the distinctions given by Berland (1935) it appears to be *E. plebeja*, a species already recorded from Tonga and from Fiji. The two immature males probably belong to the same species.

Nephila flagellans L. Koch

3 Females, 1 male. Tongatabu. Previously recorded.

SUMMARY

A collection of 34 species from various islands in the Tonga group includes 18 new records, bringing the total to 49. The female of the clubionid *Chiracanthium diversum* is described.

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The Hawaiian Species of *Conus* (Mollusca: Gastropoda)¹

ALAN J. KOHN²

IN THE COURSE OF a comparative ecological study of gastropod mollusks of the genus *Conus* in Hawaii (Kohn, 1959), some 2,400 specimens of 25 species were examined. Uncertainty of the correct names to be applied to some of these species prompted the taxonomic study reported here. Many workers have contributed to the systematics of the genus *Conus*; nevertheless, both nomenclatorial and biological questions have persisted concerning the correct names of a number of species that occur in the Hawaiian archipelago, here considered to extend from Kure (Ocean) Island (28.25° N., 178.26° W.) to the island of Hawaii (20.00° N., 155.30° W.).

FAUNAL AFFINITY

As is characteristic of the marine fauna of the Hawaiian Islands, the affinities of *Conus* are with the Indo-Pacific center of distribution. The Hawaiian Islands mark the northeastern limit of most of the species that occur there. Eastern Pacific species of *Conus* are entirely absent from the Hawaiian fauna.

Most of the species present in Hawaii range widely throughout the central and western Pacific Ocean, Indian Ocean, and Red Sea. The chief mode of distribution is the pelagic veliger larval stage. Drifting while attached to floating material may be a secondary mechanism. Despite the extensive distribution of most of the species occurring in Hawaii, the geographic position of the archipelago and the prevailing westerly surface

currents are factors which could plausibly effect the isolation necessary for geographic speciation.

Of the 33 species of *Conus* considered in this paper to be valid constituents of the Hawaiian fauna, about 20 occur in shallow water on marine benches and coral reefs and in bays. Of these, only one species, *C. abbreviatus* Reeve, is considered to be endemic to the Hawaiian archipelago. Less is known of the species more characteristic of deeper water habitats. Some, known at present only from dredgings about the Hawaiian Islands, may in the future prove to occur elsewhere as well, when adequate sampling methods are extended to other parts of the Indo-West Pacific region.

ECOLOGY

Since the ecology of *Conus* has been discussed in detail elsewhere (Kohn, 1959), ecological data are restricted to notes in this report.

It is a pleasure to acknowledge the constant stimulation and willing assistance of Karl W. Greene, director, Children's Museum of Honolulu, and Edwin H. Bryan, Jr., curator of collections, Bernice P. Bishop Museum, Honolulu. The collections and libraries of the following institutions were also visited, and gratitude is expressed to the persons in charge: U. S. National Museum (H. A. Rehder, J. P. E. Morrison), Academy of Natural Sciences of Philadelphia (R. T. Abbott), Museum of Comparative Zoology, Harvard University (W. J. Clench, R. D. Turner), and Bernice P. Bishop Museum (Y. Kondo). In addition, specimens were loaned to the writer for study by C. A. Allen, Mrs. Jean Bromley,

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BIBLIOGRAPHICAL NOTES

An excellent bibliographical account and collation of the major works in which species of *Conus* were described is given by Hanna and Strong (1949). Except where otherwise noted, the collations cited therein are followed in the present paper.

Catalogue of the Portland Museum. 1786. This catalogue was published anonymously, but its authorship is usually attributed to George Humphrey (Dall, 1921). The names of new species are attributed to Daniel Solander in the volume, and the same usage is followed in the present paper. A valuable discussion of this catalogue is given by Wilkins (1955), who also presents cogent reasons for attributing the names to Humphrey.

J. G. Bruguière. *Encyclopédie Méthodique. Histoire Naturelle des Vers*. 1792. Many previously undescribed species of *Conus* were named and carefully described in this work. However, the authorship to be attributed to these names has been a matter of dispute almost since the volume appeared. In the volume, Bruguière attributes the names and Latin diagnoses of species to C. H. Hwass (p. 598). Bruguière states that he himself wrote the descriptions and the "additional" synonymy (see Clench, 1942: 3). New specific names are published in the volume as, e.g. "*Conus catus* Hwass."

However, many subsequent writers (Lamarck, 1810; Dillwyn, 1817; Kiener, 1845–1850; Wood, 1856; Sowerby, 1857–1858; Schaufuss, 1869; Iredale, 1929; Tomlin, 1937; Cotton, 1945; Hanna and Strong, 1949; Hirase, 1954; and Kira, 1955) have cited such species as, e.g. "*Conus catus* Bruguière." Other

writers (Blainville, 1818; Reeve, 1843–1844; Adams and Adams, 1858; Weinkauff, 1874; Smith, 1879; Tryon, 1884; Fischer, 1887; von Martens and Thiele, 1903; Tinker, 1952; and Morris, 1952) have cited the names as they appear in Bruguière (1792). A third group of writers (Dautzenberg, 1937; Clench, 1942; Mermod, 1947; and Dodge, 1953) has cited such names as, e.g., "*Conus catus* Hwass in Bruguière."

Application of the *Règles* of the International Commission on Zoological Nomenclature (ICZN), and later provisions and clarifications of the *Règles*, does not lead to an unequivocal solution to this problem. In the decisions of the ICZN meeting in Paris in 1948, it was recommended (Bull. Zool. Nomencl. 4: 565–566, 1950) that "where in a book or paper written by one author (say author 'A') it is clearly stated that the description of one or more specified taxonomic units there named has been prepared exclusively by some other author (say author 'C'), the name or names in question are to be attributed to author 'C', not to author 'A'. The name of the taxonomic unit so described and named is to be cited by later authors as having been published by 'C in A'."

It is apparent from the remarks of Bruguière (1792: 598; see also Clench, 1942: 3) that the descriptions of the species were not prepared exclusively by Hwass, although the names and brief Latin diagnoses were. It is, however, the present author's opinion that Hwass's contribution is sufficient to justify attributing authorship of the names to him. This view is strengthened by the more recent further clarification of Article 21 (Copenhagen Decisions, 1953: 58–59), which states that "the rule set out on pages 565–566 of vol. 4 of the BULLETIN should be qualified in such a way as to make it clear that it applies only where the book or paper concerned contains a clear indication that not only the name in question was proposed by some author other than that by whom the book or paper was written but also that the indication, defini-

tion, or description on which, under Article 25, the availability of that name depends was written not by the author of the book or paper concerned but by the author to whom the name is there attributed."

For these reasons, the species of *Conus* referred to as, e.g. "*Conus catus* Hwass" in Bruguière (1792) are herein cited as, e.g. "*Conus catus* Hwass in Bruguière."

Museum Calonnianum. 1797. The names introduced in this publication were rejected in Opinion 51 of the ICZN (Smithsonian Publ. 2060, 1912: 116), but this decision has not been universally accepted. Of the names listed in the *Museum Calonnianum*, only three, all of which are synonyms, are pertinent to this paper. For the sake of completeness, they are listed in brackets in the synonymies. Authorship of the *Museum Calonnianum* is attributed to George Humphrey, following general acceptance. The problem is discussed in detail by Iredale (1937).

Museum Boltenianum. 1798. The names in this volume were accepted as nomenclatorially available in Opinion 96 of the ICZN (Smithsonian Misc. Coll., 73(4): 16-18, 1926), and their authorship was attributed to P. F. Röding in Direction 48 of the ICZN (Opinions and Declarations Rendered by the ICZN, 1: 255-264, 1956).

L. W. Dillwyn. *A Descriptive Catalogue of Recent Shells*. 1817. A number of species of *Conus* described by Chemnitz (1788, 1795) are listed in Dillwyn's catalogue. Since the specific names in Chemnitz (1788, 1795) have been rejected by Opinion 184 of the ICZN (Opinions and Declarations Rendered by the ICZN, 3: 27-35), these names became nomenclatorially available upon publication by Dillwyn (1817). (See also Bull. Zool. Nomencl., 4: 259-260, 1950.)

L. C. Kiener. *Spécies Général et Iconographie des Coquilles Vivantes*. 1845-1850. The names of species described in this work appear both on the plates and in the text. Hanna and Strong (1949) reproduce the summary of the collation of Sherborn and Woodward (1901:

218) which gives 1846 as the year of publication of the plates. This date, however, is erroneous, being presumably a typographical error. The correct date is 1845 as given in the body of the paper (Sherborn and Woodward, 1901: 217). Therefore, the names in Kiener's work should date from 1845 rather than from the dates on which they appeared in the text.³

Tomlin (1937) has given the most complete catalogue of the genus *Conus*. Some 2,700 names are listed, including both extant and fossil species. Earlier catalogues of Recent species are given by Reeve (1843-1849), Kiener (1845-1850), Sowerby (1857-1858), and Tryon (1884).

Earlier published lists of the species of *Conus* in Hawaii are those of Garrett (1878), Edmondson (1933, 1946), Tinker (1952, 1958), and Greene (1953). Extensive unpublished lists compiled by W. A. Bryan in 1919, and by E. H. Bryan, Jr. in 1956, have been made available to the writer by E. H. Bryan, Jr.

SYNONYMY

The synonymies consist of the first known publication of all known different names, authors, and combinations which have been applied to the species, listed chronologically. Subsequent references to the same name are not given, with the exception of errors and emendations, in order to conserve space. It is perhaps unfortunate that some of the references are to distributional lists and museum catalogues, which in many cases lack taxonomic information. These are included primarily because specific names first published in some of the museum catalogues have been recognized as available by the ICZN. Furthermore, in addition to their historical importance, such lists and catalogues are in some cases the source of errors which have been perpetuated in the subsequent literature.

Many specific names of *Conus* were introduced by authors who did not consistently use the binominal system. These names are

³ The author is grateful to Dr. Harald A. Rehder for having pointed out this discrepancy.

thus invalid (see Opinions and Declarations Rendered by the ICZN, 3: 27–35; 5: 265–279) and have not been included in the synonymies. Among the post-Linnean authors responsible for such names are Martini (1773), Chemnitz (1788, 1795), Meuschen (1778, 1787), and Martyn (1784–1792).

In cases of generic changes by subsequent authors, the name of the author of the species has been placed in parentheses throughout, whether or not this was done by the author of the generic change.

Described varieties of listed valid species are not included in synonymies. However, if the listed valid species itself has been described as a variety of another species, that entry is included in the synonymy.

In cases of published erroneous identification of specimens, the notation "(error)" follows the entry.

Genus *CONUS* Linné

Shell obconical, turbanate; whorls enrolled upon themselves, attenuated anteriorly. Spire usually short, smooth or coronate. Aperture elongate, narrow, effuse at the base, without teeth; outer lip smooth, sharp, with a sutural sinus:

Conus abbreviatus Reeve

Fig. 33 in Plate 2

Conus abbreviatus Reeve, 1843, *Conch. Icon.*, 1: pl. 16, sp. 86.

Conus abbreviatus Sowerby, 1857, *Thes. Conchyl.*, 3: 10 (as "*C. abbreviatus* Nuttall MS., Reeve C.I." on pl. 4, fig. 84).

Conus coronatus Dillwyn var. *abbreviatus*. Weinkauff, 1874, *Jahrb. Deutsch. Malak. Ges.*, 1: 250.

Conus miliaris Hwass var. *abbreviatus*. Tryon, 1884, *Man. Conch.*, 1: 22, pl. 5, fig. 89.

Stephanoconus abbreviatus (Reeve). Kaicher, 1956, *Indo-Pacific Sea Shells*, Sect. 5, pl. 2, fig. 4.

DESCRIPTION: Shell small but sturdy. Body whorl striate, the striae as raised ridges near

the base, impressed and widely spaced elsewhere. Aperture fairly narrow, flaring somewhat towards the anterior, or basal end. Base attenuated. Shoulder coronate; spire depressed, coronate, striate. Color bluish gray, with pale flesh-colored transverse bands in the middle of the body whorl and at the shoulder; with rows of rather distantly spaced small brown dots encircling the body whorl. Aperture purplish brown within, with a light median band. Periostracum thin, yellow, translucent. In life, foot pale brown; siphon pale brown, tinged with pink.

LENGTH: To 60 mm., but usually smaller.

TYPE LOCALITY: Oahu.

REMARKS: It is believed that this species is endemic to the Hawaiian archipelago. It is known from Midway Island and all of the main islands, where it is usually rather common on marine benches. Larger specimens are found on sandy substrata of coral reef platforms.

Conus miliaris Hwass and *C. coronatus* Gmelin, neither of which occurs in Hawaii, are the most closely related species. *C. abbreviatus* may be distinguished from both by the regular arrangement and small size of the brown dots, by the characteristic bluish-gray ground color, and by the absence of irregular longitudinal white flecks (as in *C. miliaris*) or brown blotches (as in *C. coronatus*).

Pleistocene fossils of *C. abbreviatus* are known from Oahu (Ostergaard, 1928), Maui, and Molokai (Ostergaard, 1939).

Conus acutangulus Lamarck

Fig. 37 in Plate 2

Conus acutangulus Lamarck, 1810, *Ann. Mus. Hist. Nat. Paris*, 15: 286.

Leptoconus acutangulus. Adams and Adams, 1853, *Gen. Rec. Moill.*, 1: 251.

Conus acutangulus Sowerby, 1857, *Thes. Conchyl.*, 3: 11.

(?) *Conus crebrisulcus* Sowerby, 1857, *Thes. Conchyl.*, 3: 21, pl. 14, fig. 321.

Conus turriculatus Sowerby, 1866, Thes. Conchyl., 3: 328, pl. 27, figs. 643, 644.

Conus gemmulatus Sowerby, 1870, Proc. Zool. Soc. Lond., 1870: 257, pl. 22, fig. 8.

Conus acutangulus Bruguière. Paetel, 1883, Catal. Conch.-Samml. Paetel, p. 50.

Conus acutangulus Hwass. Tryon, 1884, Man. Conch., 6: 76.

Conus acutanculus Friedberg, 1911, Rozprawy Wiadomości Muzeum Imienia Dzieduszyckich (Moll. Mioc. Poloniae), 14: 47.

Conus eugrammatus Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 85.

Conasprella acutangulus (Lamarck). Cotton, 1945, Rec. South Austral. Mus., 8: 272.

Conus eugrammatus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.

Asprella acutangulus (Lamarck). Kuroda, 1956, Venus: Jap. Jour. Mal., 19: 88.

DESCRIPTION: Shell small, rather thin. Body whorl elongate, bearing rather distantly and irregularly spaced incised spiral lines marked by small punctures. Aperture narrow, outer lip protracted. Shoulder angular, ridged; spire elevated, turreted, concave, striate, compris-

ing at least one third of the total shell length; apex sharp. Early whorls smooth, succeeding whorls with slender protracting curved axial riblets which fuse to form strong nodules at the shoulder, the nodules becoming less conspicuous on the latest whorls. Color of body whorl white to pale buff, marked with interrupted broad brown spiral bands either side of the center. Rows of brown dots between the striae mark the light area between the brown bands. Spire marked by distantly spaced rather regular broad brown spots. Periostracum grayish white, bearing lamellae on the fine riblets of the spire.

LENGTH: 30 mm.

TYPE LOCALITY: "Mers des grandes Indes."

REMARKS: Specimens of *C. acutangulus* have been collected in Hawaii by dredging in comparative shallow water and to a depth of 200 fathoms.

Conus bullatus Linné

Fig. 1

Conus bullatus Linné, 1758, Syst. Nat., ed. 10, p. 717.

PLATE 1

References are given to the shells figured. The dimensions given are shell length \times maximum diameter.

FIG. 1. *Conus distans* Hwass in Bruguière. 75 \times 43 mm. Off Rabbit (Manana) Island, off Oahu. USNM coll., No. 484738.

FIG. 2. *Conus textile* Linné. 80 \times 44 mm. Waikiki, Oahu. C. E. Cutress coll.

FIG. 3. *Conus pennaceus* Born. 64 \times 35 mm. Keaukaha, Hilo, Hawaii. USNM coll., No. 338584.

FIG. 4. *Conus quercinus* Solander. 80 \times 49 mm. Honolulu Harbor Channel, Oahu. USNM coll., No. 338584.

FIG. 5. *Conus striatus* Linné. 107 \times 53 mm. Waikiki, Oahu. C. E. Cutress coll.

FIG. 6. *Conus miles* Linné. 67 \times 39 mm. Waikiki, Oahu. C. E. Cutress coll.

FIG. 7. *Conus imperialis* Linné. 69 \times 36 mm. Lahaina, Maui. USNM coll., No. 484735.

FIG. 8. *Conus spiceri* Bartsch & Rehder. 113 \times 62 mm. Midway Island. USNM coll., No. 523700.

FIG. 9. *Conus marmoreus* Linné. 96 \times 54 mm. Honolulu Harbor entrance, Oahu, 5-8 fathoms. USNM coll., No. 338163.

FIG. 10. *Conus leopardus* (Röding). 143 \times 86 mm. Waimea Bay, Oahu. C. E. Cutress coll.

FIG. 11. *Conus vexillum* Gmelin. 88 \times 54 mm. Kahala, Oahu. USNM coll., No. 338510.

FIG. 12. *Conus pulchricus* Hwass in Bruguière. 48 \times 27 mm. Honolulu, Oahu. USNM coll., No. 338195.

FIG. 13. *Conus smirna* Bartsch & Rehder. Holotype. 61 \times 23 mm. off Lanai, 257-312 fathoms. USNM coll., No. 173226.

FIG. 14. *Conus vitulinus* Hwass in Bruguière. 56 \times 31 mm. Keokey, Hawaii. USNM coll., No. 338549.

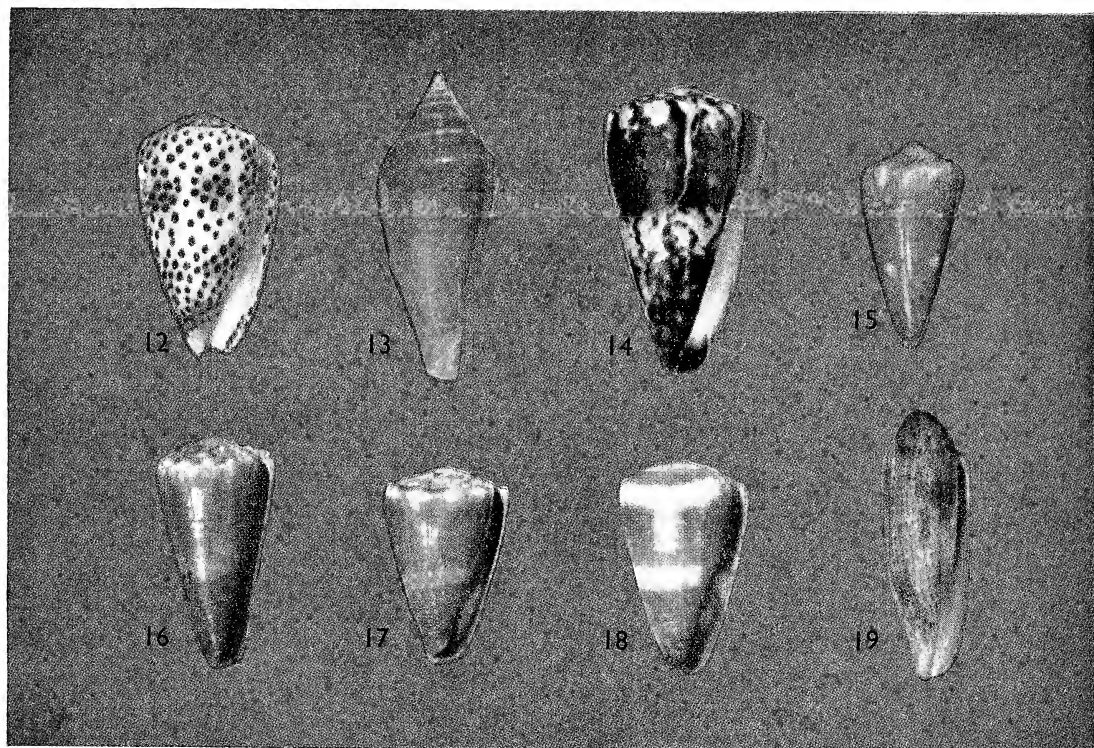
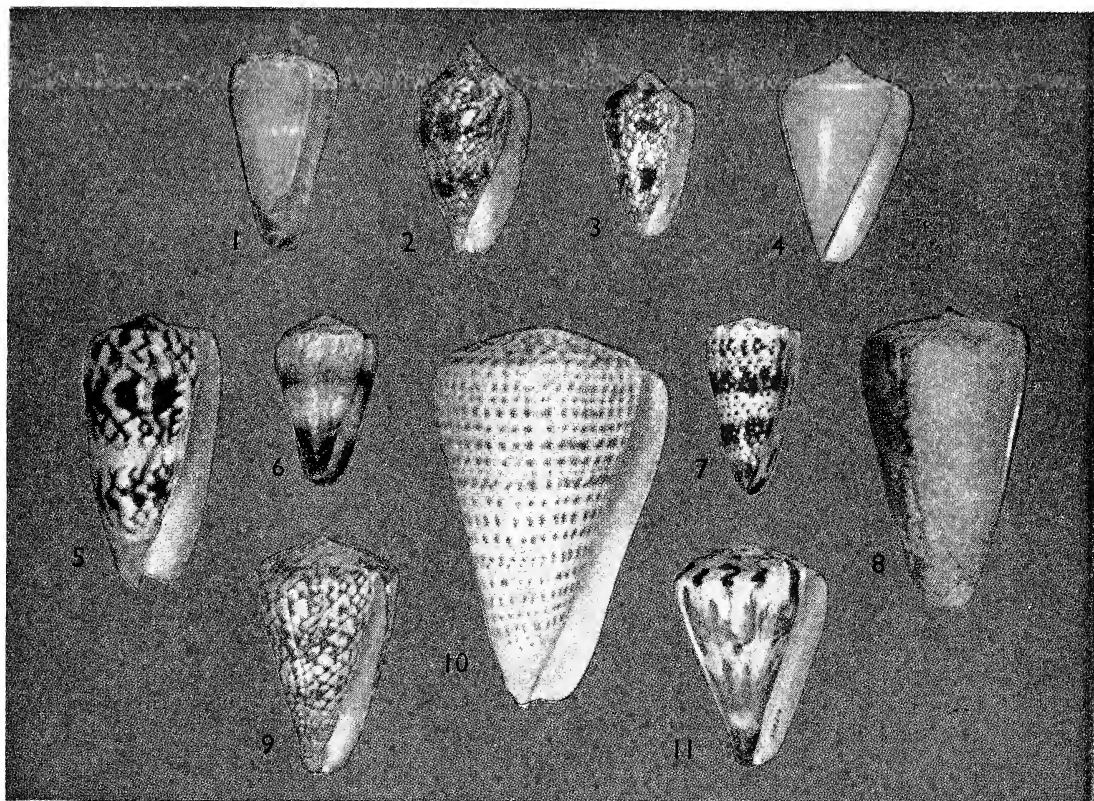
FIG. 15. *Conus litoglyphus* Hwass in Bruguière. 41 \times 19 mm. Honolulu Harbor entrance, Oahu, 5-8 fathoms. USNM coll., No. 338538.

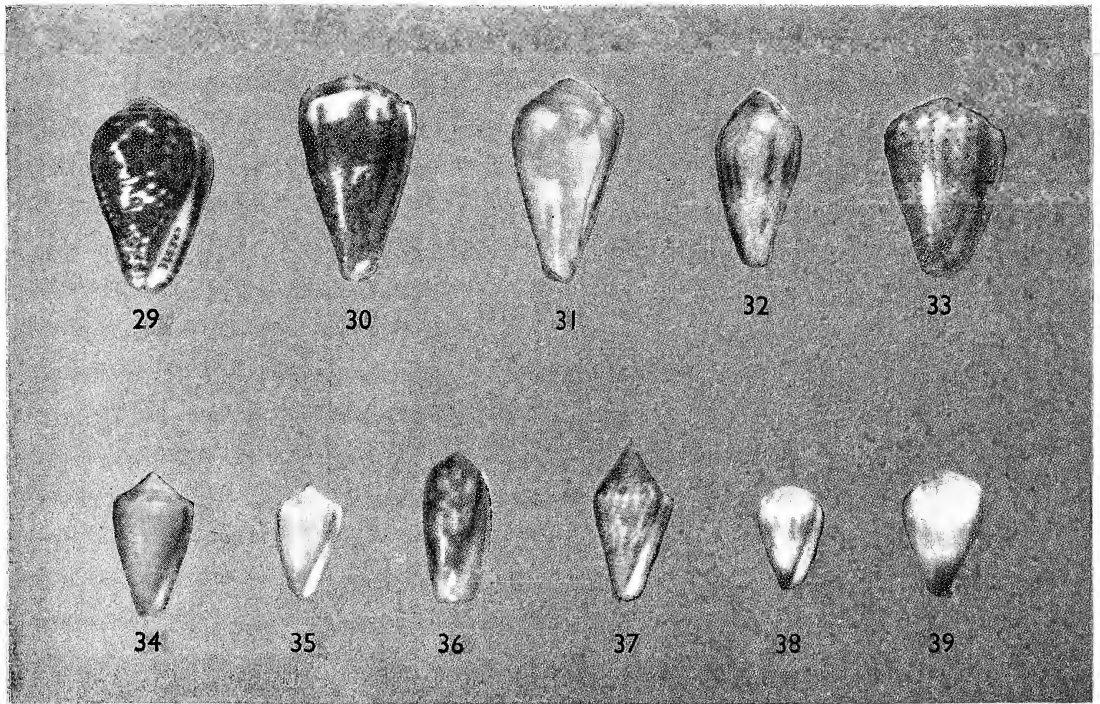
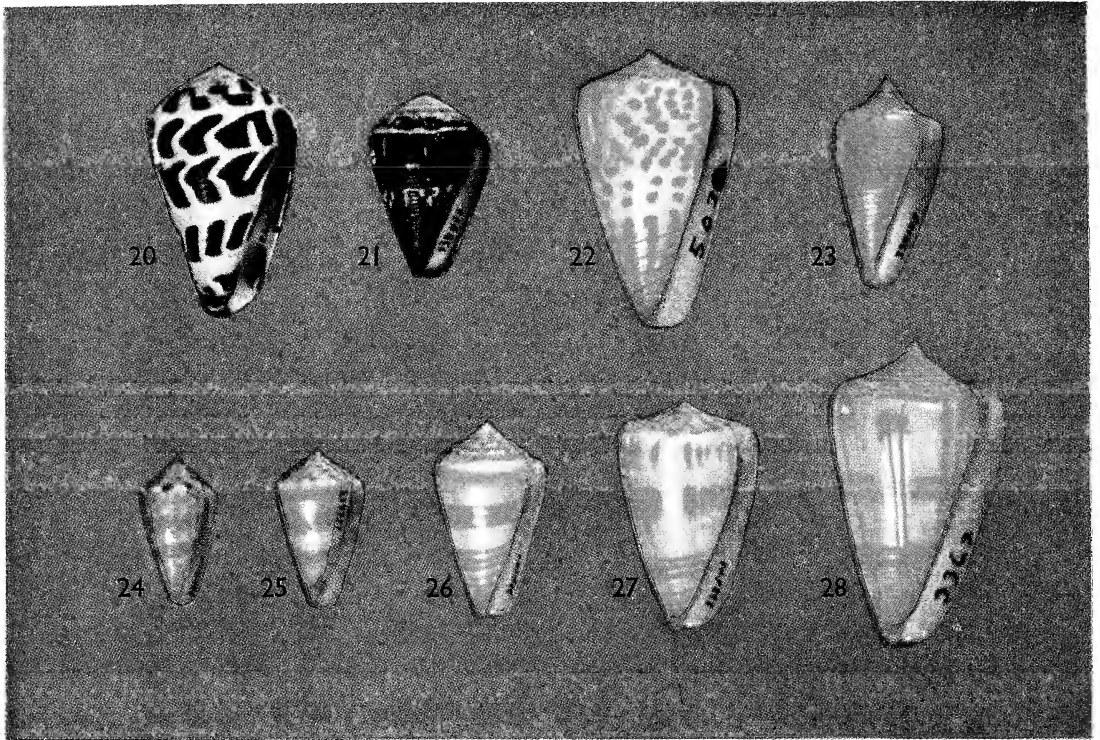
FIG. 16. *Conus moreletii* Crosse. 46 \times 23 mm. Kailua, Oahu, 12-15 feet. USNM coll., No. 484249.

FIG. 17. *Conus lividus* Hwass in Bruguière. 39 \times 23 mm. Honokowai, Maui. USNM coll., No. 338531.

FIG. 18. *Conus flavidus* Lamarck. 42 \times 25 mm. Honokowai, Maui. USNM coll., No. 338522.

FIG. 19. *Conus nussatella* Linné. 53 \times 17 mm. Kuhio Bay, Hilo, Hawaii. USNM coll., No. 338577.





Conus nubecula Gmelin, 1791, Syst. Nat., ed. 13, p. 3396.

Cucullus nubecula (Gmelin). Röding, 1798, Mus. Boltenianum, p. 46.

Cucullus parvus Röding, 1798, Mus. Boltenianum, p. 46.

Cucullus laganum Röding, 1798, Mus. Boltenianum, p. 51.

Conus bullatus Lamarck. Sowerby, 1833, Conch. Illus., p. 2, pt. 29, fig. 23.

Textilia bullatus. Swainson, 1840, Treat. Mal., p. 312.

Leptoconus bullatus (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 253.

Textilia bullata (Linné). Cotton, 1945, Rec. South Austral. Mus., 8: 261.

DESCRIPTION: Shell rather thick but not heavy, ovate-oblong, the maximum diameter not at the shoulder but about one third of the distance from shoulder to base. Body whorl glossy, with impressed, rather widely spaced transverse striae basally. Shoulder rounded, smooth; spire obsoletely striate, canaliculate. Ground color white or pale pink, clouded with orange brown subtrigonal markings often fused to form three broad, rather poorly defined transverse bands, separated by areas of sparser, irregularly placed similar

markings. Spire marked irregularly with orange brown and pink or pinkish white. Interior of aperture pinkish orange. Periostracum thin.

LENGTH: The most recently collected specimen from Hawaii (see below) measures 62 × 29 mm.

TYPE LOCALITY: None.

REMARKS: Very few specimens of *Conus bullatus* are known from the Hawaiian Islands. A single shell in excellent condition was dredged off Nanakuli, Oahu, but whether or not it was alive is not known (D. Thaanum, *in litt.*). In November, 1957, a living specimen (Fig. 1) was collected half-buried in sand at a depth of 100 feet off Diamond Head, Oahu (C. S. Weaver, *in litt.*). At least two other specimens are believed to have been collected in Hawaii, but it has not been possible to verify the reports. In addition, a number of dead shells have been collected (K. W. Greene, *in litt.*; L. Brand, verbal communication).

Conus capitaneus Linné

Fig. 2

Conus capitaneus Linné, 1758, Syst. Nat., ed. 10, p. 713.

PLATE 2

References are given to the shells figured. The dimensions given are shell length × maximum diameter.

FIG. 20. *Conus ebraeus* Linné. 39 × 23 mm. Hilo, Hawaii. USNM coll., No. 338209.

FIG. 21. *Conus chaldaeus* (Röding). 29 × 18 mm. Hilo, Hawaii. USNM coll., No. 338477.

FIG. 22. *Conus tessulatus* Born. 42 × 25 mm. "Sandwich Is." USNM coll., No. 5038. A faded specimen.

FIG. 23. *Conus quercinus* Solander. 33 × 16 mm. Off Kaanapali, Maui, 4–12 fathoms. USNM coll., No. 338187. Juvenile specimen, showing the characteristic high spire.

FIGS. 24–28. *Conus saturatus* Reeve, showing changes in color pattern with increase in size. FIG. 24. 23 × 11 mm. Off Launiupoko Camp, Maui, 4–12 fathoms. USNM coll., No. 338546. FIG. 25. 25 × 13 mm. Off Mt. Lihau, Maui, 4–12 fathoms. USNM coll., No. 338547. FIG. 26. 32 × 17 mm. USNM coll., No. 338546. FIG. 27. 37 × 21 mm. Honolulu Harbor entrance, Oahu, 5–8 fathoms. USNM coll., No. 338541. FIG. 28. 48 × 27 mm. North Island, Pearl and Hermes Reef. Mrs. J. Bromley coll., No. 3363.

FIG. 29. *Conus catus* Hwass *in* Bruguière. 29 × 18 mm. Honokowai, Maui. USNM coll., No. 338561.

FIG. 30. *Conus rattus* Hwass *in* Bruguière. 30 × 17 mm. Honolulu, Oahu. USNM coll., No. 338516.

FIG. 31. *Conus pertusus* Hwass *in* Bruguière. 30 × 15 mm. Locality unknown. USNM coll., No. 18522.

FIG. 32. *Conus retifer* Menke. Midway Island. USNM coll., No. 524591. A faded specimen.

FIG. 33. *Conus abbreviatus* Reeve. 26 × 17 mm. Honokowai, Maui. USNM coll., No. 338488.

FIG. 34. *Conus circumactis* Iredale. 22 × 11 mm. Off Lanai, 179–253 fathoms. (Holotype of *Conus hammatus* Bartsch and Rehder). USNM coll., No. 173225. Juvenile.

FIG. 35. *Conus circumactis* Iredale. 17 × 9 mm. USNM coll. Juvenile.

FIG. 36. *Conus obscurus* Sowerby. 23 × 9 mm. Off Waikiki, Oahu, 20 feet. USNM coll., No. 484740.

FIG. 37. *Conus acutangulus* Lamarck. 24 × 10 mm. Honolulu Harbor entrance, Oahu, 6–8 fathoms. USNM coll., No. 338564.

FIGS. 38–39. *Conus sponsalis* Hwass *in* Bruguière. Kauai. USNM coll. FIG. 38. 15 × 9 mm. FIG. 39. 18 × 11 mm.

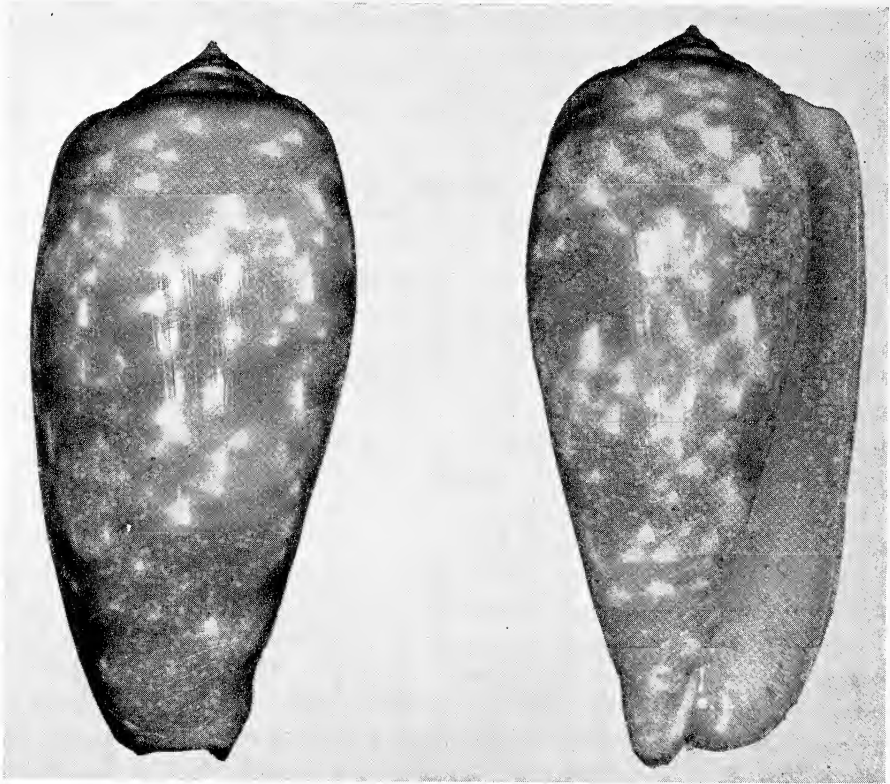


FIG. 1. *Conus bullatus* Linné, 62 × 29 mm. Collected off Diamond Head, Oahu, 17 fathoms. Shell in collection of C. S. Weaver. Photographs by the author.

Conus classarius Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 705, pl. 335, fig. 7.

[*Conus venator* Humphrey, 1797, Mus. Calonianum, p. 11.]

[*Conus agasus* Humphrey, 1797, Mus. Calonianum, p. 11.]

Cucullus capitaneus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 43.

Conus classarius Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 267.

Conus chemnitzii Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 363.

Conus capitaneus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 172.

Leptoconus capitaneus (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Conus ceciliae Crosse, 1858, Jour. Conchyl., 7: 381, pl. 14, fig. 5.

Rhizoconus capitaneus (Linné). Frauenfeld, 1869, Verh. Zool.-Bot. Ges. Wien, 19: 863.

Conus chemnitzii Dillwyn. Dautzenberg, 1937, Mem. Mus. Roy. Hist. Nat. Belg., 2(18): 171.

Lithoconus capitaneus (Linné). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 4, fig. 9.

DESCRIPTION: Shell of moderate thickness; body whorl encircled by finely punctate striae on the basal half, the striae more distinct and separated by low ridges basally; aperture rather narrow, the sides parallel. Shoulder angular, smooth; spire rather low, obtuse, striate; apex pointed. Color of body whorl variable, yellow or olive yellow to orange brown or olive brown, encircled by several dark brown dotted lines and two broad white bands, interrupted by dark brown blotches, at the shoulder and centrally on the body whorl. The white bands may also be crossed by closely spaced longitudinal wavy brown

lines. Young individuals may lack the two white bands. Spire tessellated with alternate brown and white blotches, continuing to form band on body whorl at shoulder. Outer lip thin; aperture violet within. Periostracum rather thin but opaque, encircled by raised transverse ridges.

LENGTH: The only two specimens known from the Hawaiian Islands (Fig. 2) measure 31×21 mm. and 19.5×11.5 mm.

TYPE LOCALITY: Asia.

REMARKS: This species was not known to occur in the Hawaiian area until the collection of a living specimen (Fig. 2, right) by Mrs. A. M. Harrison at a depth of 15–20 feet off Nanakuli, Oahu, in April, 1958. A second, smaller specimen (Fig. 2, left) was collected by Mr. A. M. Harrison at a depth of 35 feet near Kaena Pt., Oahu, on 31 August 1958.

Conus catus Hwass in Bruguière

Fig. 29 in Plate 2

Conus catus Hwass in Bruguière, 1792, Enc.

Meth. Vers, 1: 707, pl. 332, figs. 3, 4, 7.

Conus leoninus var. δ Gmelin, 1791, Syst. Nat., ed. 13, p. 3387.

Cucullus nubilus Röding, 1798, Mus. Boltenianum, p. 46.

Conus nubilus (Bolten). Link, 1807, Beschreib. Nat.-Samml. Univ. Rostock, Abt. 3, p. 105.

Conus catus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 285.

Conus discrepans Sowerby, 1833, Conch. Illus., p. 2, pt. 29, fig. 28.

Conus catus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 173.

Leptoconus catus (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 253.

(?) *Conus purus* Pease, 1862, Proc. Zool. Soc. Lond., p. 279.

Chelyconus catus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 241.

Chelyconus catus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 6, fig. 10.

DESCRIPTION: Shell stout, solid, bulbous. Body whorl striate, the striae raised, rounded, usually obsolete near the shoulder, and granular near the base. Aperture rather broad, the sides almost parallel. Shoulder rounded, smooth; spire obtuse, deeply striate. Apex sharp, rose-colored, but often eroded. Color of body whorl and spire brown with irregular white flecks or splotches. Aperture white with brown margin. Periostracum thin, yellow, translucent. In life, foot mottled brown on buff. "Pale cinereous, varied with delicate brown mottlings, which are most conspicuous on the muzzle" (Garrett, 1878).

LENGTH: To 40 mm.

TYPE LOCALITY: Several localities are given with the original description, the first two of which, "Saint-Domingue" and Martinique, are almost certainly in error. The species described as *Conus catus* is restricted to the Indo-West Pacific region although it resembles *Conus ranunculus* Hwass in Bruguière, a western Atlantic species.

REMARKS: *Conus catus* is less variable with respect to shell characteristics in Hawaii than in other parts of the Pacific and Indian oceans. It occurs intertidally on benches and rocky shores and subtidally as well. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus chaldaeus (Röding)

Fig. 21 in Plate 2

Conus princeps Linné. Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 134. (error).

Conus princeps var. β . Gmelin, 1791, Syst. Nat., ed. 13, p. 3378.

Conus ebraeus Linné var. E. Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 619, pl. 321, figs. 1, 7, 8.

Cucullus chaldaeus Röding, 1798, Mus. Boltenianum, p. 42.

Conus chaldaeus (Bolten). Link, 1807, Beschreib. Nat.-Samml. Univ. Rostock, Abt. 3, p. 106.

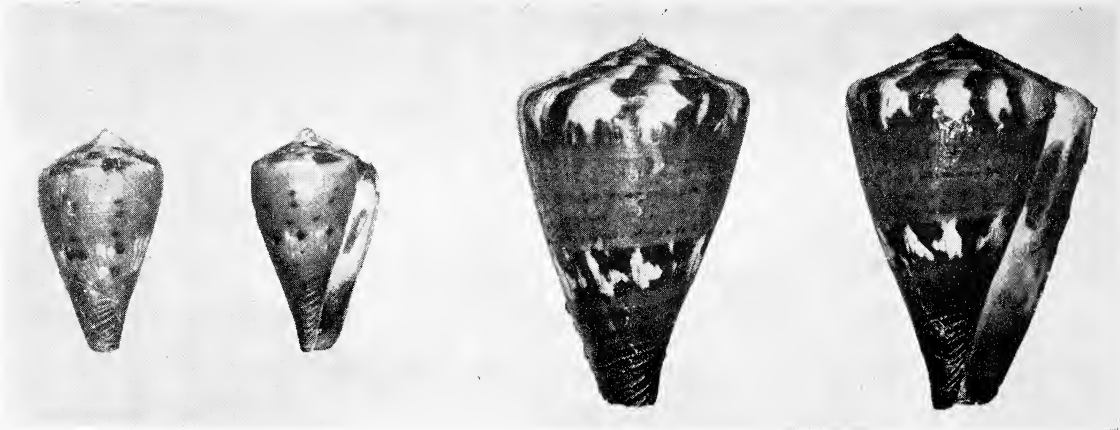


FIG. 2. *Conus capitaneus* Linné. Left, 19.5 × 11.5 mm. Specimen collected by A. M. Harrison near Kaena Pt., Oahu, 6 fathoms. Right, 31 × 21 mm. Specimen collected by Mrs. A. M. Harrison near Nanakuli, Oahu, 3 fathoms. Photographs by the author.

- Conus vermiculatus* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 34.
- Conus ebraeus* Linné var. C. Dillwyn, 1817, Descr. Cat. Rec. Shells, p. 399.
- Conus ebraeus* Linné var. D. Dillwyn, 1817, Descr. Cat. Rec. Shells, p. 399.
- Conus hebraeus* Linné var. β. Reeve, 1843, Conchol. Icon., 1: pl. 19, fig. 104a.
- Conus hebraeus* Linné var. *vermiculatus* Lamarck. Kiener, 1846, Spéc. Gén. Icon. Coq. Viv., 2: 46, pl. 8, fig. 3.
- Conus ebraeus* Linné var. *vermiculatus* Hwass. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 249.
- Conus ebraeus* Linné var. *vermiculatus* Lamarck: Crosse and Marie, 1874, Jour. Conchyl., 22: 340.
- Conus hebraeus* Linné var. *vermiculatus* Hwass. Kobelt, 1878, Illus. Conchyl., p. 92.
- Conus vermiculatus* Bruguière. Fischer, 1891, Bull. Soc. Hist. Nat. Autun, 4: 132.
- Conus ebraeus* Linné var. *vermiculata* Lamarck. Couturier, 1907, Jour. Conchyl., 55: 126.
- Cucullus chaldaeus* Bolten. Iredale, 1929, Mem. Queensl. Mus., 9: 282.
- Virroconus chaldaeus* (Bolten). Cotton, 1945, Rec. Austral. Mus., 8: 236.
- Conus chaldeus* (Röding). Tinker, 1952, Pacific Sea Shells, p. 44.
- Conus chaldens* (Röding). Dietrich and Morris, 1953, Nautilus, 67: 17, pl. 4, fig. 19.
- Virroconus chaldeus* (Röding). Kira, 1955, Coloured Illus. Shells Japan, p. 72.
- Stephanoconus chaldeus* (Röding). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 10.
- Conus ebraeus chaldaeus* Röding. Hertlein and Emerson, 1957, Amer. Mus. Novit., No. 1859: 3.

DESCRIPTION: Shell rather small but extremely thick and sturdy. Body whorl transversely striate, the striae obsoletely tuberculate near the base, becoming strongly so near the shoulder; aperture narrow. Shoulder coronate; spire moderately elevated, tuberculate, striate; apex often eroded. Color mostly black, with narrow, irregular, usually interrupted white bands at the shoulder and centrally on the body whorl, the black areas also interrupted by intermittent vertical white streaks. Aperture bluish white, the external color pattern visible at the outer lip. Periostracum rather thin, yellow, translucent. In life, foot black, with a broad central longitudinal tan stripe on the sole. Siphon and rostrum black, tipped with red.

LENGTH: Usually less than 40 mm. A specimen collected by the author at Waikiki, Oahu, measures 44 mm.

TYPE LOCALITY: None.

REMARKS: This species is closely related to *Conus ebraeus* and is regarded as a variety of that species by some recent workers (e.g. Dodge, 1953). It differs from *C. ebraeus* in being generally smaller, having a tuberculate surface, and having the black flammules confluent so as to cover most of the shell. The two species are sympatric over a wide range. Hawaiian specimens are easily distinguishable. In other areas, the two species tend to approach each other more closely morphologically but do not intergrade. Lamarck's (1810) statement that the two species are constantly distinct is correct.

C. chaldaeus occurs most commonly near the outer edge of marine benches. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus circumactis Iredale

Figs. 34 and 35 in Plate 2; Fig. 3

Conus cinctus Swainson, 1822, Zool. Illus., ser. 1, 2: pl. 110. (non *cinctus* Bosc, 1801.)

Conus pulcbellus Swainson, 1822, Zool. Illus., ser. 1, 2: pl. 114. (non *pulcbellus* Röding, 1798.)

Rhizoconus pulcbellus (Swainson). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

(?) *Conus connectens* A. Adams, 1854, Proc. Zool. Soc. Lond., 1854: 136.

Conus circumactis Iredale, 1929, Mem. Queensl. Mus., 9: 281.

Conus hammatus Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 86.

Dauciconus circumactis (Iredale). Cotton, 1945, Rec. South Austral. Mus., 8: 246.

Conus hammatus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.

Leptoconus circumactis (Iredale). Kuroda, 1956, Venus: Jap. Jour. Mal., 19: 73.

DESCRIPTION: Shell rather thin; body whorl slightly concave near the base on the left side, spirally striate with the striae obsolete and impressed toward the shoulder but stronger and with widely spaced low knobs basally. Aperture narrow, widening slightly basally; outer lip thin. Shoulder angular, smooth or



FIG. 3. *Conus circumactis* Iredale. Specimens dredged by C. A. Allen off southern shore of Oahu, 8-60 fathoms. Left, 21 × 12 mm.; center, 25 × 13 mm.; right, 34 × 18 mm. Photographs by M. Miyamoto.

extremely obsoletely coronate. Spire low; apex nipplelike, especially in young specimens; whorls finely striate, separated by a deeply impressed suture. Color of body whorl pale yellow or yellowish brown, with large white blotches forming a band at the shoulder and another at the middle; body whorl also encircled by narrow brown lines, which are usually interrupted to form dots and dashes; base violet or pink; interior of aperture bluish or pinkish white. Spire white or pinkish white, sparsely maculated with brown. Periostracum rather thick, yellowish brown and opaque in young specimens, yellow and somewhat translucent in older individuals.

LENGTH: 35 mm.

TYPE LOCALITY: Amboina.

REMARKS: All specimens of *C. circumactis* known from the Hawaiian Islands have been collected by dredging. The holotype of *C. hammatus* Bartsch and Rehder, here considered the juvenile of *C. circumactis*, was dredged off Kauai in about 200 fathoms. C. A. Allen collected thirteen specimens from depths of 8–60 fathoms off the southern shore of Oahu.

Of the other species of *Conus* in Hawaii, *C. vitulinus* is most closely related to *C. circumactis*. The latter can be distinguished by its pale ground color, pink or violet base, and yellowish brown periostracum. *C. circumactis* can be distinguished from *C. litoglyphus* by the narrow interrupted transverse brown lines and the pink or violet base in the former.

Conus distans Hwass in Bruguière

Fig. 1 in Plate 1

Conus distans Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 634, pl. 321, fig. 11.

Conus distans Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 38.

Virroconus distans (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 254.

Rhizoconus distans (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 75.

Virgiconus distans (Bruguière). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 291.

Stephanoconus distans (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 16.

DESCRIPTION: Shell large, elongate, slightly concave in profile. Body whorl smooth or encircled with obsolete impressed lines; aperture narrow, the sides parallel. Shoulder coronate; spire short, coronated with obtuse rounded tubercles. Color of body whorl yellowish tan, obsoletely banded with white or pale bluish white at the center and near the shoulder. Tubercles of the spire white, depressed areas between them dark brown. A purplish brown stain usually present near the base. Interior of aperture light violet with a lighter central band, darker violet at the base. The violet of the interior is deeper in juvenile specimens, which are generally more colorful. Periostracum thick, olive green, with transverse rows of tufted ridges on body whorl. In life, foot brown; siphon light tan, mottled with brown; rostrum dark brown, tipped with yellow; tentacles light brown; penis orange.

LENGTH: 120 mm.

TYPE LOCALITY: New Zealand. In error (see Wilkins, 1955: 106).

REMARKS: *C. distans* occurs chiefly at the outer areas of reef platforms and in depths of one or more fathoms.

Conus ebraeus Linné

Fig. 20 in Plate 2

Conus ebraeus Linné, 1758, Syst. Nat., ed. 10, p. 715.

Conus hebraeus Linné. Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 142.

Cucullus ebraeus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 42.

Conus quadratus Perry, 1811, Conchology, pl. 24, fig. 5. (non *quadratus* Röding, 1798.)

Conus hebraeus Hwass. Blainville, 1818, Dict. Sci. Nat., 10: 249.

Conus hebraeus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 170.

Conus hebreus. Montrouzier, 1856, Ann. Soc. Imp. Agr. Lyon, 8: 416.

Coronaxis hebraeus (Linné). Frauenfeld, 1869, Verh. Zool.-Bot. Ges. Wien, 19: 863.

Virroconus ebraeus (Linné). Iredale, 1930, Mem. Queensl. Mus., 10: 80.

Stephanoconus ebraeus (Linné). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 9.

DESCRIPTION: Shell solid; body whorl smooth, becoming encircled with obsolete raised ridges toward the base; outer lip of aperture flaring slightly basally. Shoulder coronate, often obsoletely so; spire of moderate height, often somewhat eroded, indistinctly coronate. Color white with usually three rows of large angular rhomboidal black flammules, with another row encircling the shoulder. Aperture with clouded bands corresponding with the exterior markings. Periostracum thin, yellow, translucent. In life, foot black, with a broad longitudinal central buff stripe on the sole. Siphon and rostrum black, tipped with a narrow red margin.

LENGTH: This species attains greater length in the Hawaiian Islands than in other parts of its extensive range. Specimens exceeding 50 mm. are often found. A specimen collected by the author at Diamond Head, Oahu, measures 56 mm. in length.

TYPE LOCALITY: India.

REMARKS: One of the most abundant species of *Conus* in the Hawaiian Islands, *C. ebraeus* is the dominant species on intertidal benches and occurs also on reef platforms. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus flavidus Lamarck

Fig. 18 in Plate 1

Conus flavidus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 265.

Conus virgo Linné var. Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 362.

Dendroconus flavidus (Lamarck). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.

Conus neglectus Pease, 1860, Proc. Zool. Soc. Lond., pt. 28: 398. (non *neglectus* A. Adams, 1853.)

Conus flavidus Bruguière. Issel, 1869, Malacologia del Mar Rosso, p. 143.

Lithoconus flavidus (Lamarck). Brazier, 1877, Proc. Linn. Soc. New South Wales, 1: 288.

Lithoconus peasei Brazier, 1877, Proc. Linn. Soc. New South Wales, 1: 288.

Conus lividus Hwass var. *flavidus* Lamarck. Smith, 1879, Phil. Trans. Roy. Soc. Lond., 168 (extra volume): 477.

Virgiconus flavidus (Lamarck). Cotton, 1945, Rec. South Austral. Mus., 8: 254.

DESCRIPTION: Shell thick and heavy. Body whorl transversely striate, the striae more pronounced and raised toward the base; aperture narrow. Shoulder rather square, smooth; spire low, striate. Color of body whorl usually olivaceous or yellowish brown banded with white and/or bluish white at the shoulder and below the middle. Base stained dark violet. Aperture violet, with a light central band and yellow margin. Periostracum gray, transversely ridged in young specimens, smooth in older individuals. In life, upper surface of foot reddish brown, mottled with brown; remainder of foot and rostrum light yellowish brown mottled with darker brown; tip of siphon yellow, followed proximally by black and yellow bands; remainder of siphon yellow mottled with black. Tentacles white to yellow.

LENGTH: 50 mm.

TYPE LOCALITY: None.

REMARKS: *C. flavidus* is one of the commonest species of *Conus* on Hawaiian coral reefs. Pleistocene fossils have been collected on Oahu by Ostergaard (1928) and the writer and on Molokai by Ostergaard (1939).

Conus imperialis Linné

Fig. 7 in Plate 1

Conus imperialis Linné, 1758, Syst. Nat., ed. 10, p. 712.

Conus fuscatus Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 126.

Cucullus imperialis (Gmelin). Röding, 1798, Mus. Boltenianum, p. 37.

Cucullus corona-ducalis Röding, 1798, Mus. Boltenianum, p. 38.

Cucullus regius Röding, 1798, Mus. Boltenianum, p. 38. (non *regius* Gmelin, 1791.)

Conus viridulus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 31.

Conus imperialis Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 157-158, figs. 128, 129.

Conus fuscatus Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 157-158, figs. 130, 131.

Conus viridulus Linné. Adams and Adams, 1853, Gen. Rec. Moll., 1: 247.

Conus queketti Smith, 1906, Ann. Natal Govt. Mus., 1: 22, pl. 7, fig. 1.

Cucullus imperialis (Linné). Kira, 1955, Coloured Illus. Shells Japan, p. 72.

Rhombus imperialis (Linné). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 289.

DESCRIPTION: Shell large and sturdy, body whorl elongate, striate basally; outer lip thin. Shoulder coronate; spire low, strongly coronate. Ground color of shell white, with numerous interrupted light and dark brown bands on the spire as well as on the body whorl. Two broad yellowish brown bands encircle the body whorl. The band nearer the shoulder is broader. Both bands contain several narrow revolving dark brown lines interrupted by white. Color of base pale blue, often as narrow interrupted revolving lines. Base of aperture stained with a dark purple marginal band. Periostracum thin, yellow, translucent, but often obscured by epizooic coralline algae in nature. In life, exposed soft parts red, speckled with black.

LENGTH: 90 mm.

TYPE LOCALITY: None.

REMARKS: *C. imperialis* occurs on reef platforms and to a depth of at least 30 fathoms. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus leopardus (Röding)

Fig. 10 in Plate 1

(?) *Conus litteratus* Linné var. β Born, 1778,

Ind. Rer. Nat. Mus. Caes. Vind., p. 128.

Conus litteratus Linné var. β Born, 1780, Test. Mus. Caes. Vind., p. 149.

Conus litteratus Linné var. D Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 638, pl. 324, fig. 4.

Conus litteratus Linné var. G Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 638, pl. 324, fig. 3.

Conus litteratus Linné var. I Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 638, pl. 323, fig. 5.

Cucullus leopardus Röding, 1798, Mus. Boltenianum, p. 41.

Conus literatus var. B. Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 357.

Conus millepunctatus Lamarck, 1822, Hist. Nat. Anim. sans Vert., 7: 461. (non *millepunctatus* Röding, 1798.)

Conus litteratus Linné var. *millepunctatus* Lamarck. Anton, 1839, Verzeichniss, p. 105.

Conus mille punctatus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 167.

Conus millepunctatus Linné. Mörch, 1852, Catal. Conchyl. Yoldi, p. 66.

Dendroconus millepunctatus (Lamarck). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.

(?) *Leptoconus leopardus*. Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Conus millepunctatus Bruguière. Sowerby, 1857, Thes. Conchyl., 3: 23, pl. 7, fig. 151.

Conus millipunctatus Lamarck. Theobald, 1860, Catal. Rec. Sh. Mus. Asiat. Soc. Bengal, p. 23.

Conus literatus Linné var. *millepunctatus* Lamarck. Tryon, 1884, Man. Conch., 6: 10, pl. 2, fig. 19.

Conus millepunctatus Hwass. Von Martens and Thiele, 1903, Beschr. Gastrop. Deutsche Tiefsee Exp., p. 136.

Cucullus pardus Bolten. Iredale, 1929, Mem. Queensl. Mus., 9: 282. (error. *pardus* Röding, 1798 = *litteratus* Linné, 1758.)

Conus litteratus Linné var. *millepunctata* Lamarck. Dautzenberg and Bouge, 1933, Jour. Conchyl., 77: 78.

Conus millepunctatus Lamarck var. *aldrovandi* Dautzenberg, 1937, Mém. Mus. Roy. Hist. Nat. Belg., 2(18): 171. (non *aldrovandi* Risso, 1826.)

Conus litteratus pardus (Bolten). Suvatti, 1938, Molluscs of Siam, p. 39.

Conus litteratus pardus (Röding). Kira, 1955, Coloured Illus. Shells Japan, p. 72.

Lithoconus leopardus (Röding). Kaicher 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 13.

DESCRIPTION: Shell massive, conical. Body whorl with very obscure striae; base truncate; aperture rather narrow, the sides parallel. Shoulder smooth; spire depressed, spirally canaliculate and striate. Color of body whorl cream white, with many encircling rows of oblong bluish brown to black spots. One or two rows of small spots often alternate with one or two rows of large ones. The spots are more pronounced in smaller individuals. The body whorl of juvenile specimens is dark cream with narrow transverse white bands on which the dark spots are superimposed. The latter are more square than in adult specimens. Specimens 15 cm. or more in length may be almost completely unmarked. Color of aperture white or pale orange, sometimes yellow at the base. Periostracum olive brown, very thick, opaque. In life, exposed soft parts yellowish white, mottled with brown.

LENGTH: Ordinarily 150–200 mm. This species is the largest representative of the genus in Hawaii. A specimen in the collection of Mr. C. S. Weaver of Honolulu measures 221 × 124 mm.

TYPE LOCALITY: None.

REMARKS: *Conus leopardus* may be distinguished from *C. litteratus* Linné, its closest relative, by the following characteristics: *C. litteratus*, which does not occur in Hawaii, attains a length of only about 5 inches. It generally reaches its maximum width anterior of the shoulder, rather than at the shoulder, as in *C. leopardus*. The base of *C. litteratus* is pointed rather than truncate, and it typically

bears a black smudge at the base of the aperture. The spots are more nearly similar in size and more square, and the shell typically bears two broad yellow bands.

C. leopardus is occasionally found on reef platforms but occurs more commonly in depths of one fathom or more in bays and offshore. It is known to occur to a depth of 12 fathoms. Pleistocene fossils of *C. leopardus* are known from Oahu (Ostergaard, 1928).

Conus litoglyphus Hwass in Bruguière

Conus capitaneus var. δ . Gmelin, 1791, Syst. Nat., ed. 13, p. 3377.

Conus capitaneus var. ζ . Gmelin, 1791, Syst. Nat., ed. 13, p. 3377.

Conus litoglyphus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 692, pl. 338, fig. 8.

Cucullus cinamomeus Röding, 1798, Mus. Boltenianum, p. 43.

Cucullus orleanus Röding, 1798, Mus. Boltenianum, p. 44.

Conus subcapitaneus Link, 1807, Besch. Nat.-Samml. Univ. Rostock, Abt. 3, p. 103.

Conus lithoglyphus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 280.

Conus lithoglyphus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 175.

Conus lacinulatus Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 108, fig. 2, p. 312.

Conus carpenteri Crosse, 1865, Jour. Conchyl., 13: 302, pl. 9, fig. 1.

(?) *Conus seychellensis* Nevill, 1874, Jour. Asiatic Soc. Bengal, 43(2): 22.

Conus lithoglyphus Reeve. Tomlin, 1937, Proc. Malac. Soc. Lond., 22: 268.

Dauciconus ermineus (Born). Cotton, 1945, Rec. South Austral. Mus., 8: 246.

Conus lithographus. Platt, 1949, Natl. Geog. Mag., 96: 53, fig. 2.

Conus inermis Born. Tinker, 1952, Pacific Sea Shells, p. 40.

Lithoconus ermineus (Born). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 4, fig. 10.

DESCRIPTION: Shell elongate; body whorl faintly and distantly striate toward the base,

the striae absolutely tuberculate. Aperture very narrow, the sides parallel. Color of body whorl dull yellow, reddish brown, or chestnut, often darker at the base, banded at the center and shoulder with rows of white blotches. Spire with alternate brown and white maculations on each whorl. Interior of aperture white.

LENGTH: 50 mm.

TYPE LOCALITY: "Mers des grandes Indes."

REMARKS: This species has often been referred to as *Conus ermineus* Born (Dautzenberg, 1937). Although Born did not provide a figure of *C. ermineus* and his brief description has been held by some (Burch, 1955) to be inadequate, the first figure reference given by Born (Valentyn, 1773: pl. 5, fig. 47) is a fairly good representation of the species under discussion. However, as was first pointed out by Brauer (1878), the two specimens on which Born's original description was based (Naturhistorisches Museum, Vienna, Nos. 4051 and 4052) are not conspecific with *C. litoglyphus* Hwass. Born's specimens are of the species later described by Lamarck (1810: 281) as *C. narcissus*.

Conus litoglyphus occurs rarely on Hawaiian reefs. It has been collected at a depth of 30 fathoms.

Conus lividus Hwass in Bruguière

Fig. 17 in Plate 1

Conus rusticus var. β Gmelin, 1791, Syst. Nat., ed. 13, p. 3383. (non *rusticus* Linné, 1758.)

Conus lividus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 630, pl. 321, fig. 5.

Conus rusticus Linné (Gmelin). Schreibers, 1793, Conchylienkenntniss, 1: 26.

Cucullus monachos Röding, 1798, Mus. Boltenianum, p. 39.

Conus plebejus Link, 1807, Besch. Nat.-Samml. Univ. Rostock, Abt. 3, p. 106.

Conus lividus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 36.

(?) *Conus balteatus* Sowerby, 1833, Conch. Illus., p. 3, pt. 37, fig. 58.

Conus lividus Lamarck. Quoy and Gaimard, 1834, Voy. *Astrolabe* Zool., 3: 98, pl. 53, figs. 19-21.

Conus sanguinolentus Quoy and Gaimard, 1834, Voy. *Astrolabe* Zool., 3: 99, pl. 53, fig. 18.

Conus lividus Linné. Krauss, 1848, Die Südafrikanischen Molluscen, p. 130.

Conus rusticus Linné. Mörch, 1857, Catal. Suenson, p. 32. (error).

Conus citrinus Gmelin. Sowerby, 1857, Thes. Conchyl., 3: 4, pl. 4, fig. 70. (error).

(?) *Conus bocki* Sowerby, 1881, Proc. Zool. Soc. Lond., 1881: 636, pl. 56, fig. 7.

(?) *Conus prytanis* Sowerby, 1882, Proc. Zool. Soc. Lond., p. 117, pl. 5, fig. 1.

Conus plebeius Link. Tomlin, 1937, Proc. Malac. Soc. Lond., 22: 293.

Virgiconus lividus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 254.

Rhizoconus lividus (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 75.

Stephanoconus lividus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 13.

DESCRIPTION: Shell solid, with widely spaced transverse slightly elevated striae on the body whorl, the striae obsolete near the shoulder but strongly granulated basally. Aperture narrow, the sides parallel. Shoulder coronate; spire obtuse, coronated with large tubercles, striate, often eroded. Color olivaceous or orange brown, with tubercles of the spire and a transverse band below the shoulder white or bluish white. A central band on the body whorl light yellow, white, or bluish white. Color of aperture violet with a pale central transverse band; margin of outer lip yellow. Periostracum greenish brown, thick, opaque. In life, foot, rostrum and siphon black, finely mottled with more or less red, appearing reddish black.

LENGTH: Usually to 60 mm. A specimen 76 mm. in length, collected near Nanakuli, Oahu, is in the collection of Mr. A. M. Harrison of Honolulu.

TYPE LOCALITY: "Antilles," "Isle-de-France"

& aux Indes orientales." The first locality is undoubtedly in error. Île de France was an eighteenth-century French name for Mauritius, which was probably the source of Hwass's specimens.

REMARKS: *C. lividus* is one of the two most abundant species of *Conus* on Hawaiian coral reef platforms, the other being *C. flavidus*.

Conus marmoreus Linné

Fig. 9 in Plate 1

Conus marmoreus Linné, 1758, Syst. Nat., ed. 10, p. 712.

Conus nocturnus Solander, 1786, Cat. Portland Mus., p. 156, no. 3411.

Conus marmoratus Linné. Herbst, 1788, Hist. Verm., p. 176, pl. 43, fig. 1. (Not seen.)

Conus bandanus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 611, pl. 318, fig. 5.

Conus nocturnus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 611, pl. 318, fig. 1.

[*Conus tigrinus* Humphrey, 1797, Mus. Calonianum, p. 13.]

[*Conus nigritus* Humphrey, 1797, Mus. Calonianum, p. 13.]

Cucullus marmoreus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 38.

Cucullus proarchibalassus Röding, 1798, Mus. Boltenianum, p. 38.

Conus proarchibalassius (Bolten). Link, 1807, Besch. Nat.-Samml. Univ. Rostock, Abt. 3, p. 105.

Conus marmoreus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 29.

Conus bandanus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 29.

Conus nocturnus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 30.

Conus maculatus Perry, 1811, Conchology, pl. 24, fig. 4.

Conus bandanus Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 155-156, fig. 121.

Conus nocturnus Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 155-156, figs. 122, 123.

Coronaxis bandanus (Lamarck). Swainson, 1840, Treatise on Malacol., p. 311.

Conus proarchibalassus (Bolten). Mörch, 1852, Catal. Conchyl. Yoldi, p. 64.

Conus deburghiae Sowerby, 1857, Thes. Conchyl., 3: 2, pl. 1, figs. 6, 7.

Conus nigrescens Sowerby, 1859, Proc. Zool. Soc. Lond., pt. 27: 429, pl. 49, fig. 2.

Conus crosseanus Bernardi, 1861, Jour. Conchyl., 9: 168, pl. 6, figs. 5, 6.

Conus pseudomarmoreus Crosse, 1875, Jour. Conchyl., 23: 223, pl. 9, fig. 4.

Conus marmoreus bandanus Hwass. de Burros e Cunha, 1933, Mem. Estud. Mus. Zool. Univ. Coimbra, Sér. 1, No. 71: 10.

Coronaxis bandanus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 235.

Cucullus marmoreus (Linné). Kira, 1955, Coloured Illus. Shells Japan, p. 72.

Cucullus bandanus (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 72.

Conus marmoreus bandanus Lamarck. Katcher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 3, fig. 6.

DESCRIPTION: Shell large; body whorl obsoletely striate, its maximum diameter slightly anterior of the shoulder; aperture rather narrow, with almost parallel margins. Shoulder strongly coronate; spire depressed, coronate, striate. Large triangular pale flesh-colored markings separated by dark brown and crowded in two areas form broad irregular bands on the body whorl in specimens from the Hawaiian Islands, the anterior band being narrower. Aperture white or pale pink. Periostracum thin, yellow, translucent. In life, foot tan, siphon banded proximally from the tip with red, white, and black bands.

LENGTH: Usually to 100 mm. A specimen from Oahu in the B. P. Bishop Museum measures 139 mm.

TYPE LOCALITY: Asia.

REMARKS: Hawaiian representatives differ from typical *C. marmoreus*, in which the white markings are larger and less crowded and do not form bands. In some localities, such as New Caledonia (Crosse and Marie, 1874),

Bikini, the Philippines, both forms occur together, with intergrades. To the writer's knowledge, none of the typical forms of *C. marmoreus* have ever been collected in the Hawaiian Islands. The form found in Hawaii (and elsewhere) was described as *C. bandanus* Hwass in Bruguière. Most authorities regard the latter as a variety of *C. marmoreus*, which is probably valid in areas where both, as well as intergrades, occur. However, it is probably legitimate to consider the Hawaiian populations as belonging to the subspecies *Conus marmoreus bandanus* Hwass in Bruguière. It occurs uncommonly on Hawaiian reefs and has been collected at a depth of eight fathoms.

Conus miles Linné

Fig. 6 in Plate 1

Conus miles Linné, 1758, Syst. Nat., ed. 10, p. 713.

Cucullus miles (Gmelin). Röding, 1798, Mus. Boltenianum, p. 43.

Conus miles Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 171.

Leptoconus miles (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Rhizoconus miles (Linné). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.

Lithoconus miles (Linné). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 3.

DESCRIPTION: Shell solid, with a moderately elevated spire. Body whorl smooth except for raised granular transverse ridges near the base. Aperture narrow, the sides parallel; outer lip thin. Shoulder obsoletely coronate; spire obsoletely tuberculate or plicate, rather faintly striate, concave in young individuals to straight or convex in larger ones. Color of body whorl yellowish white, with a broad, transverse blackish brown band above the center of the body whorl, and another at the base. The bands may be divided transversely into lighter and darker portions. Above and below the upper band, shell marked by narrow threadlike longitudinal dark brown lines,

which are continuous on the spire; the lines becoming more closely spaced in older individuals. The broad brown bands, alternating with white, are visible within the aperture. Periostracum greenish brown, with transverse rows of tufted ridges on the body whorl. In life, exposed soft parts greenish black.

LENGTH: 80 mm.

TYPE LOCALITY: India.

REMARKS: *C. miles* is rare on Hawaiian coral reefs and marine benches but occurs more commonly at depths of one to several fathoms. It has been collected at a depth of 26 fathoms.

Conus moreleti Crosse

Fig. 16 in Plate 1

Conus elongatus Reeve, 1843, Conch. Icon., 1: pl. 27, fig. 157. (non *elongatus* Borson, 1820.)

Conus oblitus Reeve, 1849, Conch. Icon., 1(Emendns.): 1. (non *oblitus* Michelotti, 1847.)

Conus moreleti Crosse, 1858, Rev. Mag. Zool., Ser. 2, 10: 122.

Conus lividus Hwass var. *elongatus* Reeve. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 262.

Conus lividus Bruguière var. *moreleti* Crosse. Paetel, 1887, Catal. Conch.-Samml. Paetel, 1: 299.

Stephanoconus moreleti (Crosse). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 14.

DESCRIPTION: Shell elongate, body whorl with raised, obsoletely knobbed striae basally, otherwise smooth; aperture very narrow, the sides parallel; outer lip thin. Shoulder coronate; spire low, convex, coronate, striate. Color of body whorl yellowish brown or olive, darker at the base, with lighter transverse bands at the shoulder and at the middle. Interior of aperture deep violet, outer lip yellow. Periostracum yellowish brown, rather thin, translucent, forming tufts on the tubercles.

LENGTH: 50 mm.

REMARKS: *C. moreleti* may be distinguished from *C. lividus*, its closest relative, by its elongate shape and small and closely spaced tubercles on the shoulder. It is rare on Hawaiian reefs but occurs more commonly at depths of a few fathoms.

Conus nussatella Linné

Fig. 19 in Plate 1

Conus nussatella Linné, 1758, Syst. Nat., ed. 10, p. 716.

Conus mussatellana Linné. Schröter, 1782, Mus. Gottwald., p. 23, pl. 13, figs. 96^a, 96^b, 96^c; pl. 43, fig. 52^a.

[*Conus punctulatus major* Humphrey, 1797, Mus. Calonianum, p. 15.]

Cucullus nussatella (Gmelin). Röding, 1798, Mus. Boitenianum, p. 50.

Hermes nussatellus (Linné). Montfort, 1810, Conchyl. Syst., 2: 399.

Coni nussatellae Linné. Müller, 1836, Synopsis Nov. Gen. Spec. Var. Testaceorum Viventum, p. 122.

Conus nussatella Lamarck. Dufou, 1840, Ann. Sci. Nat., Ser. 2, 14: 178.

Hermes nussatula (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 256.

Conus nusatella Linné. Mörch, 1854, Catal. Hencks, p. 21.

Conus nusatella Linné. Weinkauff, 1873, Syst. Conch. Cab., ed. 2, 4: 151.

Hermes nussatella Linné. Schmeltz, 1874, Catal. Mus. Godeffroy, 5: 136.

Hermes nusatellata (Linné). Brazier, 1877, Proc. Linn. Soc. New South Wales, 1: 291.

Conus nussatellata Linné. Brazier, 1879, Jour. Conchol., 2: 192.

DESCRIPTION: Shell cylindrical, rather thin. Body whorl closely striate, the striae minutely granular. Aperture narrow, flaring slightly basally. Shoulder rounded; spire high, convex; apex sharp. Color yellowish white, clouded irregularly with orange brown or light purplish brown longitudinal splotches; with transverse rows of numerous small dark orange brown spots on the body whorl and

spire. Periostracum thin, yellow, translucent.

LENGTH: 60 mm.

TYPE LOCALITY: "Nussatello Insulam Asiae."

REMARKS: *C. nussatella* is a rare species in the Hawaiian Islands. Pleistocene fossils have been collected on Oahu by Ostergaard (1928) and the writer.

Conus obscurus Sowerby

Fig. 36 in Plate 2

Conus obscurus Sowerby, 1833, Conch. Illus., p. 2, pt. 29, fig. 26.

Conus obscurus Humphreys MSS. Reeve, 1843, Conch. Icon., 1: pl. 16, fig. 82.

Conus obscurus Reeve. Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 68, fig. 2, p. 347.

Nubecula obscura (Humphreys). Adams and Adams, 1853, Gen. Rec. Moll., 1: 249.

Conus tulipa Linné, juv. Pease, 1868, Am. Jour. Conch., 4: 126. (error).

Conus obscurus (Hwass) Reeve. Dautzenberg, 1937, Mém. Mus. Roy. Hist. Nat. Belg., 2: 193, pl. 3, fig. 9.

Conus halitropus Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 88.

Conus halitropus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.

Tuliparia obscura (Reeve). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 291.

Gastridium obscurum (Sowerby). Kuroda, 1956, Venus: Jap. Jour. Mal., 19: 80.

DESCRIPTION: Shell elongate-ovate, very thin. Body whorl smooth except for very fine transverse grooves basally. Aperture rather broad, flaring basally. Shoulder smooth; spire moderately elevated, striate; apex pointed. Shell marked by irregularly shaped and distributed blotches and dots of light brown; the lighter areas separating them are violet. Periostracum very thin, translucent.

LENGTH: 30 mm.

TYPE LOCALITY: Arabia.

REMARKS: *C. obscurus* occurs rarely in shal-

low water in Hawaii and is apparently more common at depths of several fathoms.

Conus pennaceus Born

Fig. 3 in Plate 1

Conus pennaceus Born, 1780, Test. Mus. Caes. Vind., p. 167, pl. 7, fig. 14.

Conus aulicus var. α Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.

Conus aulicus var. β Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.

Conus aulicus var. γ Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.

Conus aulicus var. ϵ Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.

(?) *Conus omaria* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 743, pl. 344, fig. 3.

Conus rubiginosus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 746, pl. 344, figs. 1, 2.

(?) *Conus praelatus* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 746, pl. 345, fig. 4.

(?) *Conus episcopus* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 748, pl. 345, figs. 2, 6. (In part.)

(?) *Conus crocatus* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 424.

(?) *Conus colubrinus* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 433.

Conus pennaceus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 434.

Conus omaria Hwass var. β . Reeve, 1843, Conch. Icon., 1: pl. 32, sp. 177, figs. 177a, 177b.

Conus pennaceus Lamarck. Reeve, 1843, Conch. Icon., 1: pl. 32, sp. 177.

(?) *Conus elisae* Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 64, figs. 1, 1a, p. 341.

(?) *Conus stellatus* Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 99, fig. 3, p. 225.

Conus madagascariensis Sowerby, 1858, Thes. Conchyl., 3: 43, pl. 24, fig. 582.

Conus racemosus Sowerby, 1873, Proc. Zool. Soc. Lond., 1873: 721, pl. 59, fig. 11.

Conus auratus Hwass. Ostergaard, 1928, Bull. Bishop Mus., 51: 4, 29. (error).

Darioconus racemosus (Sowerby). Cotton, 1945, Rec. South Austral. Mus., 8: 257.

Darioconus pennaceus (Born). Cotton, 1945, Rec. South Austral. Mus., 8: 257.

Conus auratus Hwass. Morris, 1952, Field Guide to Shells Pac. Coast & Hawaii, p. 202, col. pl. 7, fig. 3. (error).

Cylinder pennaceus (Born). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 7, fig. 13.

DESCRIPTION: Shell ventricose, robust, broad at the shoulder; maximum diameter equal to or greater than one half the shell length. Body whorl obsoletely striate, the striae more pronounced basally. Aperture rather broad, flaring slightly basally. Shoulder smooth, usually somewhat rounded, but variable. Spire variable, depressed to moderately elevated, concave to slightly convex, obsoletely striate; protoconch nipplelike, rose colored. Ground color reddish brown (yellow specimens are occasionally found), with narrow transverse closely spaced lines, finely dotted with white. These areas are interrupted by large white subtrigonal blotches, grouped together like scales, usually forming a central band and sometimes additional bands at the shoulder and base. Color pattern of the body whorl usually continued on the spire. Interior of aperture white or bluish white. In life, foot pale brown mottled with darker brown; tip of siphon vermillion, followed proximally by white and black bands.

LENGTH: Usually to 65 mm. A specimen in the U. S. National Museum, collected at Hilo, Hawaii, measures 82 mm. in length.

TYPE LOCALITY: China.

REMARKS: Most specimens found in Hawaii agree fairly well with the original description and figure, although there is considerable morphological variation.

C. pennaceus is extremely similar to *C. omaria* Hwass in Bruguière. Tryon (1884) and some other authors have synonymized the two. Kiener (1849-1850: 340) listed characteristics by which the two species may be distinguished, stating under *C. pennaceus*, "C'est avec le *Conus omaria* que cette espèce a le plus d'analogie; le système de coloration de ces deux coquilles est à peu près semblable;

seulement, dans l'espèce ici décrite, les grandes zones sont plutôt longitudinales que transverses, et le réseau qui les constitue n'est pas aussi nettement limité. La form d'ailleurs est également différente; elle est toujours plu raccourcies et plue ventrue." The present writer has found that these distinctions generally hold, but it would be difficult to classify a small percentage of specimens collected in Hawaii using these criteria. If the two species eventually prove to be synonymous, the name *C. pennaceus* has priority over *C. omaria*.

C. pennaceus is one of the most common species on Hawaiian coral reef platforms. Fossils are known from Pleistocene deposits on Molokai (Ostergaard, 1939, as *C. omaria*).

C. elisae Kiener, here listed questionably as a synonym, is possibly a valid species. For an account of it, see page 396.

Conus pertusus Hwass in Bruguière

Fig. 31 in Plate 2

- Conus nobilis* Linné. Schröter, 1783, Einl. Conchyl., 1: 36, pl. 1, fig. 4. (error).
Conus pertusus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 686, pl. 336, fig. 2.
Conus pertusus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 278.
Conus amabilis Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 425.
Conus festivus Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 413.
 (?) *Conus inquinatus* Reeve, 1849, Conch. Icon. Suppl., pl. 5, sp. 251.
Hermes pertusus (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 256.
Conus pertusus Lamarck. Sowerby, 1858, Thes. Conchyl., 3: 23, pl. 13, fig. 273.
Leptoconus pertusus. Schmeltz, 1874, Catal. Mus. Godeffroy, 5: 136.
Pionoconus pertusus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 249.
Rhizoconus pertusus (Bruguière). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 290.
Lithoconus pertusus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 4.

DESCRIPTION: Shell conical; body whorl encircled by distantly spaced punctate striae; aperture rather narrow, sides parallel. Shoulder smooth; spire low, convex, rather obtuse. Color rose, flaked with yellow or white, banded with two interrupted transverse rows of white or light pink blotches below the shoulder and centrally on the body whorl.

LENGTH: 40 mm.

TYPE LOCALITY: "Grandes Indes."

REMARKS: *Conus pertusus* is uncommon in Hawaii. It is known to occur subtidally to a depth of 25 fathoms.

Conus pulicarius Hwass in Bruguière

Fig. 12 in Plate 1

- Conus pulicarius* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 622, pl. 320, fig. 2.
Conus fustigatus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 623, pl. 320, fig. 1.
Cucullus punctulatus Röding, 1798, Mus. Boltinianum, p. 40.
Conus pulicarius Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 34.
Conus fustigatus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 35.
Conus pulicarius Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 174.
Conus vauitieri Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 100, fig. 3, p. 350.
Conus fustigatus Lamarck. Reeve, 1849, Conch. Icon. Temp. Index (Critical Analysis), unpaginated.
Puncticulis pulicarius (Hwass). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.
Puncticulis pulicarius (Bruguière). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 289.
 DESCRIPTION: Shell thick and solid; body whorl with impressed transverse striae basally; aperture rather narrow, sides parallel. Shoulder coronate; spire moderately elevated, striate, coronate. Color white with dark brown to black spots, the spots often crowded into two transverse bands, one on each side of the center. Spire white, marked sparingly with

brown dots. Periostracum yellow, very thin and translucent in young individuals, thicker and brown in larger specimens. In life, foot and rostrum pale tan mottled with yellowish to reddish brown; tip of siphon reddish orange, followed proximally by pale buff and black bands.

LENGTH: Usually to 60 mm. A specimen collected by W. H. Christensen at Ala Moana Reef, Oahu, measures 74 × 42 mm. A specimen collected by C. S. Weaver measures 73 × 44 mm.

TYPE LOCALITY: Pacific Ocean.

REMARKS: *C. pullicarius* occurs in patches of sand on reef platforms and in bays. It has been collected at depths exceeding 40 fathoms.

Conus quercinus Solander

Fig. 4 in Plate 1; Fig. 23 in Plate 2

Conus quercinus Solander in Cat. Portland Mus., 1786, p. 67, no. 1501.

Conus cingulum Gmelin, 1791, Syst. Nat., ed. 13, p. 3378.

Conus quercinus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 681, pl. 332, figs. 5, 6.

Conus quercinus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 276.

Conus quercinus Hwass. Blainville, 1818, Dict. Sci. Nat., 10: 249.

Conus quercinus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 172.

Dendroconus quercinus (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.

Conus ponderosus Sowerby, 1858, Thes. Conchyl., 3: 54.

Lithoconus quercinus (Bruguière). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.

Cleobula quercina (Solander). Cotton, 1945, Rec. South Austral. Mus., 8: 260.

Lithoconus quercinus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 9.

DESCRIPTION: Shell large and solid, variable in obesity. Body whorl obsoletely striate, the striae becoming more pronounced basally;

aperture rather wide, sides parallel. Shoulder smooth, rounded. Spire depressed, concave, striate; apex raised. Color of body whorl yellow, encircled with numerous closely spaced transverse threadlike brown lines; spire usually paler yellow; interior of aperture white. Periostracum thick, brown, opaque. In life, foot and siphon brownish gray, heavily speckled with black.

LENGTH: Usually to 100 mm. A specimen from Oahu in the B. P. Bishop Museum measures 134 mm.

TYPE LOCALITY: None.

REMARKS: *C. quercinus* is found in large sandy areas in bays and to depths of more than 40 fathoms.

Conus rattus Hwass in Bruguière

Fig. 30 in Plate 2

Conus rattus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 700, pl. 338, fig. 7.

Conus taitensis Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 713, pl. 336, fig. 9.

Conus capitaneus var. C. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 266.

Conus rattus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 408.

Conus taitensis Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 424.

Conus capitaneus var. B. Küster, 1837-1840, Syst. Conch. Cab., ed. 2, 4: 8, pl. 14, figs. 13, 14.

Conus tabeitisensis Hwass. Reeve, 1843, Conch. Icon., 1: pl. 15, sp. 78.

Conus rattus Lamarck. Reeve, 1843, Conch. Icon., 1: sp. 78.

Conus tabeitisensis Hwass var. *rattus* Lamarck. Catlow and Reeve, 1845, Conchol. Nomencl., p. 322.

Leptoconus rattus (Lamarck). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Leptoconus tabeitisensis (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Conus tabeitisensis Bruguière. Sowerby, 1857, Thes. Conchyl., 3: 5, pl. 2, fig. 26.

Conus viridis Sowerby, 1857, Thes. Conchyl., 3: 20, pl. 5, fig. 102.

Conus tahitiensis Bruguière. Schmelz, 1865, Catal. II Godeffroy, p. 20.

Conus rattus Solander. Schaufuss, 1869, Molluscorum Syst. Cat. Paetel, p. 45.

Conus tabitensis Bruguière. Schaufuss, 1869, Molluscorum Syst. Cat. Paetel, p. 45.

Conus ratus var. *tabitensis*. Ostergaard, 1928, B. P. Bishop Mus. Bull. 51: 29.

Conus tabitiensis Hwass (emend.). Dautzenberg and Bouge, 1933, Jour. Conchyl., 77: 89.

Rhizoconus rattus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., vol. 8, p. 252.

Conus tabitensis Hwass. Mermod, 1947, Rev. Suisse Zool., 54: 208.

Lithoconus rattus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 1.

DESCRIPTION: Shell of moderate thickness; body whorl obsoletely striate near the shoulder, but distinctly so near the base, the striae closely spaced; aperture rather narrow, sides nearly parallel. Shoulder angular, smooth; spire rather low, obtuse, striate. Color of body whorl yellowish or violet brown, with large bluish white spots and maculations forming an interrupted central band and another at the shoulder. Shell below central band densely flecked with white, above band sparsely flecked with white. Spire with alternate brown and white blotches, continuing to form band on body whorl at shoulder. Aperture violet within. Periostracum thin, yellow, translucent, smooth or with raised ridges near growing edge. In life, foot, rostrum and siphon dark olive green, mottled with black.

LENGTH: Usually to 40 mm. A specimen collected by T. H. Richert on windward Oahu, and presently in the collection of the Children's Museum of Honolulu, measures 60 mm.

TYPE LOCALITY: "Mers d'Amerique," undoubtedly in error.

REMARKS: *C. rattus* occurs not uncommonly both on intertidal benches and on subtidal

reef platforms. Pleistocene fossils are known from Oahu (Ostergaard, 1928) and Maui (Ostergaard, 1939).

Conus retifer Menke

Fig. 32 in Plate 2

Conus retifer Menke, 1829, Verz. Ans. Conch.-Samm. Malsburg, p. 68.

Conus solidus Sowerby, 1834, Conch. Illus., p. 3, pt. 56, fig. 76. (non *solidus* Gmelin, 1791.)

Cylinder solidus (Sowerby). Adams and Adams, 1853, Gen. Rec. Moll., 1: 255.

Darioconus retifer (Menke). Cotton, 1945, Rec. South Austral. Mus., 8: 258.

Cylinder retifer (Menke). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 7, fig. 10.

DESCRIPTION: Shell very thick and solid, pear-shaped. Body whorl striate; aperture with almost parallel sides. Shoulder rounded, smooth. Spire elevated, acuminate, striate. Color reticulated orange brown with large and small white triangular markings, arranged as scales, and longitudinal chocolate and orange markings mostly interrupted to form two transverse bands. Color pattern of body whorl continued on spire; apex pink. Interior of aperture white or pale pink. Periostracum very thin, pale yellow, very translucent. In life, foot mottled brown. Tip of siphon vermilion, followed proximally by white and black bands.

LENGTH: 50 mm.

TYPE LOCALITY: None.

REMARKS: *C. retifer* is uncommon in Hawaii.

Conus spiceri Bartsch and Rehder

Fig. 8 in Plate 1

Conus spiceri Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 87.

Conus spiceri Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.

DESCRIPTION: Shell large and thick; body whorl marked by fine incremental lines and closely spaced spiral threads, becoming heav-

ier and more distantly spaced basally. Aperture fairly broad, widening somewhat basally. Shoulder broad, smooth, angular. Spire low, concave, singly striate. Color pale yellow, somewhat darker basally, with obscure white transverse bands. Interior of aperture bluish white. Periostracum thick, yellowish brown.

LENGTH: 110 mm.

TYPE LOCALITY: Midway Island.

REMARKS: This species, which is rather rare, is distinguished from *C. quercinus* in that it lacks the brown spiral lines, has a flatter spire, and is only singly striate on the summit. It is distinguished from *C. distans* by lacking the brown bands and tuberculate shoulder. Its closest relative is *C. virgo* Linné, which does not occur in Hawaii. *C. virgo* is easily distinguished from *C. spiceri* by the pronounced violet color of the base in the former.

To the author's knowledge, no specimens of *C. spiceri* have been collected outside the Hawaiian Islands.

Conus sponsalis Hwass in Bruguière

Figs. 38 and 39 in Plate 2

Conus sponsalis Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 635, pl. 322, fig. 1.

(?) *Conus ceylanensis* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 636, pl. 322, fig. 10.

Conus sponsalis Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 38.

Conus nanus Sowerby, 1833, Conch. Illus., p. 1, pt. 24, fig. 6.

Conus nanus Broderip, 1833, Proc. Zool. Soc. Lond., 1833: 53.

Coronaxis nanus (Broderip). Adams and Adams, 1853, Gen. Rec. Moll., 1: 248.

Coronaxis sponsalis. Adams and Adams, 1853, Gen. Rec. Moll., 1: 248.

Conus sponsalis Solander. Von Martens and Langkavel, 1871, Donum Bismarckianum. Samml. Südsee-Conchyl., p. 31.

Conus ceylonensis Hwass var. *sponsalis*. Tryon, 1884, Man. Conch., 6: 23, pl. 6, fig. 99.

Conus ceylonensis Hwass var. *nanus* Broderip. Tryon, 1884, Man. Conch., 6: 24, pl. 6, fig. 100.

Conus nana Broderip. Paetel, 1887, Catal. Conch.-Samml. Paetel, 1: 302.

Conus ceylanensis Hwass var. *pusillus*. Mant, 1922, Nautilus, 35: 84.

Conus ceylonensis Hwass. Ostergaard, 1935, B. P. Bishop Mus. Bull., 131: 21.

Virroconus sponsalis (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 237.

Stephanoconus sponsalis (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 5.

DESCRIPTION: Shell small but thick and solid, extremely variable with respect to several characteristics. Body whorl usually obsoletely striate, the striae somewhat more pronounced basally; aperture narrow, the sides parallel. Shoulder coronated with small tubercles which may be obsolete in large specimens. Spire usually moderately elevated, inner whorls coronated, but often eroded; 0-3 striae per whorl. Ground color of basal two thirds of body whorl typically pale blue; remaining area near the shoulder white; base tipped with brownish purple. In many specimens, no other coloration is present. Some individuals, chiefly younger specimens, marked with reddish or orange brown on body whorl; these markings generally of two arrangements, one or both of which may be present on the same shell: (1) encircling narrow bands of rather distantly separated dots or dashes separated by white dashes (Fig. 39); (2) interrupted longitudinal blotches of color (Fig. 38). Tubercles white, areas between them sometimes orange brown. Interior of aperture dark violet to brown, with white bands near the shoulder and centrally; outer lip white. Periostracum thin, translucent, sometimes becoming thicker and opaque at the growing edge, or in larger specimens. In life, foot pale pink, mottled with white, darker pink at extremities. Siphon and rostrum pale pink or white, tipped with darker pink; tentacles white.

LENGTH: To 30 mm. Most specimens smaller.

TYPE LOCALITY: "Île Saint-George."

REMARKS: Specimens from Hawaiian populations agree with the original figure and Broderip's (1833) description of *Conus nanus*, which has not generally been considered a distinct species. A number of workers (Pease, 1868; Tryon, 1884; Ostergaard, 1935; Tomlin, 1937; Tinker, 1952) have considered *C. nanus* to be not specifically distinct from *C. ceylanensis*.

C. ceylanensis does not seem to be a well-known species. Specimens from many Indo-West Pacific localities in the U. S. National Museum and Museum of Comparative Zoology collections are indistinguishable from representatives of the Hawaiian populations under consideration.

Examination of specimens from many Indo-West Pacific island groups in the U. S. National Museum, Museum of Comparative Zoology, and Academy of Natural Sciences of Philadelphia, and personal observations of the writer in the Marshall Islands led to the conclusions that the widespread *C. sponsalis* is also extremely variable and that there is sufficient morphological overlap with the Hawaiian forms for the latter to be considered conspecific with *C. sponsalis*. However, since most Hawaiian specimens are morphologically distinguishable from most specimens from other parts of the central and western Pacific, the Hawaiian populations may validly be accorded subspecific rank and termed *C. sponsalis nanus* Sowerby.

Tryon (1884: 24), who was also uncertain of the distinction between *C. sponsalis* and *C. ceylanensis*, considered *C. nanus* a variety of the latter in his arrangement but considered the possibility that both were varieties of *C. sponsalis*. Ostergaard (1935) also listed "*Conus ceylonensis sponsalis*," under which he stated, "I believe that this shell intergrades with *C. ceylonensis* Hwass and should therefore be termed a variety of that species, as Tryon places it."

Although the identity of *C. ceylanensis* remains problematical, the present writer is inclined to agree that it is probably conspecific

with *C. sponsalis*. In this case, the name *sponsalis* has page priority, and there seems no reason why it should not take precedence over *ceylanensis*. It is hoped that collections in Ceylon and other Indian Ocean areas, to be made by the writer in the near future, will contribute towards a more definitive solution to this question.

C. sponsalis is one of the most abundant species of *Conus* on intertidal benches in Hawaii. Pleistocene fossils are known from Oahu (Ostergaard, 1928) and Molokai (Ostergaard, 1939).

Conus striatus Linné

Fig. 5 in Plate 1

Conus striatus Linné, 1758, Syst. Nat., ed. 10, p. 716.

Cucullus striatus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 50.

Conus striatus Lamarck. Quoy and Gaimard, 1834, Voy. Astrolabe Zool., 3: 89, pl. 52, figs. 10, 10¹.

Leptoconus striatus (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 254.

Tuliparia striata. Gray, 1857, Guide Moll. Brit. Mus., 1: 5.

Conus floridus Sowerby, 1858, Thes. Conchyl., 3: 47, frontispiece, fig. 558.

Cbelyconus striatus (Linné). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.

Conus tulipa Linné var. *floridus* Sowerby. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 284.

Phasmoconus striatus (Linné). Cotton, 1945, Rec. South Austral. Mus., 8: 260.

Dendroconus striatus (Linné). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 292.

DESCRIPTION: Shell large, rather thin, elongate-ovate, the maximum diameter not at the shoulder but about one fifth of the distance from shoulder to base. Body whorl with fine, closely spaced transverse striae; aperture broad, flaring gradually toward the base. Shoulder angular, smooth. Spire striate,

canaliculate, usually concave, often extremely so and depressed below the shoulder, a peculiarity not typically found in specimens from other areas. Ground color pinkish white, irregularly clouded with blotches of brown or purplish brown composed of closely spaced transverse lines. Spire tessellated with brown and white. Interior of aperture white. Periostracum thin, yellow, translucent. In life, foot, siphon and rostrum tan mottled with brown.

LENGTH: Usually to 110 mm. A specimen measuring 120 × 53 mm. is in the collection of C. S. Weaver.

TYPE LOCALITY: "Hitoe."

REMARKS: Specimens from the Hawaiian Islands are characterized by having the spire depressed often to such an extent that the apex does not extend beyond the shoulder of the body whorl. In juvenile specimens, the spire is elevated and the sides of the aperture almost parallel.

C. striatus occurs uncommonly on Hawaiian reefs. It is typically found associated with a sand substratum. Pleistocene fossils of *C. striatus* have been collected by the author on Oahu.

Conus suturatus Reeve

Figs. 24–28 in Plate 2

Conus suturatus Reeve, 1844, *Conch, Icon.*, 1: pl. 45, sp. 250; suppl. pl. 3, fig. 250b.

Dendroconus suturatus (Reeve). Adams and Adams, 1853, *Gen. Rec. Moll.*, 1: 250.

Conus turbinatus Sowerby, 1858, *Thes. Conchyl.*, 3: 25, pl. 10, fig. 227.

Lithoconus hawaiiensis Bartsch and Rehder. Kaicher, 1956, *Indo-Pacific Sea Shells*, Sect. 5, pl. 5, fig. 6.

DESCRIPTION: Shell solid; body whorl obsoletely striate toward the shoulder, the striae more pronounced, impressed but with an adjacent ridge, widely spaced toward the base. In young specimens, the striae are more pronounced over the entire body whorl. Aperture narrow, sides parallel. Shoulder angular,

smooth; spire elevated in younger specimens, less so in larger ones, deeply striate, characterized by a ridge on each whorl at the junction of the preceding whorl. Ground color white, with broad transverse bands of orange brown (in smaller specimens) or orange pink (in larger specimens) on the body whorl. Base stained with pale orange brown or pale rose. Interior of aperture white. In smaller specimens, narrow bands of orange brown rectangles encircle the body whorl. Spire maculated with orange brown and white. Periostracum smooth, dark brown, opaque.

Most specimens from Hawaii are characterized by having the spire more elevated than those of the shells described and figured by Reeve.

LENGTH: To 50 mm.

TYPE LOCALITY: Port Essington, Australia.

REMARKS: *C. suturatus* is very closely related to *C. tessulatus*. In the latter, the rows of square or quadrangular blotches persist in adult specimens and vary from orange brown to, more usually, pink. In *C. suturatus*, this pattern is present in young specimens but is gradually superseded by the broad solid orange pink transverse bands mentioned in the description, and the transverse rows of rectangles are usually lost, as the shell grows larger. Some specimens of the two species may be virtually indistinguishable. In young *C. suturatus*, the broad transverse bands typically underly the juvenile pattern, the entire body whorl is usually striate, and the basal striae are accompanied by an adjacent ridge. In young *C. tessulatus* all areas between the rectangular blotches are typically white, impressed spiral striae occur only basally, and the areas between the striae are typically flat. The upper portion of the shell is smooth. Older, larger specimens of these two species are usually distinguishable by differences in color pattern cited in the accompanying descriptions.

C. suturatus is not common in shallow water in Hawaii, but many specimens have been

dredged in 4–50 fathoms off the major islands.

C. ambiguus Reeve (1844, *Conch. Icon.*, 1: pl. 44, sp. 244) appears to be extremely similar and possibly identical. Some specimens collected in Hawaii have been labeled *C. ambiguus*. A definitive statement concerning *C. ambiguus* will not be made here, pending study of type material.

Conus tessulatus Born

Fig. 22 in Plate 2

Conus tessulatus Born, 1778, *Ind. Rer. Nat. Mus. Caes. Vind.*, p. 131.

Conus virgo var. γ Gmelin, 1791, *Syst. Nat.*, ed. 13, p. 3376.

Conus tessellatus Born. Bruguière, 1792, *Enc. Meth. Vers.*, 1: 641.

Cucullus pavementum Röding, 1798, *Mus. Boltanium*, p. 41.

Conus tessellatus Lamarck. Menke, 1828, *Synopsis Methodica Molluscorum*, p. 45.

Conus tessellatus Lamarck. Dufou, 1840, *Ann. Sci. Nat.*, Ser. 2, 14: 173.

Conus desselatus Lamarck. Reichenbach, 1842, *Land.-, Süssw.- u. See-Conch.*, p. 51, pl. 17, figs. 376, 377.

Conus tessellatus Bruguière. Kiener, 1845, *Spéc. Gén. Icon. Coq. Viv.*, 2: pl. 17, fig. 1, p. 68.

Dendroconus tessellatus (Born). Adams and Adams, 1853, *Gen. Rec. Moll.*, 1: 250.

Conus tessalatus Born. Theobald, 1860, *Catal. Rec. Sh. Mus. Asiat. Soc. Bengal*, p. 24.

Conus tessellatus Born. Weinkauff, 1874, *Jahrb. Deutsch. Malak. Ges.*, 1: 245.

Conus tessellatus Bruguière. G. R. Batalha, 1878, *Catal. Coll. F. R. Batalha*, p. 25.

Conus tessellatus Hwass. Dautzenberg, 1893, *Bull. Soc. Zool. France*, 18: 80.

Conus edaphus Dall, 1910, *Proc. U. S. Natl. Mus.*, 38: 223.

Conus tessullatus Born. Hirase, 1954, *Illus. Handbk. Shells*, p. 88, pl. 113, fig. 17.

Lithoconus tessulatus (Born). Kaicher, 1956, *Indo-Pacific Sea Shells*, Sect. 5, pl. 5, fig. 11.

DESCRIPTION: Shell fairly thick and stout.

Body whorl smooth near the shoulder, bearing rather widely spaced impressed striae basally; base grooved; aperture narrow, the sides parallel; outer lip thin. Shoulder smooth, angular; spire concave, deeply striate, characterized by a ridge on each whorl at the junction of the preceding whorl; apex pointed. Ground color white, body whorl encircled by rows of quadrangular pinkish orange spots, usually crowded to form two transverse bands. Base characteristically stained with violet. Spire tessellated with pink and white. Interior of aperture white, violet at the base. In life, "yellowish white, foot mottled with brownish buff, anteriorly spotted with black; creeping disk buff yellow with darker veins; siphon creamy yellow tinged with brown, edged with yellow, with a transverse black spot at the anterior end" (Garrett, 1878).

LENGTH: 35–40 mm.

TYPE LOCALITY: Africa.

REMARKS: This species is extremely rare in shallow water in the Hawaiian Islands although it is widely distributed throughout the Indo-West Pacific region and reaches the west coast of Mexico (Hanna and Strong, 1949). Only one specimen collected alive in the Hawaiian Islands is known with certainty to the writer. It was collected by S. Sato in Haleiwa Bay, Oahu, depth 25 feet, and is in the Children's Museum of Honolulu, on loan from Mrs. Jean Bromley.

C. tessulatus was recorded from Hawaii by Garrett (1878). Dautzenberg (1937: 244) states that it was also recorded from Hawaii by P. Fischer, but no further reference is given. Three specimens in the U. S. National Museum, collected by the U. S. Exploring Expedition, are labeled "Sandwich Is." (and are shown in Plate 2, Fig. 22), but this locality datum is not to be considered reliable (J. P. E. Morrison, verbal communication).

Conus textile Linné

Fig. 2 in Plate 1

Conus textile Linné, 1758, *Syst. Nat.*, ed. 10, p. 717.

- Conus undulatus* Solander in Cat. Portland Mus., 1786, p. 180, no. 3866.
- Conus archiepiscopus* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 747, pl. 345, fig. 5; pl. 346, figs. 1, 7.
- Cucullus auriger* Röding, 1798, Mus. Boltanium, p. 49.
- Cucullus gloria-maris* Röding, 1798, Mus. Boltanium, p. 49. (non *Conus gloria-maris* Chemnitz, 1777.)
- Cucullus textile* (Gmelin). Röding, 1798, Mus. Boltanium, p. 50.
- Conus panniculus* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 435.
- Cylinder textile* (Linné). Montfort, 1810, Conchylogie Systematique, 2: 391.
- (?) *Conus pyramidalis* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 438.
- Conus gloria-maris* Perry, 1811, Conchology, pl. 25, no. 5. (non *gloria-maris* Chemnitz, 1777.)
- Conus rete-aureum* Perry, 1811, Conchology, pl. 25, no. 5.
- Conus textiles* Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 177.
- Conus textilis*. Gray, 1842, Fig. Moll. Anim., pl. 10, fig. 1.
- Conus victoriae* Reeve, 1843, Conch. Icon., 1: pl. 37, figs. 202a, 202b.
- Conus verriculum* Reeve, 1843, Conch. Icon., 1: pl. 38, figs. 208a, 208b.
- Conus concatenatus* Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 110, fig. 1, p. 362.
- Conus telatus* Reeve, 1848, Conch. Icon., 1: suppl. pl. 1, fig. 270.
- Conus scriptus* Sowerby, 1858, Thes. Conchyl., 3: 41, pl. 23, fig. 563.
- Conus tigrinus* Sowerby, 1858, Thes. Conchyl., 3: 41, pl. 23, fig. 569.
- (?) *Conus condensus* Sowerby, 1866, Thes. Conchyl., 3: 326, pl. 26, fig. 622.
- Conus paniculus* Lamarck. Paetel, 1873, Catal. Conch.-Samml. Paetel, p. 51.
- Cylindrus textile* (Linné). Morelet, 1889, Jour. Conchyl., 37: 133.
- Darioconus textile* (Linné). Cotton, 1945, Rec. South Austral. Mus., 8: 257.
- Darioconus textilis* (Linné). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 291.
- DESCRIPTION: Shell large, ventricose, rather thin, subcylindrical-ovate. Maximum diameter of about one half shell length is reached about one fifth of the distance from shoulder to base. Body whorl transversely striate, the striae fine and closely spaced; aperture broad, flaring basally. Shoulder smooth; spire elevated, concave, acuminate, striate. Ground color white, with undulating longitudinal brown lines, interrupted by white triangles arranged as scales, and broad orange brown maculations disposed to form two or three interrupted transverse bands on the body whorl; the maculations streaked longitudinally with waved darker brown lines. Spire similarly marked. Interior of aperture white. Periostracum thin, yellow, translucent. In life, foot mottled brown on white. Tip of siphon reddish orange, followed proximally by bands of white and black; remainder of siphon white with closely spaced narrow brown bands.
- LENGTH: To 100 mm.
- TYPE LOCALITY: Banda Islands.
- REMARKS: *C. textile* is rare in Hawaiian waters. It is found occasionally on reef platforms and to depths of at least 12 fathoms.

Conus vexillum Gmelin

Fig. 11 in Plate 1

- Conus vexillum* Gmelin, 1791, Syst. Nat., ed. 13, p. 3397.
- (?) *Conus sumatrensis* Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 655, pl. 327, fig. 8.
- Cucullus canonicus* Röding, 1798, Mus. Boltanium, p. 43. (non *Conus canonicus* Hwass in Bruguière, 1792.)
- Conus vexillum* Linné. De Fremery, 1802, Mus. Meyer., p. 82. (Not seen.)
- Conus vexillum* Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 268.
- (?) *Conus leopardus* Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 364. (non *leopardus* Röding, 1798.)

Conus sulphuratus Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 66, fig. 3; pl. 78, fig. 4; p. 130.

Leptoconus vexillum. Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Conus planorbis Born. Oostingh, 1928, Misc. Zool. Sumatrana, no. 28: 4. (error. Fide Misc. Zool. Sum., no. 49: 6.)

Rhizoconus vexillum (Gmelin). Cotton, 1945, Rec. South Austral. Mus., 8: 251.

DESCRIPTION: Shell large, rather thin. Body whorl obsoletely striate; aperture rather broad, sides parallel. Shoulder broad, angular, smooth. Spire moderately elevated, obtuse, somewhat canaliculate, striate. Color of body whorl white, broadly banded with yellowish brown, stained with darker brown at the base, with irregular chocolate longitudinal wavy lines which often branch and are partially interrupted to form a white band at the middle and another at the shoulder. Spire white with yellow apex and broad radiating chocolate bands, some of which are continuous on the body whorl. Interior of aperture white. Periostracum dark green, thick, opaque; ridged. In life, foot and siphon greenish black.

LENGTH: To 135 mm.

TYPE LOCALITY: None.

REMARKS: Although this species was first reported from Hawaii as *C. vexillum* (Garrett, 1878), it has generally been known in Hawaii as *C. sumatrensis*. Examination of specimens in the U. S. National Museum and in collections made by the author in Micronesia as well as Hawaii revealed morphological overlap and intergrades between typical specimens of both species. Further confusion is found in the literature. Kiener (1847: 81) stated under *C. sumatrensis*, "Coquille qui par sa forme se rapproche de la précédente [*C. vexillum*]; elle est reconnaissable surtout par ses lignes longitudinales ramifiées." Tryon (1884: 39) stated, on the other hand, under *C. vexillum*, "Spire often variegated with white and chestnut broad flames, the latter often overlaying also the lighter chestnut of the body whorl." Most authorities have considered the two as

distinct species. The figures given in Reeve (1843: pls. 1 and 3) show extreme variants, while the specimens figured by Sowerby (1857: pl. 7) are hardly distinguishable.

C. vexillum is a relatively uncommon species on Hawaiian reefs. It is known to occur to a depth of 25 fathoms. Pleistocene fossils are known from Molokai (Ostergaard, 1939, as *C. sumatrensis*).

Conus vitulinus Hwass in Bruguière

Fig. 14 in Plate 1

Conus vitulinus Hwass in Bruguière, 1792, Enc. Meth. Vers, 1: 648, pl. 326, fig. 3.

Conus vitulinus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 265.

Conus vulpinus Schubert and Wagner, 1829, Syst. Conch. Cab., 12: 56, pl. 222, fig. 3073. (non *vulpinus* Hwass in Bruguière, 1792.)

Conus vulpinus Wagner var. A. Küster, 1837-1840, Syst. Conch. Cab., ed. 2, 4: 29, pl. 3, fig. 7. (non *vulpinus* Hwass in Bruguière, 1792.)

Conus planorbis var. *vitulinus* Hwass. Mörch, 1852, Catal. Conchyl. Yoldi, p. 69.

Dauciconus vitulinus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 246.

Leptoconus vitulinus (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 36.

Lithoconus vitulinus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, no. 7a.

DESCRIPTION: Shell thick and solid. Body whorl obscurely striate near the shoulder, the striae becoming more pronounced and granular basally. Aperture narrow, the sides parallel. Shoulder angular, smooth; spire depressed, slightly canaliculate, striate. Color of body whorl usually deep reddish or purplish brown, darker at the base, with white bands mottled with ground color at the shoulder and below the center; the bands contain one to several rows of brown dots. In large specimens, the reddish brown areas often interrupted by longitudinal white blotches. Spire arcuately tessellated with brown and white. Perios-

tracum gray, thick, opaque, closely striate transversely. In life, visible portions of foot and siphon bright lemon yellow.

LENGTH: 70 mm.

TYPE LOCALITY: Indian Ocean.

REMARKS: Small specimens of this species closely resemble *C. litoglyphus*. *C. vitulinus* may be distinguished by having striae above the central band, rows of brown dots on the white bands, and absence of a pointed apex.

C. vitulinus is a relatively uncommon species on Hawaiian reefs. It is known to occur to a depth of 30 fathoms. Pleistocene fossils are known from Molokai (Ostergaard, 1939).

A single specimen labeled *Conus planorbis* Born in the collection of the B. P. Bishop Museum (No. 68990) was dredged in Honolulu Harbor. The Museum of Comparative Zoology contains another specimen (No. 146332) collected at Midway Island by J. Chalean, apparently alive when collected. These specimens are extremely similar to, and may be synonymous with, *C. vitulinus*, as has been suggested by some workers (p. 395).

POSSIBLE ADDITIONAL VALID SPECIES
IN HAWAII

Conus elisae Kiener

Fig. 4

Conus elisae Kiener, 1845, Spéc. Gén. Icon.

Coq. Viv., 2: pl. 64, figs. 1, 1a, p. 341.

(?) *Conus stellatus* Kiener, 1845, Spéc. Gén.

Icon. Coq. Viv., 2: pl. 99, fig. 3, p. 225.

DESCRIPTION: Shell subcylindrical; maximum diameter slightly more than one half the length. Body whorl obsoletely striate, the striae slightly more pronounced and as raised ridges toward the base. Aperture rather broad, flaring slightly basally. Shoulder smooth, rounded. Spire moderately elevated, obtuse, straight or slightly convex, obsoletely striate. Color dark reddish brown, as many closely spaced and intersecting longitudinal lines separated by small white spots; occasionally with larger white subtrigonal blotches as in



FIG. 4. "*Conus elisae* Kiener," 35 × 19 mm. Specimens collected by C. E. Cutress on Rabbit Island, off Oahu. Photograph by C. E. Cutress.

C. pennaceus; two broad transverse bands either side of the center appear to be superimposed on this pattern. These bands are more solidly colored and are similar to the reddish brown areas of *C. pennaceus* in that they bear narrow transverse closely spaced lines finely dotted with white. Color pattern of the spire similar to that of the bands on the body whorl. Interior of aperture bluish white.

LENGTH: Specimens in the U. S. National Museum and Academy of Natural Sciences of Philadelphia range from 15.5 mm. to 27 mm. in shell length. The specimen illustrated in Figure 3 measures 35 × 19 mm.

TYPE LOCALITY: None.

REMARKS: *Conus elisae* was first reported from Hawaii by Weinkauff (1874). Recently, a number of specimens agreeing with the description and figure of this species have been collected on the islands of Kauai and Niihau. Sowerby (1858: 43) considered this species to be synonymous with *C. pennaceus*, a conclusion with which the present writer has been inclined to agree. However, no specimens intermediate in character between

Kiener's *C. elisae* and typical *C. pennaceus* have been found, despite an increasing number of specimens collected during the past year. Moreover, the microhabitat of the Hawaiian specimens referred to seems to differ from that of typical *C. pennaceus*. The former are typically found buried as deep as six inches under sand (A. H. Cornelison, verbal communication) while the latter are typically found on or partly buried in sand under rocks (Kohn, 1959). It seems reasonable at the present time to consider *C. elisae* as a possibly valid species. The problem requires further investigation.

UNIQUE RECORD FROM HAWAII

Conus smirna Bartsch and Rehder

Fig. 13 in Plate 1

This species is known only from a single specimen, the type, described by Bartsch and Rehder (1943). It was dredged near Lanai ("Ranai") in 257–312 fathoms by the U. S. Fisheries steamer "Albatross."

SPECIES KNOWN IN HAWAII ONLY FROM COLLECTION OF DEAD SPECIMENS

To the author's knowledge, there are no records of living specimens of the following species from the Hawaiian archipelago.

Conus aulicus Linné

C. auratus is probably a synonym of *C. aulicus*.

Ostergaard (1928) listed *C. auratus* as occurring in the fossil state on Oahu. The present writer is quite convinced that the species referred to was *C. pennaceus*, since Ostergaard (1928) also mentions the normal habitat of living specimens. However, at least one fossil specimen of *C. aulicus* is known from Oahu. It was collected about five feet above high tide mark near Nanakuli by E. C. Jones in March, 1954. It is at present in the collection of the Children's Museum of Honolulu (No. 2747).

Specimens now considered to be narrow-shelled variants of *C. pennaceus* because of the abundance of intergrades were listed as *C. auratus* by Edmondson (1933). Edmondson (1946) cited both *C. auratus* and *C. omaria*. The same figure of a rather typical shell of *C. pennaceus* was labelled *C. auratus* by Edmondson (1933) and "*Conus omaria* (?)" in the 1946 edition.

Specimens of *C. aulicus* were collected by the Tanager Expedition at Kure (Ocean) Island and Pearl and Hermes Reef and are in the collection of the B. P. Bishop Museum (Nos. 66438, 66439, 66205). A shell from Midway Island which is quite fresh in appearance but was empty when collected is in the collection of C. A. Allen.

Conus aureus Hwass in Bruguière

A number of well-preserved shells of this species have been collected on beaches along the windward coast of Oahu.

Conus auricomus Hwass in Bruguière

This species has been known erroneously as *C. clavus* Linné (see Dodge, 1953). Several specimens have been collected from dredged material at Honolulu, Oahu, and at Midway Island. *C. magnificus* Reeve, recorded by Garrett (1878) from the Hawaiian Islands, is probably synonymous. A label, "*Conus magnificus* Reeve. Hawaiian Ids.," is present in the Garrett collection in the B. P. Bishop Museum, but no shell is present.

Conus cylindraceus Broderip and Sowerby

Several shells have been collected from dredged material at Midway Island. No specimens are known from the main Hawaiian Islands (Thaanum, *in litt.*).

Conus fabula Sowerby

(= *Conus scabriusculus* Dillwyn?)

The only known specimen, probably a subfossil, was collected at Makua, Oahu, by W. C. Ross.

Conus tenuistriatus Sowerby

Some authors have considered this species synonymous with (Tryon, 1884) or a variety of (Couturier, 1907; Dautzenberg, 1933) *Conus glans* Hwass *in* Bruguière. Several dead specimens have been dredged and a few have been collected on beaches in the Hawaiian Islands.

Conus tulipa Linné

Ostergaard (1928) reported collection of several fossil specimens, one of which is figured, of *Conus tulipa*. The identification of a fossil specimen, presumably collected by Ostergaard, in the Hawaii Marine Laboratory reference collection, has been verified by the writer as *C. tulipa*. Ostergaard (1928) referred to a "live immature specimen" of *C. tulipa* collected in Hawaii by C. H. Edmondson. It is possible that the specimen referred to was a *C. obscurus*, as several older specimens of that species were labeled *C. tulipa*. However, a single juvenile specimen of *C. tulipa* (No. 20), collected at Waikiki Reef, Oahu, is in the Hawaii Marine Laboratory reference collection. It is not known whether or not this specimen was alive when collected, but it is in fresh condition. A number of shell fragments of *C. tulipa* have also been collected on Hawaiian beaches.

UNVERIFIED AND INACCURATE RECORDS
FROM THE HAWAIIAN ISLANDS

Conus arenatus Hwass *in* Bruguière

A single beach specimen, labeled "Hawaii. coll. W. H. Pease," is in the U. S. National Museum (No. 5038). No other specimens are known from the Hawaiian Islands, and the record may be in error as to locality.

Conus aristophanes Sowerby

This species, considered by Tomlin (1937) and others as synonymous with *C. coronatus* Gmelin, was described by Sowerby (1858) from the Philippine and Hawaiian islands. The latter locality is almost certainly in error.

Conus atramentosus Reeve

This is the type species of the genus *Lovellona* of Iredale (1917). Thiele (1931) considers *Lovellona* a section of the genus *Mitromorpha* A. Adams (1865) and places it in the subfamily Cytharinae of the family Conidae. Other authorities place *Mitromorpha* in the family Pleurotomidae (Simroth, 1896-1907).

Conus cancellatus Hwass *in* Bruguière

The type locality of this species is given in Bruguière (1792: 713) as "l'isle d'Owhyhée dans l'océan pacifique." This is presumably an error, since no specimens from the Hawaiian Islands are known to the writer, although there is some resemblance to *C. acutangulus*. *C. cancellatus* is found in Japan.

Conus emaciatus Reeve

This species, considered by Tomlin (1937) and others as a juvenile of *C. virgo* Linné, was reported from the Hawaiian Islands by Sowerby (1858: pl. 12, sp. 191). This reference may be in error, since no specimens from Hawaii are known to the writer or D. Thaanum (*in litt.*).

Conus fusiformis Pease

Pease (1860) described this species from the Hawaiian Islands. It belongs to the genus *Mitromorpha*. (See under *C. atramentosus*.)

Conus miliaris Hwass *in* Bruguière

A specimen in the U. S. National Museum (No. 338481) now labeled "*Conus miliaris* Hwass" was collected by D. Thaanum at Keaukaha, near Hilo, Hawaii. Three live specimens were found in a sand pocket in the reef and apparently none have been collected since (Thaanum, *in litt.*). The specimens were first labeled by W. H. Dall as a variety of *C. abbreviatus*. The single discovery of three individuals in a small area suggests a small, isolated, aberrant population with possible fixation of atypical morphological character-

istics by genetic drift. The circumstances of collection thus lend support to Dall's conclusion that the specimens represent a variant of *C. abbreviatus*. However, the specimens agree quite completely on morphological grounds with typical *C. miliaris*, which is otherwise not known to occur in the Hawaiian Islands. It is possible that the specimens under consideration may have hatched elsewhere and have been carried ashore on Hawaii by currents during the pelagic larval stage. In either event, the population has apparently not become established in Hawaii.

The Museum National d'Histoire Naturelle, Paris, contains two additional specimens labeled "Kauai (Sandwich) Rémy 1857."

Conus parvus Pease

Pease (1868) having discovered that *C. fusiformis* was preoccupied, renamed that species *C. parvus*. See under *C. fusiformis*.

Conus virgo Linné

Although Garrett (1878) reported this species from the Hawaiian Islands, there is no specimen in the Garrett collection in the B. P. Bishop Museum, and no other records are known to the writer. Demond (1957) also lists this species from Hawaii.

SUMMARY

The gastropod genus *Conus* is represented by 33 species in the Hawaiian archipelago. This number comprises only species of which more than one individual has been collected alive in the area between Kure (Ocean) Island and the island of Hawaii. Synonymies, descriptions, type localities, and notes are given for each of these species.

One possibly additional valid species, a unique record of one species, seven species known in Hawaii only from the collection of dead specimens, and unverified and inaccurate records of nine species from the Hawaiian Islands, are cited.

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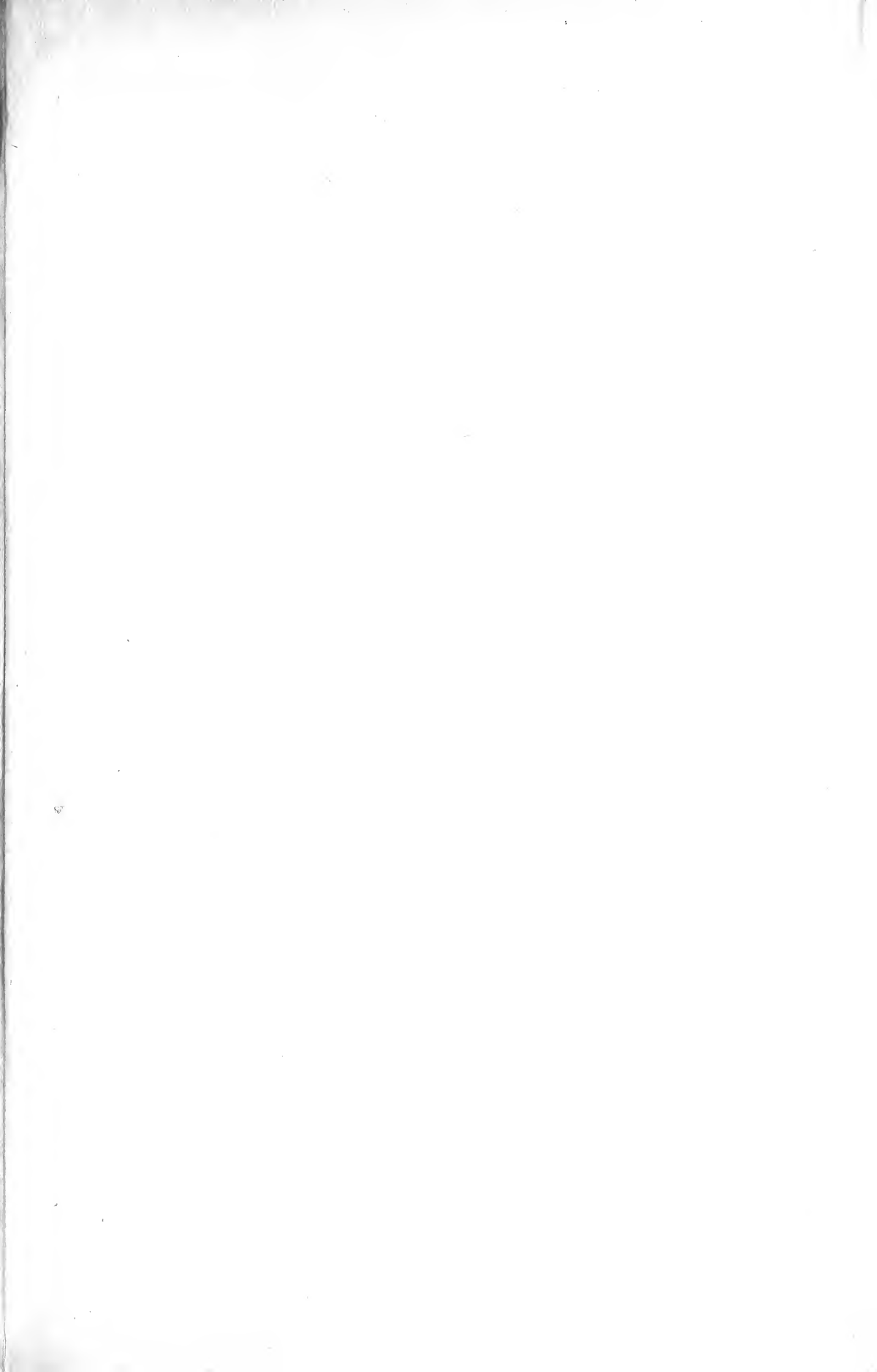
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