Ceylon J. Sci (Bio. Sci.) Vol. 10, No 1, April 1972

A Review and Revision of the Systematics of the Genera *Hydroides* and *Eupomatus* together with an Account of their Phylogeny and Zoogeography

by

T. Gottfried Pillai

*Fisheries Research Station, Colombo, Ceylon**

(With six text figures)

INTRODUCTION AND CRITICAL REVIEW

The genus *Hydroides* was established by Gunnerus in 1768, with *H. norvegica* Gunnerus as the genotype. Although two centuries have passed since then, there is at present no unanimity of opinion with regard to the systematics of the many similar species that have been described since then. *Hydroides*, which differs from the genus *Serpula* Linne 1758 only with regard to the structure of the operculum, was described as possessing a two-tiered operculum, with the proximal portion or "infundibulum" being funnel-like as in *Serpula* and the distal portion or "corona" consisting of a crown of spines bearing lateral processes. In 1844 Philippi established another genus, *Eupomatus*, with *E. uncinatus* Philippi as the genotype, for a similar serpulid with a two-tiered operculum but with the coronal spines lacking lateral processes. Since then a few other generic names have been proposed for other similar forms, but two main conflicting views prevail today. One is that all forms with a two-tiered operculum and with the other characters resembling the genus *Serpula* should be included under a single genus *Hydroides*. The other is that these serpulids fall into one or the other of the two genera *Hydroides* and *Eupomatus*, depending on whether the coronal spines bear lateral processes or not, respectively.

Morch (1863) believes that such differences as the occurrence or lack of lateral processes on the coronal spines, and whether the spines are all alike or one is different from the other, are only of sub-generic value. He establishes the genus *Eucarphus*, with *E. cumingii* as the genotype, to include forms with terminal lateral processes on the coronal spines. However, Claparède (1870) includes the species *lunulifera* Claparède (1870) which possesses terminal lateral processes on the spines within the genus *Eupomatus*, and also describes the species *Eupomatus trypanon* possessing lateral processes on its opercular spines. This species later proved to be *H. norvegica* Gunnerus.

In 1878, Grube describes two new species of serpulids under the genus *Serpula*, namely, *Serpula furcifera* and *Serpula minax* from the Philippines, although both species possess two-tiered opercula as in the *Hydroides/Eupomatus* group and agree with the latter in other features as well. Bush (1904) creates the genus *Glossopsis* for *Serpula minax* Grube and another genus *Schizocraspedon* for *Serpula furcifera* Grube, while describing species with

---

*Present Address: United Nations Development Programme, Tunisia.

lateral processes on the coronal spines under the genus *Hydroides*. On the other hand Gravier (1908) considers *Hydroides* to be a sub-genus of *Serpula* in describing *Serpula (Hydroides) uncinata* Philippi and; in doing so, does not recognize the genus *Eupomatus* which was established by Philippi for the species *uncinatus*.

Pixell (1913) attempts the first major review of the genera *Hydroides* and *Eupomatus*. She considers the genus *Glossopsis* Bush as redundant and that the species *Serpula minax* for which it was created falls naturally within the scheme proposed by her. She also states that *Eucarphus* Morch must be included under the genus *Hydroides* and retains the genus *Eupomatus*, differentiating the former from the latter on the presence or absence, respectively, of lateral processes on the coronal spines. Thirteen species are included under the genus *Hydroides* and seven are included under *Eupomatus*. The first sub-division within each genus, in the table given by Pixell, is based on whether the coronal spines are similar or dissimilar.

Chamberlin (1919) recognizes the genera *Hydroides* Gunnerus, *Eupomatus* Philippi *Eucarphus* Morch, *Schizocraspedon* Bush and *Glossopsis* Bush. He considers *Polyphragma* Quatrefages 1865 as a synonym of *Eupomatus* and *Codonytes* Quatrefages 1865 as a synonym of *Eucarphus* Morch. Chamberlin's basis for separation of *Hydroides* and *Eupomatus* agrees with that of Pixell (1913). He describes *Eucarphus* as possessing a crown of blunt spines with a single lateral process on either side at the tip. *Schizocraspedon* is defined as possessing an operculum forming two deep funnels, one above the other, with the edge of each sub-divided into branched processes. *Glossopsis* is defined as possessing an operculum forming a deep funnel with each process of the edge terminating in a knob and bearing a long curved process which arises from the the centre of the funnel.

Fauvel (1927) recognizes a single genus *Hydroides* and includes the species *H. uncinata* Philippi, *H. helmatus* Iroso, *H. lunulifera* Claparède and *H. norvegica* Gunnerus under it. Monro (1933) recognizes a single genus *Hydroides* and describes the species *uncinata* Philippi, *lunulifera* Claparède, *exaltata* Marenzeller under it. Day (1934) and Okuda (1937) accept a single genus *Hydroides*. However, Fauvel (1953) regards *Eupomatus* as a sub-genus of *Hydroides* and includes *H. exaltatus* Marenzeller under it. Tebble (1955) recognizes a single genus *Hydroides*.

Rioja (1957) discusses at length the difficulties of delimiting the genera *Hydroides* and *Eupomatus* owing to the enormous variability in the form of the opercula. He also draws attention to the following : There are wide discrepancies in the use of the criteria for separation of the species of the two genera by the various authors who have dealt with them. In many cases the characters cannot be uniformly applied to all the processes of the same crown. Secondly, it is difficult to establish a proper grouping of the different species of *Hydroides* and *Eupomatus* by virtue of their affinities. Nevertheless, Rioja retains the two genera *Hydroides* and *Eupomatus*, differentiating them on the same basis as proposed by Pixell (1913). He also mentions that all the species of *Eupomatus* from the American Atlantic are close to *E. uncinatus* Philippi.

Day (1957) and Dew (1959) recognize a single genus *Hydroides*, while Rioja (1958) and Hartman (1959) retain the two genera, *Hydroides* and *Eupomatus*. Hartman (1959) also recognizes the genus *Schizocraspedon* Bush for *H. furcifera* (Grube). Under the genus *Eupomatus*, Hartman includes twenty-three species among which are *E. uncinatus*, *E. albiceps*, *E. exaltatus*, *E. helmatus*, *E. novaepommeraniae*, *E. sanctae-crucis* and *E. lunulifera*. It will be recalled that while Claparède (1870) includes the species *lunulifera* under *Eupomatus*, Pixell (1913) includes it under *Hydroides*. Under the genus *Hydroides* Hartman includes twenty-two species among which is *H. ezoensis* Okuda. Moreover, it will be noted that *H. ezoensis* does not possess lateral processes on the spines of the corona, but possesses a row of medial processes along each radius leading to a marginal tooth. Owing to the absence of lateral processes on the spines, this species should be included under the genus *Eupomatus* if the sub-division of this group into two genera is correct.

Pillai (1960) and Day (1961) recognize a single genus *Hydroides*, while Jones (1962) retains the two genera *Hydroides* and *Eupomatus*. Jones divides the various species of *Eupomatus* into four groups and gives some indication of the possible lines along which the *Eupomatus* group could have taken place. In the first group he includes species in which the coronal spines are not all of the same size as regards their thickness or length or both. The species included in this group are *E. albiceps*, *E. dianthus*, *E. exaltatus*, *E. helmatus*, *E. inermis* and *E. ralumnianus*. In the second group are included species in which the spines of the corona are spread centrifugally or are erect, not incurving. The species are *E. elegantulus*, *E. fusicola*, *E. gracilis*, *E. humilis*, *E. lunulifera*, *E. novae-pommeraniae*, *E. protulicola* and *E. uncinatus*. The third group contains species in which the spines of the corona are asymmetrically arranged. They are *E. dipoma* and *E. similis*. The fourth group consists of species in which the coronal spines have T-shaped apices, namely, *E. dirampha*, *E. gairacensis*, *E. intereans*, *E. spongicola* and *E. alalateralis*.

Laubier (1965) states that the great variability of the operculum does not justify the division proposed by Pixell (1913) and prefers to retain the single genus *Hydroides*. Pillai (1965), Straughan (1965 & 1967) and Nelson-Smith (1967) also recognize the single genus *Hydroides* for this group of serpulids.

SUMMARY OF VIEWS

From the foregoing survey of the views expressed on the *Hydroides/Eupomatus* group of serpulids it is evident that their systematics is still not settled. One view prevailing today is that all the species of this group of serpulids fall under two genera, namely, *Hydroides* and *Eupomatus*, depending on whether the spines of the corona bear lateral processes or not, respectively. The second view is that all the species of this group fall under a single genus *Hydroides*. A third view, which was proposed by Morch (1863) and followed by Fauvel (1953) is that differences in the opercula which are generally used to separate genera, are only of sub-generic value.

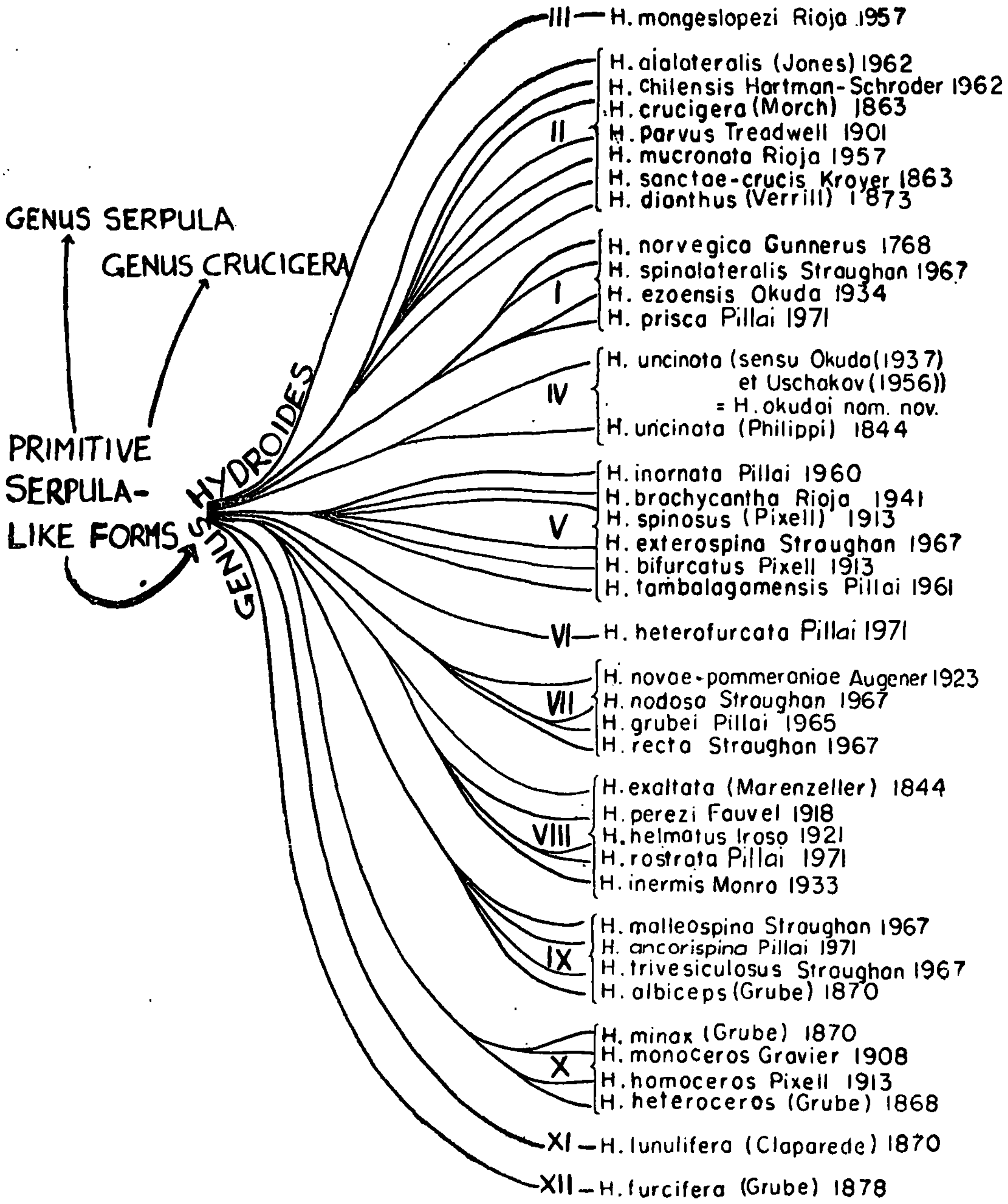

Fig. 1 :— A phylogenetic chart of the genus *Hydroides*.

SURVEY OF THE OPERCULAR ORNAMENTATIONS WITHIN THE GROUP

In order to determine which of these views is correct, it is necessary to survey not only the occurrence of the criteria presently used to separate genera among the various species of the *Hydroides/Eupomatus* group, but also other similar characters which have hitherto been ignored, and also to discuss the validity of separating genera on the basis of such criteria.

The species belonging to the *Hydroides/Eupomatus* group are similar to the genus *Serpula* in all major respects, except with regard to the operculum. The operculum in *Serpula* consists of a funnel-like structure or *infundibulum* bearing a number of pointed or rounded teeth along its rim. In the *Hydroides/Eupomatus*, on the other hand, the operculum consists of a *Serpula*-like infundibulum surmounted by a crown of spines, which is characteristic for any given species. The genus *Crucigera* Benedict (1887) is also similar to *Serpula* in all respects, except with regard to the operculum which bears a cross-like expansion at the base of the *Serpula*-like infundibulum.

The differentiation of the genera *Hydroides* and *Eupomatus* is based on whether the spines of the corona bear lateral processes or not, respectively. A comparative study of the species comprising this group, many of which have been recently discovered, however, reveals that the initial points of contrast lie in the marginal teeth of the infundibulum. In most species the marginal teeth of the infundibulum are simple and pointed. In *H. uncinata* (Philippi) 1844 (Fig. 2), each marginal tooth possesses a medial spur (Nelson-Smith, 1967). In *H. heterofurcata* each marginal tooth ends in a small but distinct claw-like segment (Fig. 3). Another group of species, consisting of *H. heteroceros* (Grube) 1868, *H. homoceros* Pixell (1913), *H. minax* (Grube) 1878, *H. monoceros* Gravier (1908), *H. malleospina* Straughan (1965), *H. albiceps* (Grube) 1870, *H. trivesiculosus* Straughan (1967) and *H. ancorispina* Pillai (1971) bear T-shaped terminal processes at the ends of the radii of the infundibulum. A further group of species is represented by *H. furcifera* (Grube) 1878, in which each marginal tooth of the infundibulum is forked and the prongs are extremely elongated.

With regard to the coronal spines, there are four main types of arrangement found in the *Eupomatus* group. The first is represented by *H. prisca* (Fig. 2), in which the operculum consists of two, simple, super-imposed *Serpula*-like funnels. The marginal teeth of the corona are similar to those of the infundibulum and are devoid of any ornamentation. The second group consists of species like *H. grubei* Pillai (1965) and *H. nodosa* Straughan (1965), which possess a reduced number of simple elongate coronal spines which are devoid of any processes. The third group consists of species like *H. dianthus* Verrill (1874) and *H. inornata* Pillai (1960) in which the coronal spines are ornamented only by a single basal process each (Fig. 2). The fourth group consists of species like *H. ezoensis* Okuda (1934) and *H. spinosus* Pixell (1913). It is noteworthy that Pixell (1913) and Hartman (1959) include the latter species under *Hydroides* although its coronal spines lack lateral processes.

Certain groupings can also be recognized within the genus *Hydroides* (*sensu* Pixell, 1913). In one group, represented by *H. mucronata* Rioja (1957), the coronal spines lack medial and basal processes, but possess a pair of lateral processes about half-way up the spine

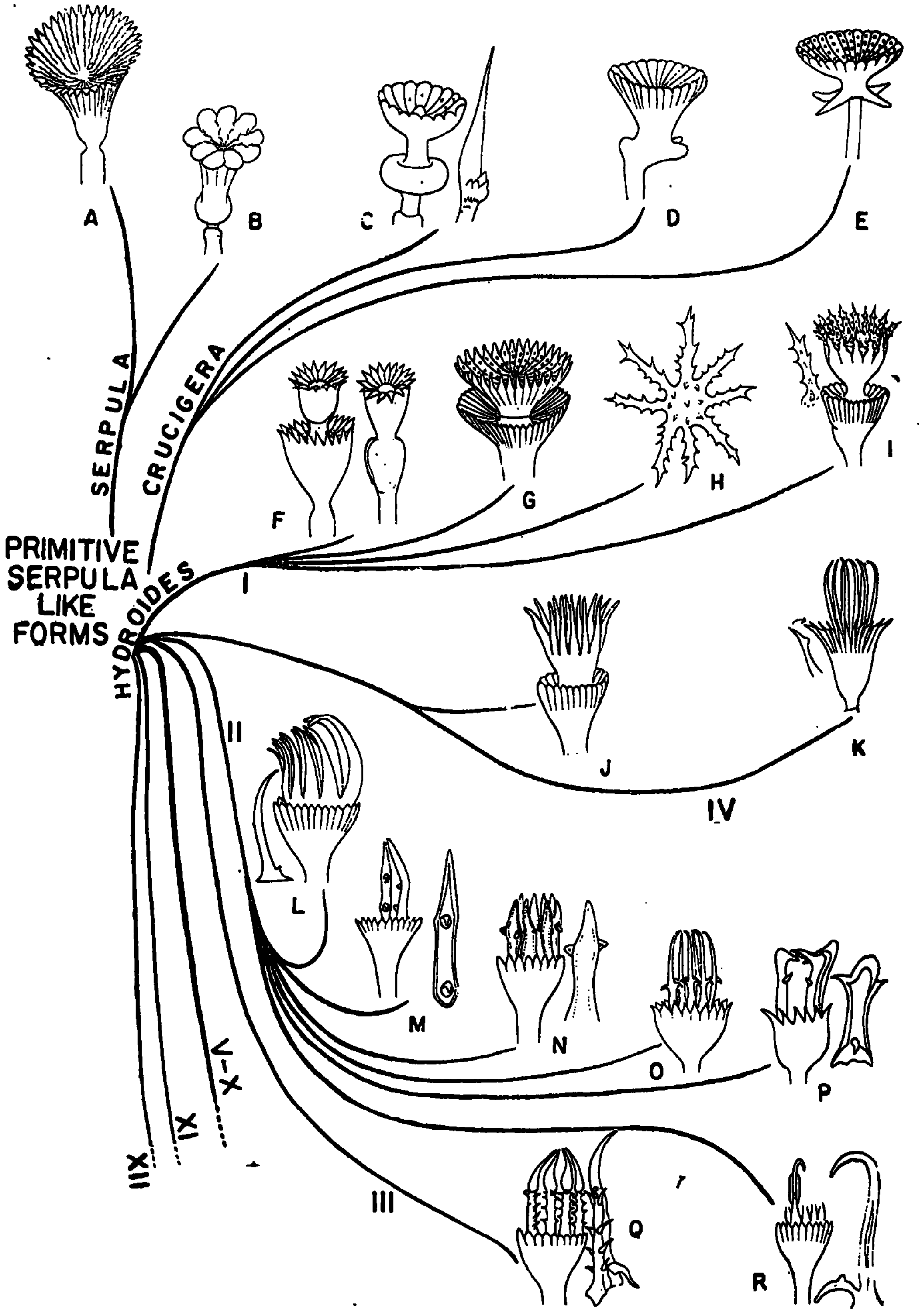

Fig. 2 :- Phylogenetic chart of the genus *Hydroides* showing groups I - IV and the relationships to the genera *Serpula* and *Crucigera*. A, *Serpula vermicularis*. B, *S. willeyi*. C, *Crucigera loveni*. D, *C. zygophora*. E, *C. websteri*. F, *H. prisca*. G, *H. ezoensis*. H, *H. spinalateralis*. I, *H. norvegica*. J, *H. okudai nom. nov*. K, *H. uncinata*. L, *H. dianthus*. M, *H. sanctae-crucis*. N, *H. mucronata*. O, *H. crucigera*. P, *H. parvus*. Q, *H. mongeslopezi*. R, *H. alalateralis*. (For details see text).

(Fig. 2). In the second group there are species such as *H. parvus* Treadwell (1901), *H. tambalagamensis* Pillai (1961) and *H. exterospina* Straughan (1961) which possess a single pair of lateral processes about half-way up the spine and a basal process each, in addition (Fig. 3). Thirdly, there are forms such as *H. mongeslopezi* Rioja (1957) which possess several pairs of lateral processes and a basal process on each coronal spine. Finally, there is *H. norvegica* Gunnerus (1768) which possesses a row of median processes on each coronal spine, in addition to several pairs of lateral processes and a basal process. Jones (1962) has drawn attention to the fact that there are species in which one coronal spine is different from the rest with regard to size alone, or both size and form.

It therefore becomes open to serious questioning as to why, when there are so many different conditions pertaining to the marginal teeth of the infundibulum and the spines of the corona, the presence or absence of lateral processes only, and on the spines of the corona alone, should be chosen for differentiating genera within this group of serpulids. In the absence of any other supporting characters, particularly with regard to the setation, these differences in the ornamentation of the coronal spines must necessarily be of specific significance only. As pointed out by Rioja(1957) there are instances in which the presence or absence of lateral processes cannot be uniformly applied to all the processes of the same crown. An example is *H. albiceps* (Grube) 1870 which is included under the genus *Eupomatus* (*vide* Willey, 1905, and Hartman, 1959) although the most dorsal spine, which is also different from the rest in size and shape, bears a pair of lateral extensions, while the remaining spines lack any ornamentation.

PHYLOGENETIC CONSIDERATIONS

Rioja (1957) states that it is difficult to establish a proper grouping of the different species of *Hydroides* and *Eupomatus* by virtue of their affinities. The nearest approach to a phylogenetic grouping is by Jones (1962) in his first group under the genus *Eupomatus*, in which he includes the species *E. albiceps*, *E. dianthus*, *E. exaltatus*, *E. inermis* and *E. ralumnianus*. In this group of species the spines of the corona are not all of the same size as regards their thickness or length or both.

A very significant clue to the phylogeny of the group, however, has hitherto been overlooked. It is the evolution and occurrence of heptaspiny in the corona of certain species. The presence of this seven-spined condition in several species of both the genera *Hydroides* and *Eupomatus* is, as will be seen presently, further evidence of the artificial nature of the sub-division into these two genera. Since the evolution of the heptaspinous condition, because of the other specializations often associated with it, would have been from forms possessing more than seven spines, it would be appropriate to consider species showing the latter condition first.

The most primitive species of this group are likely to have had a two-tiered operculum in which both the infundibulum and the corona were simple, similar to each other and *Serpula*-like. Indeed a species of this type, *H. prisca*, has been described earlier (Pillai 1971).

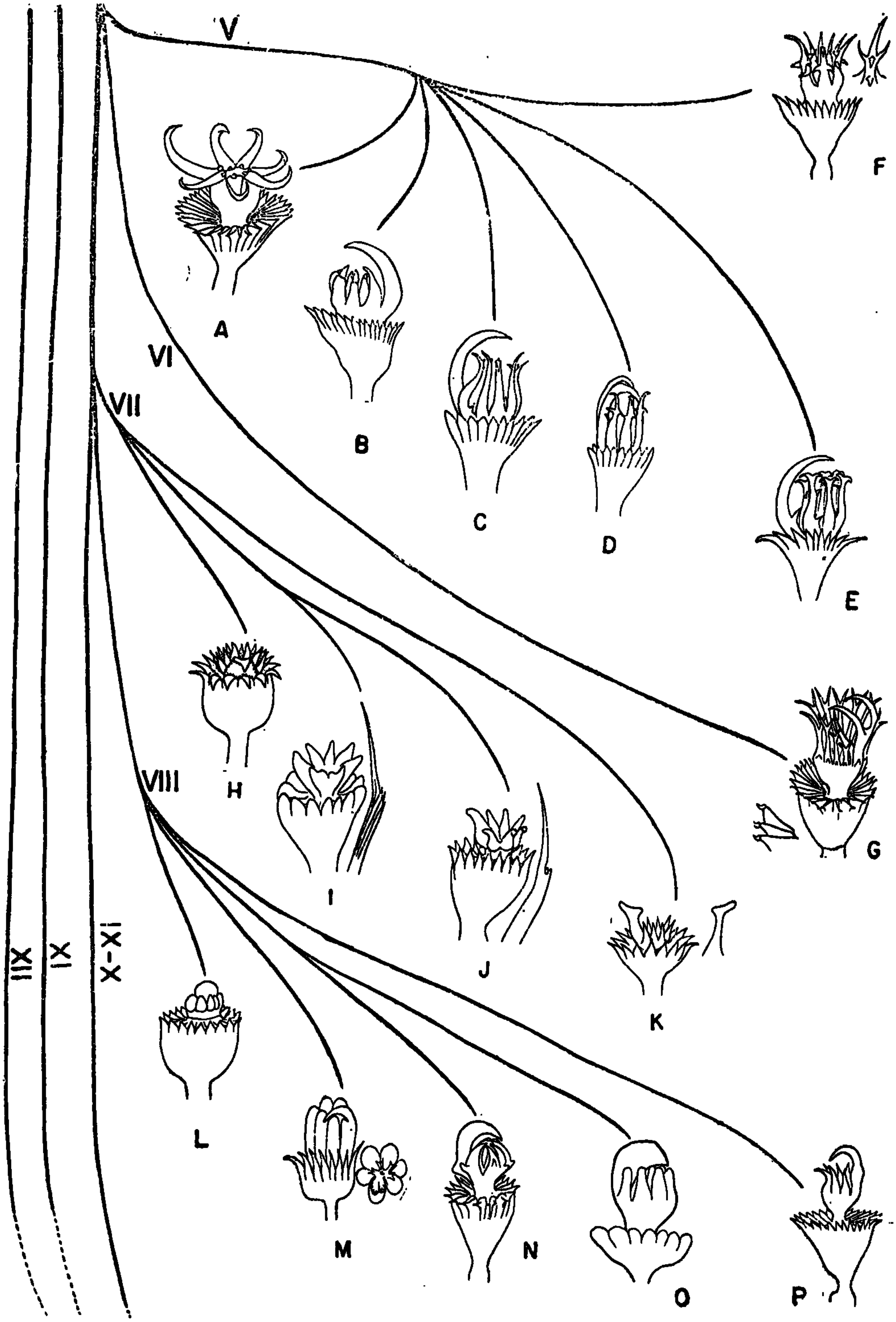

Fig. 3 :- Phylogenetic chart of the genus *Hydroides* showing groups V-VIII. A, *H. inornata.* B, *H. brachycantha* C, *H. spinosus.* D, *H. spinalateralis.* E, *H. bifurcatus.* F, *H. tambalagamensis.* G, *H. heterofurcata.* H, *H. novaepommeraniae.* I, *H. nodosa.* J, *H. grubei.* K, *H. nodosa.* L, *H. inermis.* M, *H. perezi,* N, *H. ancorispina.* O, *H. helmatus.* P, *H. exaltata* (For details see text).

As further evidence of the primitiveness of this species, one encounters specimens which offer a clue as to the method of evolution of the typical operculum of *Hydroides* from a simple *Serpula*-like form (Fig 2). In the abnormal specimens of *H. prisca* (Fig. 2) the corona is similar to that of normal specimens of the same species, but the infundibulum is represented by a swelling which resembles the swelling found below the operculum of certain species of the allied genus *Crucigera* as, for example, *C. inconstans* Straughan (1967). Indeed if these irregular specimens of *H. prisca* alone were discovered, they would most probably have been assigned to the genus *Crucigera*. The genus *Crucigera* therefore represents an intermediate condition between the genera *Serpula* and *Hydroides*. The irregular specimens of *H. prisca* indicate that the genera *Crucigera* and *Hydroides* are likely to have been evolved by the swelling of the opercular stalk below the operculum of primitive *Serpula*-like forms. While this swelling developed into a fully formed secondary infundibulum in the genus *Hydroides*, it developed into a cruciform, knee-like or irregular swelling in certain species which are grouped together under the genus *Crucigera*. In the latter group the primary infundibulum continues to serve a protective function in closing the tube after withdrawal of the worm within it. In the genus *Hydroides*, however, the protective function is taken over by the new structure, the secondary infundbulum, while the primary infundibulum is available for modification into defensive armature for preventing intruders from entering the tube.

It would appear therefore that the primitive forms which gave rise to the genus *Serpula* also gave rise to the genera *Crucigera* and *Hydroides* which retained the setal characteristics of *Serpula* but developed different types of opercula. A phylogenetic chart showing the possible lines of evolution within the genus *Hydroides* is presented in Figure 1. Group I consists of four species besides *H. prisca* namely, *H. uncinata* (*sensu* Okuda, 1937, et Uschakov, 1956) from Japan, *H. ezoensis* from Japan (Okuda, 1934), *H. spinalateralis* from Eastern Australia (Straughan, 1967 and *norvegica* which was originally recorded from Norway (Gunnerus, 1768 ; *in* Hartman, 1959) but later proved to be cosmopolitan species (Tebble, 1955 ; Nelson-Smith and Gee, 1966). *H. uncinata* (*sensu* Okuda et Uschakov), with its simple spindly coronal spines (Fig. 2) is more specialised than *H. prisca* and may well represent a form which is similar to the ancestors from which the remaining species of *Hydroides* would have been evolved. The corona of *H. ezoensis* differs from that of *H. prisca* in possessing a row of short medial spines along each radius. This condition is already foreshadowed in *Serpula loveni* Kinberg (Fig. 2) which, owing to its possession of a large swelling below the operculum, may well be referred to the genus *Crucigera*. In *H. spinalateralis* the corona consists of a reduced number of larger spines, each bearing lateral processes and a basal spine (Fig. 2). *H. norvegica* has evolved all three types of processes, lateral, medial and basal. *H. uncinata* Philippi (Fig. 2) possesses a more advanced operculum than *H. uncinata* (*sensu* Okuda et Uschakov). The marginal teeth of its infundibulum bears a short subterminal process each, and its coronal spines are all alike, hooked inwards terminally, and bear a basal process each. This species therefore appears to be the result of a separate line of evolution originating from forms which gave rise to *H. uncinata* (*sensu* Okuda et Uschakov). The two forms appear to be distinct species, and the latter is accordingly named *H. okudai* nom. nov., in the present account.

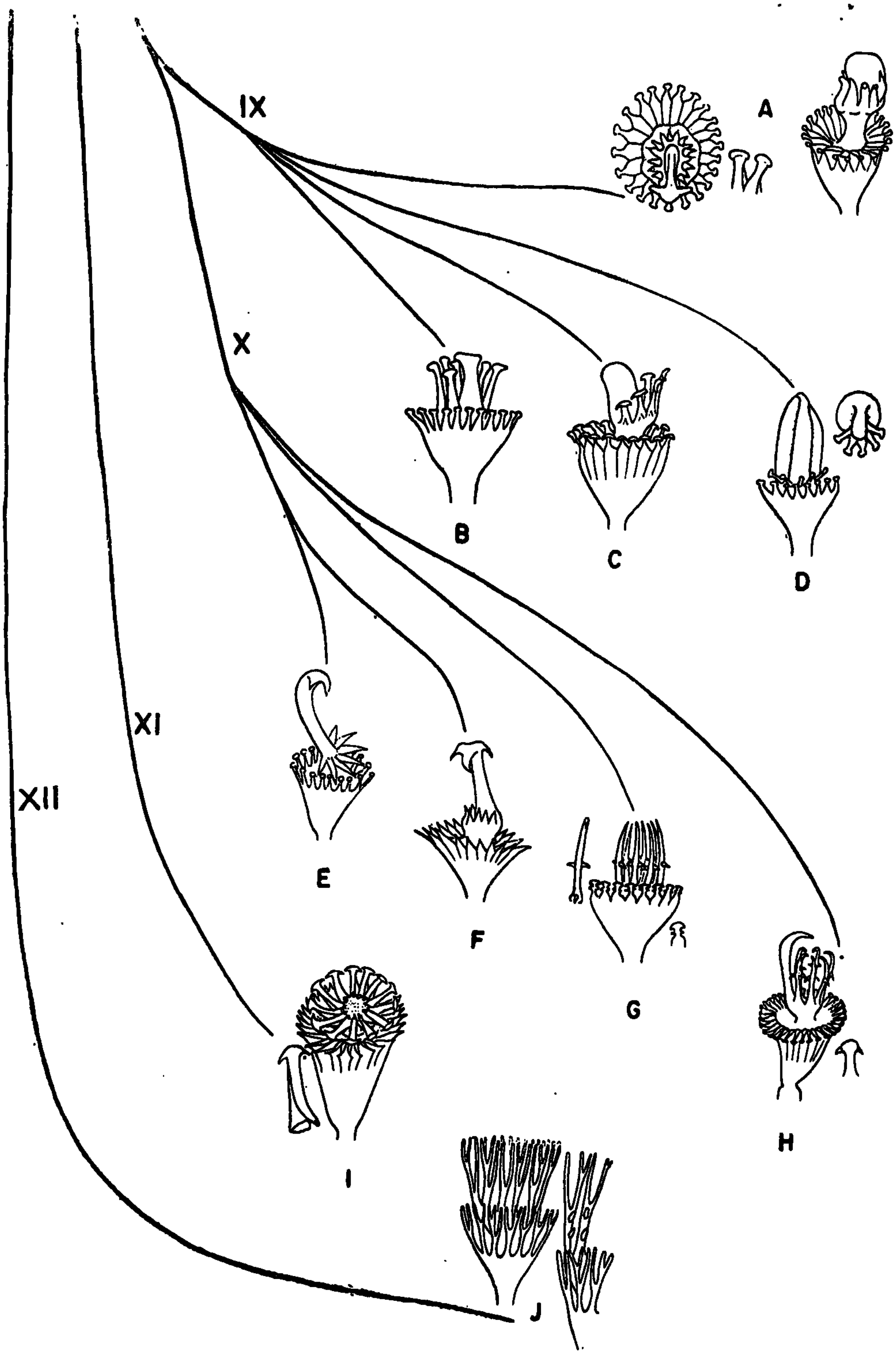

Fig. 4 :- Phylogenetic chart of the genus *Hydroides* showing groups IX-XII. A. *H. exaltata*. B. *H. malleospina*. C, *H. ancorispina*. D, *H. trivesiculosus*. E, *H. minax*. F, *H. monoceros*. G, *H. homoceros*. H, *H. heteroceros*. I, *H. lunulifera*. J, *H. furcifera* (For details see text).

From the stem forms which gave rise to the preceding group of species, the genus *Hydroides* appears to have evolved into two main categories. In one, the corona possesses a large number of spines which are all alike, while in the other, the most dorsal coronal spine is different from the rest with regard to size or form or both, and the total number of coronal spines is normally seven or in a few cases tends to be around seven.

In the first main category are species such as *H. dianthus*, *H. mucronata*, *H. sanctae-crucis*, *H. parvus*, *H. crucigera*, *H. chilensis* and *H. alalateralis* which possess a large number of coronal spines which are all alike. In *H. dianthus* which was discovered from the Atlantic Coast of North America (Verrill, 1874; *in* Hartman 1959), the coronal spines are devoid of lateral processes and bear only a basal spur each. *H. mucronata* from the Gulf of Mexico (Rioja, 1957) possesses coronal spines which are ornamented by a pair of lateral processes only. In *H. sanctae-crucis* from the West Indies (Kroyer, 1863; *in* Hartman, 1959), the coronal spines lack lateral processes, but each possesses two medial processes, one of which is basal. In *H. parvus* from Puerto-Rico (Treadwell, 1901; *in* Hartman, 1959), Mexican Coast of Gulf of Mexico (Rioja, 1957 & 1958), and Trinidad (Hartman, 1944), the coronal spines bear a pair of pointed lateral processes and a basal process each, and are distally bent inwards, being knuckleshaped at the bend. *H. crucigera* from Puntarenas, Costa Rica (Morch, 1863 ; *in* Hartman, 1959) and the Gulf of Mexico (Rioja, 1957), possesses coronal spines which bear a pair of pointed lateral processes each. *H. chilensis* from Chile (Hartman-Schroder, 1962), is closely related to *H. crucigera*. The coronal spines are stouter than those of *H. crucigera*, and possess a long basal spur each in addition to a pair of lateral processes. In *H. alalateralis* from Jamaica (Jones, 1962), the coronal spines bear a pair of wing-like lateral processes and a long basal process each.

The second main category of species occurs from the tropical Indo-West-Pacific to the Mediterranean and consist of species in which the most dorsal coronal spine is different from the rest and the total number of spines is normally seven. From the phylogenetic chart presented in Figure 1 it will be seen that these species are best discussed under the separate groups into which they are divided, on the basis of structural similarities of the opercula. Group V (Fig. 3) consists of species in which the number of coronal spines is normally seven or tends to be seven, and in which the most dorsal spine is or, tends to be, different from the rest with regard to size, direction of curvature, form, or a combination of these features. Examples of this group are *H. inornata*, *H. brachycantha*, *H. spinosus*, *H. bifurcatus*, *G. exterospina* and *H. tambalagamensis*. In *H. inornata* from Ceylon (Pillai) 1960 and Eastern Australia (Straughan, 1967*a*, as *H. gradata* and *H. basispinosus*), the number of spines is normally seven but there may sometimes be an additional spine or two. Each coronal spine lacks lateral processes and bears only a small basal spur. The most dorsal spine is different from the rest with regard to size only, being much larger than the ventral spines but only slightly larger than the adjoining spines. *H. brachycantha* was originally reported from the Pacific Coast of Mexico (Rioja, 1941 ; *in* Hartman, 1959) and later from Eastern Australia (Dew, 1959) and Levilla Gizedo Islands, off the Pacific Coast of Mexico (Rioja, 1959). Its inwardly curved coronal spines tend to be seven in number, each with lateral processes, and the most dorsal spine is larger than the rest which possess claw-like terminal projections. In *H. spinosus* from the Red Sea (Pixell, 1913) and Gold Coast (Tebble, 1955)

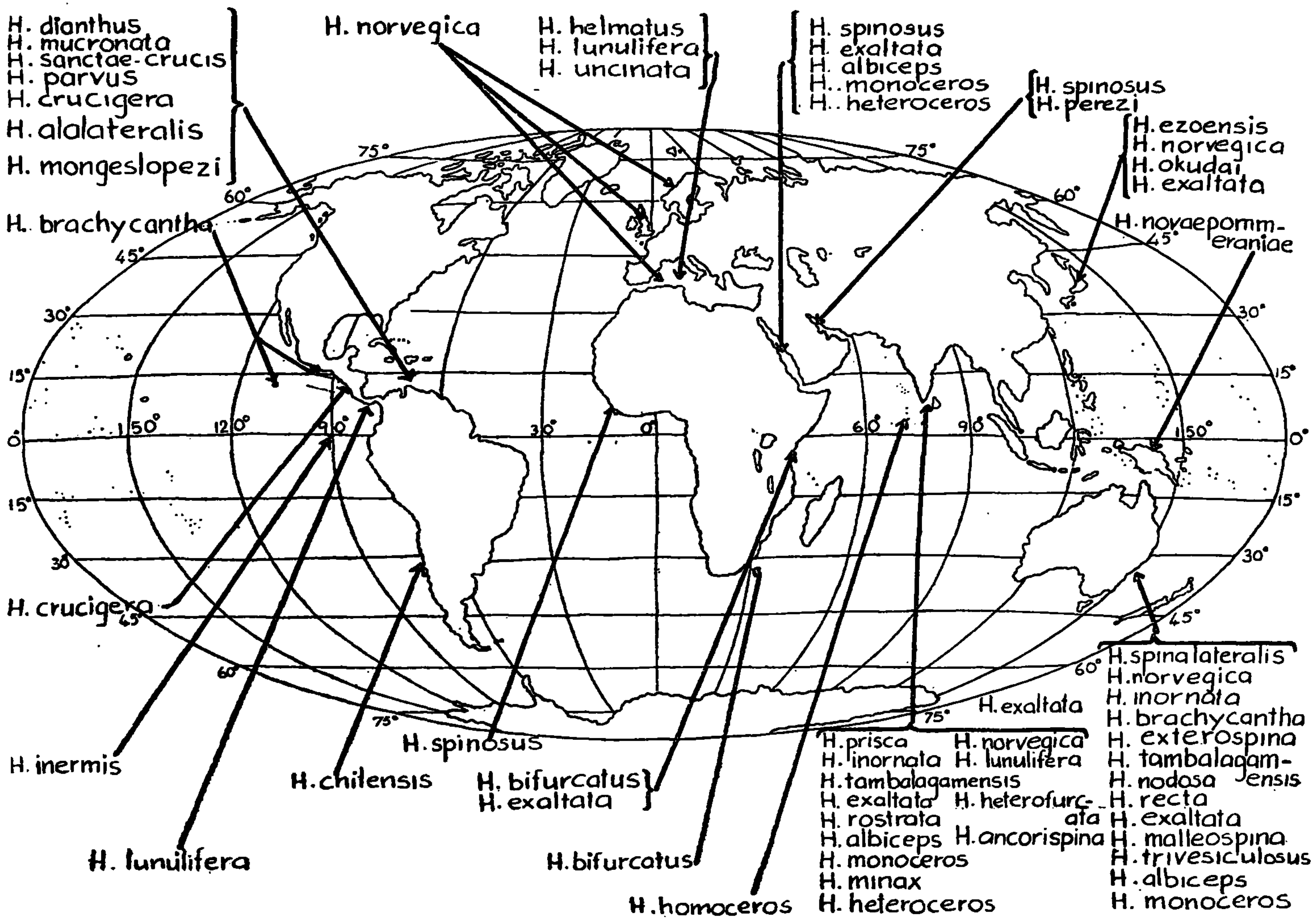

Fig. 5 :- Map (Mollweide's equal area projection) showing the world distribution of the species of *Hydroides*.

the most dorsal coronal spine is different from the rest with regard to size as well as direction of curvature and ornamentation. In *H. bifurcatus* from the Indian Ocean (Pixell, 1913) and Natal and Mozambique, South Africa (Day, 1951), the most dorsal coronal spine is different from the rest with regard to size and form. While the former lacks lateral processes, the latter spines possess terminal lateral processes. In *H. exterospina* from Queensland (Straughan, 1967*b*) the most dorsal, coronal spine is different from the rest with regard to size, form and direction of curvature, but the number of spines is nine. In *H. tambalagamensis* from Ceylon (Pillai, 1961) and Queensland, Australia (Straughan 1967*b*) all the coronal spines, which number seven, are alike in being outwardly curved, and in possessing a pair of lateral processes and two medial processes, one of which is basal.

Group VII (Fig. 3) consists of species such as *H. novaepommeraniae*, *H. nodosa*, *H. grubei*, and *H. recta*. In *H. novaepommeraniae* from New Guinea (Augener, 1923 ; *in* Hartman, 1959) and Eastern Australia (Dew, 1959), the corona consists of seven spines of which the most dorsal spine is larger and more sharply curved outwards than the rest. They are not ornamented by lateral or other accessory processes. In *H. nodosa* from Eastern Australia (Straughan, 1967), the corona consists of six or seven smooth spines, each with a rounded basal projection. They are more or less of equal size. *H. grubei* from the Philippines (Pillai, 1965) is closely related to *H. nodosa* but differs from the latter with regard to the collar setae, shape of the infundibular teeth and the spines of the corona. The coronal spines in *H. grubei* are seven in number and alike in form. They are all devoid of any accessory processes and the most dorsal spine is larger than the rest. In *H. recta* from Eastern Australia (Straughan 1967) the most dorsal spine is larger than the rest and bears a sub-terminal swelling. The remaining spines are all smooth. *H. nodosa* and *H. grubei* appear to be more closely related to each other than to the other two species.

Group VIII (Fig. 3) consists of species such as *H. exaltatus*, *H. perezi*, *H. rostrata*, *H. helmatus* and *H. inermis* in which the most dorsal coronal spine is fleshy or vesicular. In *H. exaltatus* from Japan (Marenzeller, 1944; *in* Hartman, 1959), Ceylon (Willey, 1905) India, Red Sea, Zanzibar (Fauvel, 1953, Augener, 1914) ; Eastern Australia (Dew, 1959) and Solomon Islands (Dew, 1959), the most dorsal spine is inwardly curved. The remaining spines are smooth and outwardly curved. In *H. helmatus* from the Mediterranean (Iroso, 1921 ; *in* Hartman, 1959) the most dorsal coronal spine is thick, beak-like, inwardly-curved, and bears a dorsal swelling. The remaining spines are smooth and club-shaped. In *H. rostrata* from Ceylon (Pillai, 1971), the most dorsal coronal spine is similar to that of *H. helmatus*, but the remaining spines are also beak-like, inwardly-curved and are ornamented by an external basal spine each. Furthermore, the infundibular teeth of *H. helmatus* are rounded lobes, while those of *H. rostrata* are pointed. In *H. perezi* from the Persian Gulf (Fauvel, 1918 ; *in* Hartman, 1959) and Eastern Australia (Straughan, 1967), the most dorsal coronal spine is different from the rest in possessing an inwardly-curved, pointed, terminal hook. The remaining spines are in the form of concave, swollen valves. *H. helmatus* and *H. rostrata* appear to be more closely related to each other than to remaining members of this sub-group. In *H. inermis* from the Galapagos Islands (Monro, 1933 ; *in* Hartman 1959) the corona is heptaspinous as well as heterospinous. The coronal spines are simple, short, fleshy, triangular swellings.

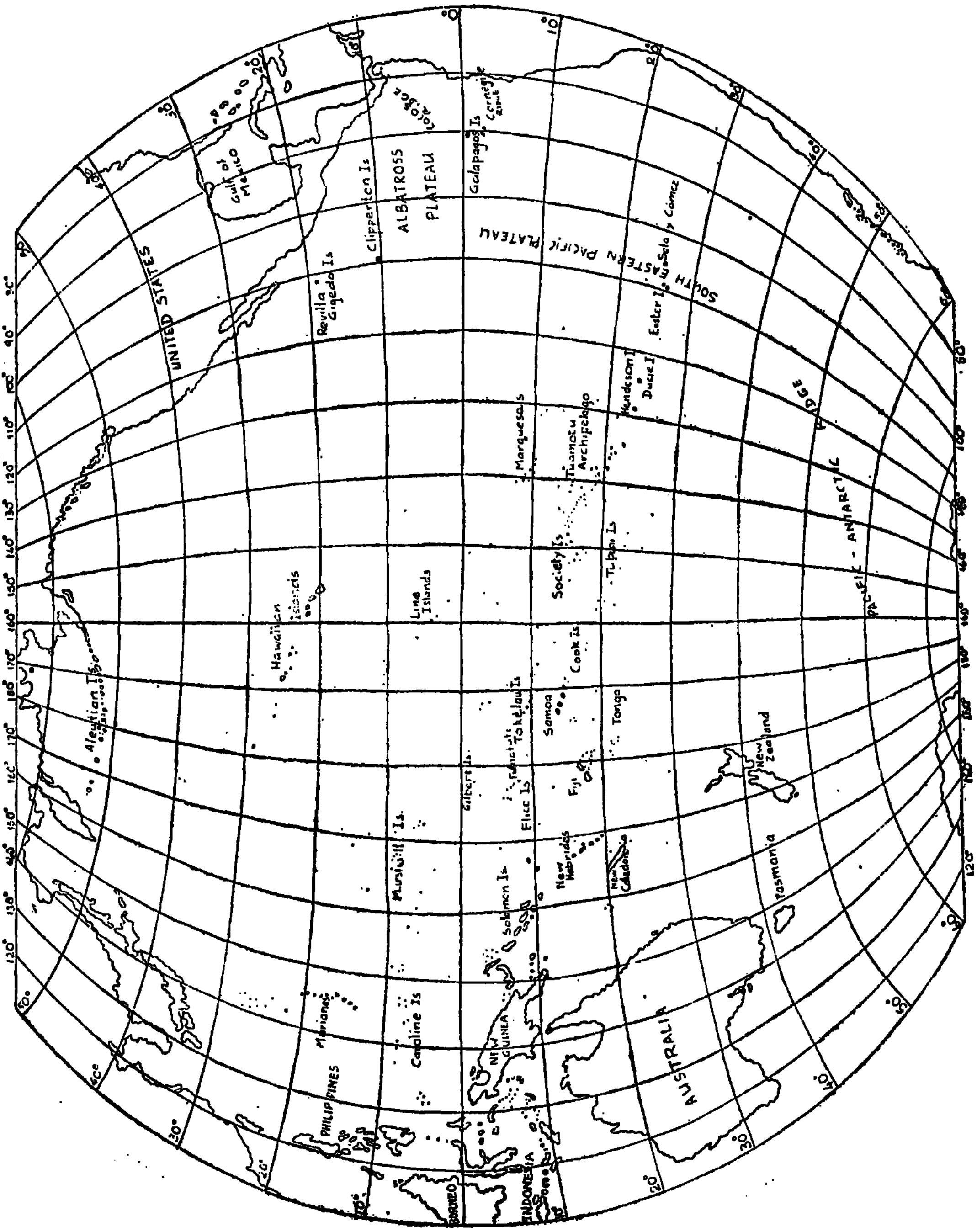

Fig. 6 :- Map (Lambert's azimuthal equal area projection) showing the Pacific Ocean Islands.

Group IX (Fig. 4) consists of the species *H. malleospina*, *H. ancorispina*, *H. albiceps* and *H. trivesiculosus*, in all of which the most dorsal coronal spine is vesicular and the marginal teeth of the infundibulum bear T-shaped or crescentic terminal processes. *H. malleospina* from Eastern Australia (Straughan, 1967) *H. ancorispina* from Ceylon (Pillai, 1971) and *H. trivesiculosus* from Eastern Australia (Straughan, 1967*b*), have an additional feature in common ; their coronal spines also bear terminal lateral processes and, in this respect appear to be more closely related to each other than to *H. albiceps*. In *H. malleospina* all seven coronal spines bear T-shaped terminal processes and the most dorsal spine is larger than the rest. In *H. ancorispina* the infundibular teeth and six out of the seven coronal spines bear crescentic terminal processes. The seventh coronal spine is an oblong, laterally compressed, fleshy column which is larger than the remaining spines and devoid of accessory processes. In *H. trivesiculosus*, the most dorsal coronal spine is a large, tri-lobed, fleshy column devoid of accessory processes. The remaining coronal spines bear small T-shaped terminal expansions which are similar to those of the marginal infundibular teeth. In the fourth species included in this sub-group, namely, *H. albiceps* from the Red Sea (Grube, 1870 ; *in* Hartman, 1959), Ceylon (Willey, 1905) and Eastern Australia (Straughan, 1967), the infundibular teeth bear terminal swellings which are similar to those of *H. trivesiculosus* and a large fleshy dorsal coronal spine which is also similar to that of the latter species However, the remaining coronal spines lack terminal swellings.

Group X (Fig. 4) consists of species such as *H. minax*, *H. monoceros*, *H. homoceros* and *H. heteroceros* in which the marginal teeth of the infundibulum end in T-shaped or anchor-shaped processes. *H. minax* from the Philippines (Grube, 1878) and Ceylon (Willey, 1905) and *H. monoceros* from the Red Sea (Gravier, 1908 ; *in* Hartman, 1959), India, Zanzibar, (Fauvel) 1953, Eastern Australia (Straughan, 1967) and Ceylon (Pillai, 1971), are very similar to each other. Hartman (1959) states that these two species may perhaps be synonymous. During the present studies specimens of the two species were compared and the following differences were noticed : *H. minax* is much smaller than *H. monoceros* and the component parts of the operculum are also smaller. The terminal T-shaped swellings of the infundibular teeth are very distinct in *H. minax*, but are absent in *H. monoceros*. Straughan's (1957, p. 217) figure of the operculum of the latter agrees with this observation. However, further studies of intermediate specimens appear to be necessary with a view to ascertaining whether these two groups of specimens are growth forms of the same species or not. In *H. homoceros* from the Maldive Archipelago, Indian Ocean (Pixell, 1913), the infundibular teeth possess a pair of sub-terminal lateral processes each, in addition to the crescentic terminal process. The coronal spines are, however, all alike and this feature appears to be a retention of a primitive character. Each coronal spine bears a pair of lateral processes and a median basal spine. In *H. heteroceros* from the Red Sea (Grube, 1868 ; *in* Hartman, 1959), India, Zanzibar (Fauvel, 1953) and Ceylon (Willey, 1905), the infundibular teeth bear anchor-shaped terminal processes, and the most dorsal coronal spine differs from the remaining six spines in being much larger and lacking lateral processes.

Six species of *Hydroides* cannot be included under any of the groups hitherto discussed. They are H. *mongeslopezi*, *H. lunulifera*, *H. heterofurcata*, *H. furcifera* and *H. uncinata*. They do not form any satisfactory groups among themselves and are therefore assigned to a separate group each (Fig. 1). *H. mongeslopezi* from the Gulf of Mexico (Rioja, 1957) has 8-11 coronal spines, each bearing about four pairs of lateral processes externally, and a long basal process. It is significant that certain other species from the same region, such as *H. alalateralis* and *H. chilensis*, also possess similar, long basal spines.

H. lunulifera was originally recorded from the Mediterranean (Claparède, 1870 ; *in* Hartman, 1959) and later from the Panama Canal (Rioja, 1923 ; *in* Nelson-Smith, 1967), India (Fauvel, 1932) and Ceylon (Pillai, 1971). Its corona bears 11-14 spines which are alike in size and form, each bearing a short basal process and terminating distally in a crescentic process. According to Nelson-Smith (1967), this species occurs on hulls of ships and buoys, besides shells and stones. It appears therefore that the present distribution of this species, particularly across the Atlantic may, to some extent, be the result of its having been transported on the hulls of ships.

In *H. heterofurcata* of Group VI (Fig. 3) from Ceylon the corona bears about eleven spines, of which the most dorsal spine is trifurcate and larger than the remaining spines which are bifurcate. The marginal teeth of the infundibulum end in a small clawlike segment each. In possessing a large number of coronal spines this species retains a primitive feature. However, it has also developed advanced features in the specialization of its most dorsal coronal spine and the unique form of its infundibular teeth. There are no other known species of *Hydroides* with this combination of characters and it is best therefore to retain this species in a group by itself.

In *H. furcifera* from the Philippines (Grube, 1878), both the infundibulum and the corona bear several branched processes (Fig. 4). The processes of the corona, however, differ from those of the infundibulum, in possessing a series of short medial processes, proximally. There are no known species of *Hydroides* with a similar operculum. *H. furcifera* is therefore best retained within a separate group by itself.

H. uncinata, which was originally recorded from the Mediterranean (Philippi, 1844 ; *in* Hartman, 1959), was accurately figured only quite recently (Nelson-Smith, 1967). The operculum is unique in that each marginal tooth of the infundibulum bears a small inner basal excresence (Fig. 2). The spines of the corona are long, slender, pointed and hooked inwards distally. It is possible that the specimens figured by Okuda (1937) and Ushakov (1956), in which the tips of the coronal spines are not hooked and are outwardly directed, belong to a different species. According to Hartman (1956) each coronal spine of *H. uncinata* bears a small pointed basal spur, which is visible when the spines are pushed apart. This species is also retained in a separate group by itself. *H. uncinata* has also been reported from Berbera in the Gulf of Aden (Treadwell, 1925; *in* Hartman, 1959) and Gulf of Panama (*in* Nelson-Smith, 1967). It is noteworthy that it is sometimes found on ships' hulls (Nelson-Smith, 1967).

GENERAL CONCLUSIONS ON THE PHYLOGENY OF HYDROIDES

The simplest known species of *Hydroides* living today is *H. prisca,* in which the corona and infundibulum are similar and *Serpula*-like. This species affords a clue as to the possible method of evolution of the genera *Hydroides* and *Crucigera* from simple *Serpula*-like ancestors. The genus *Hydroides* appears to have been evolved by the swelling of the opercular stalk immediately below the funnel-like operculum of a *Serpula*-like ancestor to form a secondary funnel or infundibulum. The latter took on a function of closing the tube, while the primary infundibulum became available for modification as an additional protective structure. The genus *Crucigera* would therefore include forms in which the swelling below the operculum of *Serpula*-like forms failed to develop into a funnel-like structure, but resulted in other shapes. *Serpula loveni* Kinberg (Fig. 2) appears to be one such form, and may well be included under the genus *Crucigera.* Except with regard to these differences in the operculum, all three genera, *Serpula, Crucigera* and *Hydroides,* agree with regard to the other generic characters, including the setation.

The initial stages in the evolution of complexity in the corona may well have occurred in ancestral forms similar to *H. okudai,* in which the corona bears relatively simple, spindly processes without any ornamentation. There appear to be at least twelve main lines along which speciation has occurred within the genus *Hydroides.* However, all these lines of evolution have resulted in two main categories. In one, the corona possesses a large number of spines which are all alike, while in the other, the most dorsal coronal spine is different from the rest with regard to size, or form, or both, and the total number of coronal spines is normally seven in almost all the species, and is often seven or around seven in the rest. In some groups belonging to the latter category, complexity of structure has occurred not only in the spines of the corona, but also in the marginal teeth of the infundibulum.

Groups I-IV and XI-XII include species in which the corona bears a large number of spines which are all alike. In Group I, *H. ezoensis* and *H. prisca* possess nearly similar opercula and therefore appear to be more closely related to each other than to the other species of the group. The corona of *H. norvegica* is more complicated than that of *H. spinalateralis,* and both species appear to be closely related to each other. *H. okudai,* with its corona bearing simple spindle-like spines, appears to have evolved as a separate line from the ancestral forms which gave rise to *H. prisca.* In Group II, a gradual increase in complexity of coronal structure can be seen from *H. mucronata* to *H. chilensis,* all of which appear to be more closely related to each other than to *H. dianthus* and *H. alalateralis.* The latter appears to have evolved independently of the other species of the group, from the stem forms which gave rise to *H. dianthus.* Groups III, IV, XI and XII, with their single species *H. mongeslopezi, H. uncinata, H. lunulifera* and *H. furcifera,* respectively, are all primitive in possessing a large number of coronal spines which are alike. They also possess complexities of structure in the corona or operculum, or both, which are peculiar to each of them, and therefore appear to be the result of separate lines of evolution originating from the ancestral stem forms of Group I.

The second major category consists of Groups V-X in which, except for two species, one coronal spine is different from the rest with regard to size, or form, or both, and the number of species is normally seven. In Group V, there is a gradual increase in complexity of corona structure from *H. inornata* to *H. bifurcatus*. In *H. tambalagamensis*, however, which is one of the exceptions referred to above, the number of coronal spines is seven, but there has been failure to develop a differentiated spine. *H. heterofurcata* of Group VI is the other exception. It possesses a large number of coronal spines, of which the most dorsal spine is trifurcate and the rest are bifurcate. The infundibular teeth terminate in small claw-like processes. There are no other known species which bear resemblance to this species and it therefore appears to have been evolved as an independent side branch from the stem forms which gave rise to Groups V-X.

All species in Groups I-VI, with the exception of *H. prisca* and *H. ezoensis* from Group I, possess coronal spines which are elongate, whereas the coronal spines in Groups VII-IX are comparatively short and much simpler with regard to their ornamentation. In Group VII (Fig. 3), *H. nodosa* and *H. grubei* are more closely related to each other than to the other species. The corona of *H. novaepommeraniae* bears a resemblance to that of *H. prisca*, except for the reduction in the number of coronal spines and the enlargement of one of them in the former. It appears therefore that this group originated from the stem forms which gave rise to *H. prisca*.

In Group VIII (Fig. 3), there is a gradual increase in the complexity of the corona, especially of its most dorsal spine from *H. exaltatus* to *H rostrata*, and a simplification in *H. inermis*. The species *H. helmatus* and *H. rostrata* appear to be more closely related to each other than to the other species of the group. From the general simplicity of the corona of these species, it would appear that this group originated as a branch from the stem forms which gave rise to Group VII.

The species of Group IX (Fig. 4) are characterized by the possession of T-shaped or anchor-shaped terminal processes on the coronal spines as well as on the infundibular teeth, whereas in Group X (Fig. 4) only the infundibular teeth bear such terminal processes. However, in both these groups there is heptaspiny and differentiation of the most dorsal coronal spine, as in Groups VII and VIII, and therefore appear to have evolved from forms which gave rise to the latter groups. Furthermore, in possessing T-shaped or anchor-shaped terminal processes in either the corona and the infundibulum or in the infundibulum alone, Groups IX and X appear to have had a common origin.

GEOGRAPHICAL DISTRIBUTION OF THE GENUS HYDROIDES

The phylogenetic scheme of the genus *Hydroides* presented above is strongly supported by the zoogeography of its species. The geographical distribution of the species (Fig. 5) indicates that *Hydroides* is essentially a stenothermal genus with a few species occurring in sub-tropical regions, at the extreme end of its range of distribution. It also affords evidence that the original stem forms of the genus *Hydroides* underwent separation into two main geographical groups, one in the tropical and sub-tropical regions of the Atlantic Coasts of North and South America, the other in comparable regions of the Eastern Atlantic, the Mediterranean and the Indo-West-Pacific, and underwent speciation independently.

The species of Groups II and III (Fig. 2) have been reported from the tropical American Atlantic, and they are all characterized by the possession of a number of spines which are all alike. The simplest species hitherto reported from the Eastern Atlantic is *H. dianthus*, in which the coronal spines are smooth hooks, and ornamented only by a basal spur each. The most specialised coronal spines occur in *H. mongeslopezi* of Group III (Fig. 2).

All the remaining species have been recorded from the Eastern Atlantic, the Mediterranian and the Indo-West-Pacific, with the exception of *H. brachycantha* and *H. lunulifera*, which have been recorded from the tropical Western Atlantic. The simplest known living species of *Hydroides*, namely, *H. prisca* and *H. okudai*, are from the Indo-West-Pacific Region. The remaining species of Group I, with the apparent exception of *H. norvegica*, is from the Indo-West-Pacific Region. *H. norvegica*, however, was originally recorded from Norway (Gunnerus, 1768 ; *in* Hartman, 1959). It was later recorded from the Mediterranean as *Eupomatus trypanon* (Claparède, 1870), Australia (Haswell, 1883), Japan, as *H. multispinosa* (Marenzeller, 1884 ; *in* Hartman, 1959), Alexandria (Pixell, 1913), India (Fauvel, 1932), Gold Coast (Tebble, 1955), South Africa (Day, 1957), and recently (Rioja, 1960) from Eastern Mexico and other places (*vide* Nelson-Smith, 1967). This species occurs very commonly in large masses on ships' hulls, buoys and harbour structures (Nelson-Smith 1967). *H. norvegica* therefore appears to have originated within this second geographical region, from the Eastern Atlantic to the Indo-West-Pacific, and undoubtedly owes its present distribution, including Eastern Mexico, to its having been transported on the hulls of ships. *H. lunulifera* was originally recorded from the Mediterranean and later from India, Ceylon and the Panama Canal (*vide* Nelson-Smith 1967). It has also been found on the hulls of ships (Nelson-Smith, 1967) and it appears, therefore, that the present distribution may, at least in part, be due to its having been transported on the hulls of ships. *H. brachycantha* was originally recorded from the Pacific coast of Mexico and later from Revilla Gigedo Islands (Eastern Pacific) and Eastern Australia (Rioja 1941, *in* Hartman 1959 ; Dew 1959). Unlike in *H. lunulifera*, the corona in this species is both heptaspinous and heterospinous. It would appear therefore that this species originated from the Indo-West-Pacific Region and has, at present, an extended range of distribution across the Pacific, from Australia to Western Mexico.

PALAEOGEOGRAPHIC CONSIDERATIONS

It has been shown in the preceding account that, with the exception of *H. norvegica* which occurs in tropical to temperate waters, the genus *Hydroides* is stenothermal. Secondly, there are two main zoogeographical concentrations of species, one from the Indo-West-Pacific to the Mediterranean and Eastern Atlantic, and the other in the tropical and sub-tropical Western Atlantic. Thirdly, there is a paucity of heptasinous-cum-heterospinous species from the latter region, while they are predominant in the Indo-West-Pacific Region.

Fourthly, the tropical Pacific coast of the Central American Region has relatively few species of *Hydroides*. Of the three species hitherto reported *H. chilensis* is not heptaspinous, while *H. brachycantha* and *H. inermis* are both heterospinous and heptaspinous.

This pattern of distribution of the species of *Hydroides* can be explained by the Tethys Sea, existence of which in ancient geological times is accepted by all palaeogeographers (*vide* Ekman, 1953 ; Stokes, 1960 ; George, 1962 ; and Fairbridge 1963, p. 87). It has been shown earlier in this account that species with a corona possessing more than seven spines are more primitive than those with a hepta-or heterospinous corona. The American Atlantic is characterized by species which are not only polyspinous but also homospinous. The occurrence of a few similar species in the Mediterranean (*H. uncinata* and *H. lunulifera*), and the Indo-West-Pacific (*H. lunulifera, H. furcifera* and *H. okudai*), indicates that they, together with the American Atlantic species, formed part of the Palaeozoic and Mesozoic Tethys Sea fauna. However, the endemic nature of the American Atlantic species indicates that they were evolved in the Western Atlantic, but that the mid-Atlantic barrier hindered their eastward spread. The post-Tertiary Atlantic depths of 6,000 to 29,000 feet, together with the paucity of suitable settling substrata and the complex of warm and cold currents, formed an efficient barrier to this stenothermal shallow-water shelf-fauna.

The species of *Hydroides* in the Indo-West-Pacific are predominantly heptaspinous. From the Indo-West-Pacific they spread westwards on the one hand towards East Africa, the Mediterranean and tropical Eastern Atlantic, and eastwards on the other, along the tropical islands of the Pacific Ocean. The occurrence of heptaspinous species in the Persian Gulf (*H. perezi*), Red Sea (*H. exaltatus*, which also occurs in India and Australia), and the Mediterranean (*H. helmatus*), indicates a spread of a very small number of species, by way of the Pliocene connection between the Indian Ocean and the Mediterranean through the Red Sea.

The heptaspinous species *H. brachycantha* reported from the Revilla Gigedo Islands in the American Pacific, appears to have crossed the East Pacific Ocean barrier. Ekman (1953) sets the furthest outposts of the Indo-West-Pacific Region in Hawaii, the Marquesas Islands and the Tuamoto Archipelago (Fig. 6). The oceanic waters, opposite the Hawaiian Islands and the Marquesas Islands, are 12,000 to 20,000 feet deep and too wide, and therefore do not appear to have provided a suitable route for the eastward spread of this species. However, the East Pacific Barrier is of least depth opposite the Tuamotu Archipelago. At the extreme eastern end of this Archipelago are Henderson Island and Ducie Island, located between longitudes 120° and 130°, and between latitudes 20° and 30° south. Between the same longitudinal limits and only a little further east, between longitudes 100° and 110°, are Easter Island and Salay Gomez Island. The waters between Ducie Island and Easter Island are mainly under 6,000 feet, partly around 9,000 to 12,000 feet, and forms part of the South Eastern Pacific Plateau.

Revilla Gigedo Islands, from which the heptaspinous species *H. brachycantha* has been reported, are approximately along the same longitude as Easter Island, but lie about 20° north of the Equator. Clipperton Island is situated approximately along the same longitude but 10° north. The Galapagos Islands, from which the heptaspinous species *H. inermis* has been reported, are situated along the Equator, but a little further east, along 100° longitude. The Albatross Plateau lies north of the South Eastern Pacific Plateau, and between its extreme northern end and the Galapagos Islands the sea is between 6,000 and 9,000 feet. Between the Galapagos Islands and the tropical American Pacific Coast are the Cocos and Carnegie Ridges which are below 6,000 feet deep and below 3,000 feet in some places. The path of migration of heptaspinous species, during some early geological period, could have been from Ducie Island to Easter Island, and northwards along the Albatross Plateau to the Galapagos Islands. From here, the migration to the American Coast could have been either through the Cocos Ridge or the Carnegie Ridge or both. From the Central American Region the migratory path to the Revilla Gigedo Islands in the North, and even to Chile in the south, along the continental shelf, would not have been difficult.

For this migratory route to have been effective it would have been necessary that the plateaux and ridges concerned should have been at considerably shallower depths than those prevailing during present times. Charles Darwin (1842), put forward the theory of subsidence of the sea floor in the Pacific, and this was confirmed by the deep borings in the Funafuti Atolls in 1897-98 by the Royal Society of London. It was shown that even at 334 metres depth, the madreporarian composition of the 5,400 metre high atolls was the same as at the surface. A subsidence of at least 300 metres of the ocean floor was conclusively proved, and this was possibly very much more (Ekman, 1953, p.9). Darwin's ideas were shown to be fundamentally correct more recently in the course of drilling operations conducted by the United States Navy and the United States Geological Survey in preparation for the hydrogen bomb tests at Eniwetok (Shepard, 1967, p.9). "There are five guyots at depths of 1000 to 1500 metres among the Austral Islands which were former active volcanoes but which became inactive and subsided to their present depths (Heezen and Menard, 1963). Another example is seen in the Marcus Necker Rise in which there were many volcanoes. Towards the Middle Cretaceous they had grown up through 4,000 metres of water and formed large islands, which have now been reduced to sea level (Heezen and Menard, 1963). " During low sea level stages of the Pleistocene and, prior to some recent tectonic subsidences, it was possible for major land mammals to migrate from China, through Taiwan and Philippines to Celebes. The geological evidence in the East Indies suggests that there were large scale subsidences during the Quaternary Period (Kueneis, 1935 ; Van Bemmelin, 1949)," (Fairbridge, 1965). Besides this, available data suggest a constant rate of subsidence of 2 cm. per 1000 years for the last 100 million years" (Heezen and Menard, 1963).

Another factor which could possibly have made this migratory route more effective would have been the increasing accumulation of ice around the poles during the Quaternary Glacial Period. As a result of this there was a general lowering of the sea surface itself, which was greater in the tropics than elsewhere (Ekman, 1953, p. 9). It has been shown that heptaspinous species of *Hydroides* evolved after the Late Tertiary climatic deterioration, the formation of the Mid-Atlantic Barrier and the closure of the Atlantic-Pacific connection across Central America. The occurrence of heptaspinous species along the Pacific Coast of America, and their absence on the Atlantic Coast of America, would therefore indicate that their occurrence in the former could have been possible only by migration from the Indo-West-Pacific, across suitable areas of the Pacific Ocean. Taking the period of evolution of heptaspinous species, and the geological sequences which followed, the Quaternary lowering of the sea surface may have made the route suggested above effective for the migration of heptaspinous species to the Galapagos Islands, the American Pacific Coast and the Revilla Gigedo Islands. The shallower depths at which the plateaux and ridges concerned existed prior to their subsidence would have enhanced the effectiveness of the Quaternary lowering of sea surface to permit this migration. The brief duration of these conditions accounts for the relatively few species that have been able to do so.

The actual distribution across the Pacific could have been effected by either, or both, of the following ways. If the Quaternary lowering of sea surface over the plateaux and ridges concerned was such that it permitted the development of shelf flora and fauna, the eastward spread would have taken place by the normal method of successively colonizing suitable adjacent areas. If, however, there still remained insurmountable deep areas during this period, the distribution could have taken place by passive migration. Ekman (1953, p. 21), states that this could have taken place in some species, " without doubt by drifting attached to seaweed or other floating material." Emery (1963) discusses known instances of rocks, some as large as 10 kilograms, being rafted by larger kelps such as *Macrocystis*, which have been dislodged from their substrata during rough weather. Smaller algae like *Ulva* and some brown algae have been known to transport attached pebbles and shells during abnormal weather. Emery draws attention to the fact that since several phyla are known to live among or on algal holdfasts, their transportation by ocean currents subsequent to rough weather can raise problems in ecology and palaeoecology. Brown algae are known from the Miocene and even the Silurian and Devonian and this method of dispersal of marine animal species could have occurred even during those geological periods.

Emery (1963) also discusses the transport of two other kinds of materials in the sea, namely, trees with cobbles, pebbles and even boulders enclosed among their roots, and pumice from volcanic areas. Such trees could be washed out to sea from rivers, or by falling directly into the sea by cliff erosion. Emery reports on such floating trees holding a boulder over three feet in diameter. "Once afloat, they have been known to be carried thousands of kilometres by ocean currents " (Emery, 1963). " Drift timber is thrown up on most islands even on those in the midst of the widest oceans ; and the natives of the coral islands in the Pacific procure stones for their tools, solely from the roots of drifted trees, these stones being a valuable royal tax " (Darwin, 1859). It is suggested here that tidal waves accompanying tectonic activity and floods following typhoons, in the Pacific area, could have contributed their share to the dislodgement of such trees and washing them out considerable distances into the sea, from where the ocean currents would have carried them to distant destinations. With regard to floating pumice, large quantities, which were produced during recent times off Mexico, were observed to have floated up to 12,000 kilometres from Mexico. "As pointed out by Ladd (1960), floating pumice may transport for long distances mollusks, and other attached invertebrates " (Emery, 1963).

In the context of the distribution of heptaspinous species of *Hydroides* from the Indo-West-Pacific area to the tropical and sub-tropical American Pacific, the foregoing methods would no doubt have played their part, if suitable shelf bridges did not exist between Ducie Island and Easter Island and northwards along the Southern Eastern Pacific Plateau to the Galapagos Islands, during post-Tertiary periods. All species of *Hydroides* are secondary, and settle on shells, stones, rocks and other similar substrata. Species of *Hydroides* occurring on such objects rafted by algae could have been carried eastwards from some island west of the mid-Pacific barrier. Rocks and stones enclosed within the roots of floating trees, and floating pumice, would sooner or later have such settlers during their drift over shelf areas, particularly during contact with reefs or rocks, and these settlers would have been carried eastwards across the Pacific. Finally, it is certain that a similar type of distribution and exchange of fauna must be taking place even now, by being carried on the hulls of ships.

SUMMARY

1. The views hitherto expressed on the systematics of *Hydroides*, *Eupomatus* and other genera are critically discussed.

2. The criteria hitherto used to distinguish these genera, as well as other similar criteria which have been hitherto ignored, are critically surveyed. The various combinations of opercular processes found among members of this group are shown to be only of specific value within a single genus *Hydroides.*

3. The phylogeny of *Hydroides is* discussed.

4. The zoogeography of the genus *Hydroides* is discussed. Except for *H. norvegica* which is cosmopolitan, the other known species are tropical to sub-tropical in their distribution. There are two main geographical concentrations of species, in the Indo-West-Pacific and the tropical American Atlantic. A relatively small number of species are found in the Mediterranean and Southern Europe, tropical African Atlantic and tropical American Pacific.

5. Palaeogeographic conditions, as well as other factors that would have brought about this distribution, are discussed.

REFERENCES

BENEDICT, J. E. 1886—Descriptions of ten species and one new genus of annelids from the dredgings of the U.S. Commission steamer 'Albatross' *Proc. U.S. Nat. Mus.*, 9, 547-553.

BENHAM, W. B. 1923-1934—The Polychaeta. British Museum (Natural History) British Antarctic ("Terra Nova") Expedition, 1910. *Nat. Hist. Rep. Zool.*, 7, 47-182.

CHAMBERLIN, R. V. 1919—The Annelida Polychaeta. *Mem. Mus. Comp. Zool. Harvard*, 48, 1-514. *pl.* I-LXXX.

CLAPAREDE, E. 1868—*Les Annelides chetopodes du Golfe de Naples.* Geneve et Bale, 1868.

1870—*Les Annelides chetopodes du Golfe de Naples.* Geneve et Bale 1870.

DAY, J. H. 1934—On a collection of South African Polychaeta with a catalogue of the species recorded from South Africa, Angola, Mozambique and Madagascar. *J. Linn. Soc. Lond.*, 39, No. 263, 15-82.

1951—The Polychaet fauna of South Africa. Part 1. The Intertidal and Estuarine Polychaeta of Natal and Mozambique. *An. Natal Mus.*, 12, Part I, 1-67.

1957—The Polychaet fauna of South Africa. Part 4. New species and records from Natal and Mozambique. *An. Natal Mus.*, 14, Part 1, 59-129.

1961—The Polychaet fauna of South Africa. Part 6: Sedentary species dredged off Cape Coasts with a few new records from the shore *J. Linn. Soc. (Zool.)*, **44**, No. 299, 463-560·

1963—The Polychaet fauna of South Africa. Part 8. New species and records from grab samples and dredgings. *Bull. Brit. Mus. (Nat Hist.), Zool.*, **10**, No. 7, 383-445.

EKMAN, S. 1953—*Zoogeography of the Sea.* Sidgwick and Jackson Ltd. London, 1-417

EMERY, K. O. 1963—Organic transportation of marine sediments. *The Sea.* Edited by M. N. Hill. **3**, 776-793.

FAIRBRIDGE, R.W. 1965—The Indian Ocean and the Status of Gondwanaland. *Progress in Oceanography.* Woods Hole Ocean. Inst. Massachusetts. **3**, 83-136.

FAULKNER, G. H. 1930-32—The anatomy and histology of bud-formation in the serpulid *Filograna implexa* together with some cytological observations on the nuclei of the neoblasts. *J. Linn. Soc. Lond. (Zool.)*, **37**, 109-190.

FAUVEL, P. 1919—Annelides Polychetes de Madagascar, de Djibouti et Golfe Persique. *Arch. Zool. Exp. et Gen,.* **58**, 315-473.

1927—Polychetes sedentaires. *Faune Fr.*, **16**, 1-494

1930—Annelida Polychaeta of the Madras Government Museum. *Bull. Madras Govt. Mus. (N.S.)Nat. Hist., Sec.* 1, No. 2, Part 1, 1-72.

1932—Annelida Polychaeta of the Indian Museum, **21**, No. 1, 1-262, Pts. 1-9.

1953—*The Annelida Polychaeta. Fauna of India.* Indian Press 1-507.

FRIEDRICH, H. 1938—Polychaeta. *Grumpe and Walgler, Tierwelt N.-u. Ostsea,* 1-200.

GEORGE, WILMA. 1962—*Animal Geography.* Heinemann, Lond., 1-142.

GRUBE, E. 1878—Annulata Semperiana. Beitrage zur Kenntnis der Anneliden-Fauna dr Philippinen nach den von Herrn Prof. Semper mitgebrachten Sammlungen. *Mem. Acad. Imp. Sci. St. Petersbourg.*, **7**, XXV, 1-300, Pts. 1-15.

HARTMAN, O. 1956—Polychaetous Annelids erected by Treadwell, 1891-1948, together with a brief chronology. *Bull. Amer. Mus. Nat. Hist.* **109**: Article 2, 239-310c p. 21.

1959—Catalogue of polychaetous Annelids of the World, Parts I & XX. *Allen Hancock Fdn. Publ. Occ. Pap*, **23**, 1-628.

HARTMAN-SCHRODER, GESA, VON. 1962—Zur Kenntnis des Eulittorals der chilenischen Pazifikkuste und der argentinischen Kuste Sudpatagonicus unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Die Polychaeten des Eulittorals. *Mitteilungen Hamburg Zool. Mus. und Inst.*, **60**, 57-167.

HASWELL, W. A. 1883—On some new Australian tubicolous annelids. *Proc. Linn. Soc. N. S. Wales.*, **7**, 633-638.

HEEZEN, B. C., AND MENARD, H.W. 1963—Topography of the Deep Sea Floor. *The Sea.* Edited by M. N. Hill. **3**, 233-280.

IMAJIMA AND HARTMAN, O. 1964—The Polychaetous Annelids of Japan. Parts 1 and 2. *Occ. Pap. Allan Hancock Fdn.* No. 26: 1:452.

JONES, M. L.1962—On some polychaetous annelids from Jamaica, the West Indies. *Bull. Amer. Mus Nat Hist.*, **126**, Article 5, 173-211.

LAUBIER, L. and PARIS, J. 1962—Annelides Polychetes. *Faune marine des Pyrenees Orientalis*, **4**, 1-80.

MONRO, C. C. A. 1933—The Polychaeta sedentaria collected by Dr. C. Crossland at Colon, in the Panama region, and the Galapagos Islands during the expedition of the S. Y. "St. George". *Proc. Zool. Soc. Lond.*, 1933 (2) : 1039-92, Figs. 1-31.

MOORE, H. B. 1962—*Marine Ecology.* John Wiley and Sons. Inc. New York. 1-493.

NELSON-SMITH, A. 1967—Catalogues of marine fouling organisms 3, Tubeworms. *O.E.C.D. Publication, Paris.* 1-79.

NELSON-SMITH, A. AND GEE, J. M 1966—Serpulid tubeworms (Polychaeta Serpulidae) around Dale, Pembrokeshire. *Field Studies*, **2**: No. 3, 331-356.

OKUDA, S. 1937—Annelida Polychaeta in Onagawa Bay and its vicinity. I. Polychaeta Sedentaria. *Sci. Rep. Tohoku Im. Univ., Ser.* 4 *(Biol.).*, **12**, 45-69, Pts. 2, 12 Fig.

1939—Annelida Polychaeta in Onagawa Bay and its vicinity. II. Polychaeta Errantia with some Addenda for Polychaeta Sedentaria. *Sci. Rep. Tohoku Imp. Univ., Ser* 6, **9**, No. 2. 1243.

OKUDA, S. AND YAMADA, M. 1954—Polychaetous annelids from Matsushima Bay. *J. Fac. Sci. Hokkaido Univ.*, **12**, No. 1-2, 175-199.

PILLAI, T. G. 1960—Some marine and brackish-water serpulid polychaeta from Ceylon including new genera and species. *Ceylon J. Sci (Biol. Sci.)*, **3**: No. 1, 1-40.

1961—Annelida Polychaeta from Tambalagam Lake, Ceylon, *Ceylon. J. Sci. (Biol. Sci.).*, **4**, No. 1, 1-40.

1965—Annelida Polychaeta from the Philippines and Indonesia. *Ceylon. J. Sci (Biol· Sci.)*, **5**, No. 2, 110-177.

PIXELL, H. L. M. 1913—Polychaeta of the Indian Ocean, together with some species from the Cape Verde Islands. The Serpulidae with a classification of the genera *Hydroides* and *Eupomatus.* *Trans. Linn. Soc. Lond. (Zool.).*, **16**, 69-92. Pts. 8-9.

RIOJA, E. 1957—Estudios Anelidologicos, 21. Observaciones acera de algunas especies de Serpulides de los generos *Hydroides Eupomatus* de las costas mexicanas del Golfo de Mexico. *An. Inst. Biol. Univ. Mex.*, **28**, 247-256.

1958—Estudios Anelidologicss, 22. Dates para el conoumento de bioclimaticos de anelidos poliquetos de las costas orientales de Mexico. *An. Inst. Biol. Univ. Mex.*, **29**, 219-301.

1959—Estudios Anelidologicos, 23. Contribucion al conocimento de los anelidos poliquetos de las islas de Revillagigedo. *An. Inst. Biol. Univ. Mex.*, 30, 243-259.

1960—Estudios Anelidologicos, 24. Adiciones a fauna de anelidos poliquetos de las costas orientales de Mexico. *An. Inst. Biol. Univ. Mex.*, 31, 289-316.

Shepard, F. B. 1967—*The Earth Beneath the Sea.* Johns Hopkins Press, U.S.A., 1-242.

Stokes, W. L. 1960—*Essentials of Earth History.* Prentice Hall International Inc., U.S.A., 1-502

Straughan, D. 1965—Marine Serpulidae (Annelida Polychaeta) of Eastern Queensland and New South Wales. *Austr. J Zool.*, **15**, 201-261.

1967—Some Serpulidae (Annelida Polychaeta) from Heron Island, Queensland. *Univ. of Queensland Pap. Great Barrier Reef Committee,* Heron Island Research Station, 1: No. 2. 27-45.

Tebble, N. 1955—The Polychaet Fauna of the Gold Coast. *Bull. Brit. Mus. (N.H.) Zool.*, 3: No. 2,59-148.

1959—On a collection of polychaetes from the Mediterranean Coast of Israel. *Bull. Res. Council. Israel,* 138: No. 1., 9-30.

(MS. received 14.2.69)