(Communicated at the meeting of May 29, 1948.)

In the course of time 56 different names have been used to indicate forms of the Hydrocoralline genus *Millepora*, which were considered as distinct species or varieties. Especially Duchassaing (1850) and Duchassaing & Michelotti (1860, 1864) regarded specimens of a growth form slightly differing from that of previously described species as separate entities, they gave new specific names to 16 West Indian forms of *Millepora*.

Several authors commented upon the extreme variation of *Millepora* as a result of external influences. DANA (1848, p. 543) already remarked: "There is much difficulty in characterizing the Millepores, on account of the variations of form a species undergoes, and the absence of any good distinctions in the cells." It is indeed extremely difficult to find characters for specific distinction, and Hickson (1898 a, b, 1899), who made elaborate studies concerning the species problem in Millepora, came to the conclusion that all the various forms are nothing else but results of the extreme possibilities for variation in the one species Millepora alcicornis L. HICKSON's studies were based on an extensive material of colonies of Millepora from various parts of the world. He tried to find characters for specific distinction in (1) the form of the corallum, (2) the size of the pores, (3) the degree of isolation of the cycles, (4) the presence or absence of ampullae, (5) the texture of the surface of the corallum, (6) the relative number of dactylopores and gastropores, (7) the anatomy of the soft parts. HICKSON failed to find distinct specific characters, and believed that the different growth forms were brought about by the various conditions of existence on the reefs only.

HICKSON's conclusions largely influenced the opinion of nearly all later investigators who published upon material belonging to *Millepora*. Almost invariably these authors remarked that the species problem in *Millepora* had been solved by HICKSON, and they identified their material as *Millepora alcicornis* L., though sometimes adding that the growth form corresponded with that of a certain form previously indicated with a separate name. Three authors expressing views different from those defended by HICKSON may be mentioned here. GRAVIER (1911) did not mention HICKSON's results and identified his material as *Millepora dichotoma* Forsk., whilst THIEL (1933) used the name *Millepora intricata* M. E. & H. for a colony of a delicately branched growth form which according to that author cannot easily be explained solely on account of influences of external conditions. CROSSLAND, who in a number of earlier papers had adopted HICKSON's

views regarding the specific unity of all the forms of *Millepora*, in a recent publication (CROSSLAND, 1941) stated that in the Red Sea there occur three well defined species of the genus. The latter statement completely agrees with KLUNZINGER'S (1879) results, who in an excellent manner described the specific characters of the three Red Sea forms, and gave the exact data of the synonymy of these three species, viz., *M. exaesa* Forsk., *M. dichotoma* Forsk., and *M. platyphylla* Hempr. & Ehrb.

In the last publication in which he gives his opinion on the variability of *Millepora*, HICKSON (1924, p. 145) writes: "The corallum assumes many variations of form. Sometimes it consists of thick massive plates, sometimes it is coarsely branched or becomes profusely ramified. These differences in form seem to be associated with differences of the immediate environment and cannot be used as characters for specific distinctions."

If this statement were right, colonies of Millepora living under the same conditions of existence always would show a highly similar growth form. On the reefs, however, often colonies of a strikingly dissimilar growth form may be found growing on the same spot, under exactly the same environmental factors. An instance of this kind is shown by the compound figured on the plate accompanying the present paper. The figure represents the region of contact of two colonies of Millepora growing side by side on the surf-swept edge of the reef of the island Edam in the Bay of Batavia. Each of the colonies with its broadest side was exposed to the full action of the waves, as they occupied the extreme seaward border of the reef. Consequently the external circumstances of the two colonies (depth of water, chemical and physical conditions of the water, exposure to wave action, lack of encumbrance by other colonies of corals) were exactly the same. In their growth form, however, the two colonies present striking differences. The one consists of vertically extending massive thick plates which among each other are combined into a more or less honeycombed mass, it is a typical representative of the species Millepora platyphylla Hempr. & Ehrb. The other colony in all essential characters corresponds with Millepora murrayi Quelch, it consists of a crowded mass of rather delicate branchlets. In their region of contact the heavier and apparently stronger colony has partly overgrown the more delicate specimen. The two colonies in their growth form are as unlike as possible, and these differences necessarily must be due to specific peculiarities, as the factors of the environment for each of the two colonies were exactly the same.

When corals of the genus *Millepora* are examined on the reefs, and attention is given to the conditions of the environment, it appears that, though really the colonies are variable to a considerable degree, this variation is restricted to certain limits. Colonies of a species which usually occurs as a decidedly ramified form under unfavourable conditions may remain rather compact and develop short stunted branches only. On the other hand colonies of a species which in its typical form grows out to thick and broad upstanding plates in an unsuitable locality may develop into a more or less branching

form. But these deviations from the typical form never become so pronounced that there might be found a continuous series of growth forms connecting the one extreme with the other. There are a number of distinct species in the genus *Millepora*, each of which is characterized by definite peculiarities which remain obvious even if the specimens are living under unfavourable conditions. An exception form, however, the incrusting growths of *Millepora*, which by covering all kinds of objects with a thin layer of corallum assume the form of their substratum. These incrusting specimens as a rule do not show sufficient characters for a specific identification.

All more or less full grown colonies of *Millepora* can be arranged in groups showing characters of sufficient value to regard these groups as distinct species. The chief characters are those of the growth form, which, however, as a result of the pronounced variability, are not always easily to be defined.

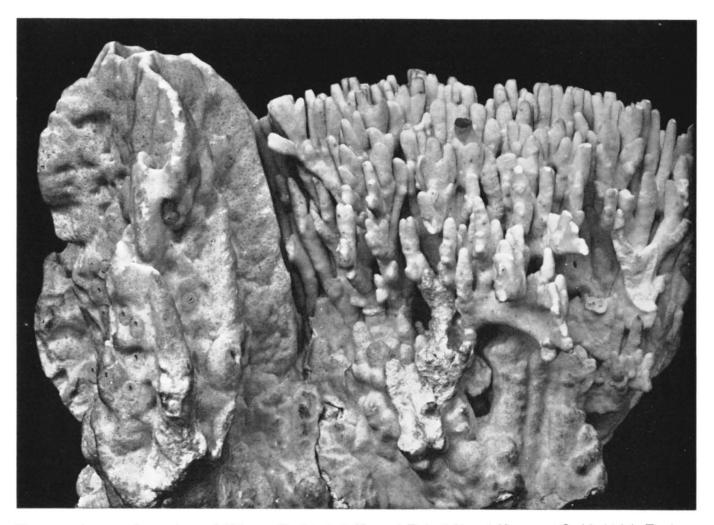
Besides the form of the corallum some of the other points in HICKSON's attempts to find specific characters may yield results of definite value, though often in a restricted sense.

If we take the extremes there is a difference in the size of the pores in the various species of *Millepora*. In *M. platyphylla* Hempr. & Ehrb. the pores invariably are large, whilst in *M. intricata* M. E. they always are small and often even difficult to detect. But in other species the size of the pores in different colonies may vary to a considerable degree, and even in parts of the same colony there may be a noticeable difference in the size of the pores.

The degree of isolation of the cycles in no manner can be used as a specific character. As HICKSON correctly observed the isolation of the cycles is highly different in various parts of one colony. It depends upon the rapidity of growth and the amount of light falling on the various parts of the corallum.

The presence or absence of ampullae cannot constitute a specific character. As a matter of fact ampullae form a part of the generative cycle of each colony, and they may be found, at least in certain parts of the year, in each specimen. On the other hand the shape of the ampullae, and especially that of the calcareous covering of these cavities, which is present before the medusae are set free, may be different in the various species, and for this reason may yield characters for a specific distinction. The available data as yet are too scanty for a decision in this respect.

The structure of the surface of the corallum in certain cases is of importance as a specific character. Many colonies of the West Indian species, M. alcicornis L., M. squarrosa Lamk., and M. complanata Lamk., have the surface profusely pitted with insignificant depressions in the centres of which there are the gastropores. But in other colonies of the same species this feature does not occur, so that then the surface of the corallum is even. It is interesting that these small depressions are found



The region of contact of two colonies of *Millepora*, *M. platyphylla* Hempr. & Ehrb. (left) and *M. murrayi* Quelch (right). The lower part of the colony of *M. murrayi* is covered with a thin layer of *M. platyphylla*. From the edge of the reef of the island Edam in the Bay of Batavia. Natural size.

in the three species only, they never occur in Indopacific species of the genus.

On the other hand many colonies of *M. platyphylla* Hempr. & Ehrb. have large parts of the surface covered with small warty excrescences on the tops of which the gastropores are found. Here again this character is not constant, as it may occur in a part of certain colonies only, and in other colonies of the same species it does not appear at all. But the occurrence of these warts is never observed in specimens belonging to other species, so that it, when occurring, is a means for identification of the specimen.

The relative number of dactylopores and gastropores does not furnish a character for specific distinction. This number to a certain degree is different in various parts of the same colony, it is highly dependent upon external conditions. Parts of vigorous growth generally show a larger amount of pores than regions of slow growth, and in various parts of one colony the relative number of dactylopores which surround each gastropore is rather variable.

The anatomy of the soft parts as yet has not given indications for specific distinctions. All the species examined in this respect have two kinds of nematocysts, larger and smaller. In the species M. alcicornis L., M. complanata Lamk., M. platyphylla Hempr. & Ehrb., M. exaesa Forsk., M. tenella Ortm., and M. murrayi Quelch these larger nematocysts have exactly the same shape, whilst their size is subject to slight variation only (length 25—30 μ). More detailed studies of the nematocysts in well preserved material perhaps may show that also here there are specific differences.

After having examined a fairly large amount of specimens from the reefs of islands in the Java Sea, and after careful studies on the material of the museums in Paris, Leiden, and Amsterdam, I came to the conclusion that at least nine species can be distinguished, each of which is characterized by distinct specific peculiarities. Moreover it appeared that almost all the forms described in previous literature could be identified as synonyms of the recognized species. A short summary of the species and their characters follows here.

Millepora alcicornis Linnaeus, 1758. Synonyms: Millepora ramosa Dana, 1848 (Millepora alcicornis var. ramosa Esper, 1790); Millepora pumila Dana, 1848; Millepora moniliformis Dana, 1848 (Millepora alcicornis var. crustacea Esper, 1790). Corallum of extremely variable form, consisting of usually flattened branches which may largely unite to form upstanding plates. The branches may, however, spread in all directions, or more or less solid masses may develop by pronounced fusion of the branches.

Millepora exaesa Forskål, 1775. Synonyms: Millepora tuberculosa Milne Edwards, 1857; Millepora gonagra Milne Edwards, 1860; Millepora nodosa Moseley, 1879 (Millepora alcicornis var. nodosa Esper, 1790). Corallum consisting of more or less rounded masses with a profusion of short and thick, knob-like branches.

Millepora dichotoma Forskål, 1775. Synonym: Millepora reticularis Milne Edwards, 1860. Corallum consisting of round branches which have a strong tendency to unite so as to form upstanding plates of a pronouncedly reticular character.

Millepora squarrosa Lamarck, 1816. Synonym: (?) Millepora foliata Milne Edwards, 1860. Corallum forming broad upstanding plates with thin edges, the surface covered with irregular ridges and tubercles, producing a frilled appearance of the colony.

Millepora complanata Lamarck, 1816. Synonym: Millepora plicata Dana, 1848 (Millepora alcicornis var. plicata Esper, 1790). Corallum consisting of flat upstanding plates with thin edges.

Millepora platyphylla Hemprich & Ehrenberg, 1834. Synonyms: Millepora verrucosa Milne Edwards, 1857; Millepora incrassata Milne Edwards, 1860 (Millepora squarrosa var. incrassata Dana, 1848); Millepora ehrenbergi Milne Edwards, 1860; Millepora truncata Vaughan, 1918 (Millepora platyphylla var. truncata Dana, 1848). Corallum forming thick upstanding plates with blunt edges. The plates have a tendency to unite in honeycombed masses.

Millepora intricata Milne Edwards, 1857. Corallum consisting of a complicated mass of thin branches spreading in all directions, and which are largely anastomosing among each other.

Millepora murrayi Quelch, 1884. Synonym: Millepora confertissima Quelch, 1886. Corallum branching in the shape of ogives with numerous vertical smaller branchlets, often forming dense masses.

Millepora tenella Ortmann, 1892. Synonym: Millepora tortuosa Dana, 1848 (the latter name is preoccupied by Millepora tortuosa Esper, 1790, which belongs to the coralline algae). Corallum rather spreadingly branching, each larger branch with numerous smaller branches in the same plane, these smaller branches rather distant from each other.

Of these nine species M. alcicornis, M. squarrosa, and M. complanata are restricted to the Atlantic region of America. M. exaesa, M. dichotoma, and M. platyphylla occur in the Red Sea and in other parts of the Indopacific region. M. intricata, M. murrayi, and M. tenella are living in the Indopacific region, but are not found in the Red Sea.

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