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## A STUDY OF SOCIALITY IN THE MADREPORARIA

GERTRUDE VAN WAGENEN AND H. J. WEHMAN

The type of sociality found in the Madreporaria is necessarily primitive. While we were making this study two criteria of sociality have been adopted and applied: first, the proximity of one corallite to another; second, organic communication between associated polyps and corallites. As the two criteria indicate, sociality is examined from the standpoint of morphology of hard parts. This is necessary because of the extent of the field covered, the absence of live specimens, and the inclusion of fossils.

The association in which there is no organic communication between the units may be called non-colonial; the association in which there is organic continuation, colonial. The non-colonial associations include simple corals growing in the same locality, colonies flourishing on the same reef, and groups of larvæ which, because of an especially favorable environment, have settled very near to each other. In the last-mentioned instance, should several of the larvæ survive their hard parts would soon approach each other and coalesce, giving the appearance of a true colony. In such a case there is usually no communication between the adjacent visceral cavities; and the term pseudo-colonial is used. Other than this simple fusion of hard parts the non-colonial and pseudo-colonial associations are of no further interest morphologically.

It is only reasonable to believe that the solitary corals preceded the colonial. The evidence of paleontology, while leaving something to be desired, is definitely in favor of this view. The most ancient of all corals, the *Archaeocyathidae*, occur in the Cambrian. They are solitary, and no trace of a Cambrian colony has yet been found. The family *Archaeocyathidae* is considered to belong to the Hexacoralla and Perforata, but for the most part the Paleozoic history of corals deals with the Tetracoralla. Of eleven genera of Ordovician Tetracoralla listed by Zittel (1913) only two were colonial (ten per cent); of twenty-eight genera from the Silurian nine were colonial (thirty-two per cent); of thirty-one genera from the Devonian eleven were colonial (thirty-five

per cent); of sixteen genera from the Carboniferous seven were colonial (forty-five per cent). From these percentages it appears that there was a gradual increase in the number of colonial genera, but there is no doubt that the majority of the Tetracoralla always remained solitary.

There are few known genera of Hexacoralla from the Paleozoic, and the greater number of these, including the *Archaeocyathidae* and several genera in the *Eupsammidae*, were solitary. The sudden extinction of the Tetracoralla at the close of the Paleozoic was followed in the beginning of the Mesozoic by a sudden increase in the number of Hexacoralla. Paleontology does not show any definite increase in the proportion of colonial to solitary genera among the Hexacoralla; but so far as is known the Hexacoralla have been predominantly colonial from the Triassic, ninety per cent of the Triassic genera listed by Zittel being colonial.

Hence it appears that in the course of geologic time a predominantly colonial type has superseded a predominantly simple type of coral.

Of the five families of Tetracoralla given by Zittel, three (*Cyathaxonidae*, *Paleocyclusidae*, and *Zaphrentidae*) contain solitary forms only. In the *Cystiphyllidae* colonies are rare; hence nearly all the compound Tetracoralla are found within the family *Cyathophyllidae*. In this family a definite progression in colony-formation may be traced.

*Heliophyllum* may serve as an example of a solitary Tetracorallum; this genus also, though rarely, forms dendroid colonies.

*Diphyphyllum* forms large colonies, but is composed of discrete columns held in place by intercolumnar braces placed at different levels throughout the colony. Reproduction is by multiple gemmation, and in some species at least the parent polyp dies. Since the columns are separated by a space which may be as great as their own diameter, and since there is no trace of interstitial tissue other than the occasional bridges, it would appear that only a few neighboring polyps were continuous over newly-formed braces.

*Cyathophyllum* represents a further step toward the formation of a compact colony. Connecting braces are not present, and a fairly distinct progress is traced from species like *C. cespitosum* in which the column walls diverge, through forms such as *Cyathophyllum calvini* in which the perfect cylindrical column walls become flattened where two are in contact, to forms like *C. hexa-*

*gonum* in which the assumption of a definite hexagonal shape is caused by maximum crowding of calices.

In the species *Lithostrotion canadense*, although the calices have taken on the hexagonal shape, each column remains distinct, the walls of adjacent columns being merely applied to each other. In *Acervularia* and other genera the walls of adjacent columns have coalesced and the common wall brings about the closest union between polyps attainable without actual confluence.

Colonies may arise in two ways: by budding and by fission. Stolonization is to be considered as a type of budding. These two lines of development from solitary corallite to colonial form may be illustrated in the Perforata within the single family *Eupsammidae* by the genera *Balanophyllia*, *Heteropsammia*, *Lobopsammia*, *Dendrophyllia* and *Rhizopsammia*.

THE SOLITARY PHASE. *Balanophyllia* may be taken as a typical example of a solitary coral, and this, as well as other solitary forms, is often found in pseudo-colonial groups.

COLONIES ARISING BY FISSION. An example of a genus that has abandoned the solitary form and is in process of becoming colonial is *Heteropsammia*. One species, *H. michelini*, invariably occurs with two calices, partly imbedded in coenenchyma. Another species, *H. multilobata*, has made further progress, always having a greater number of calices than two. A further departure along the same line is shown by *Lobopsammia*, in which there is repeated fission, resulting in a cespitose colony.

COLONIES FORMED BY BUDDING. *Balanophyllia* forms new individuals by budding, as do other solitary corals; and it is easy to see that a colony might arise in the first instance by retention of a bud. The genus *Rhodopsammia* shows a primary stage in colony formation by retaining lateral buds which in turn may bud, and the grand-daughter buds being likewise retained, the result is a dendroid colony of a simple type. A more advanced stage is illustrated by the genus *Dendrophyllia*, some species of which on the one hand build up by successive gemmations dendroid colonies of considerable complexity (*D. nigrescens*, etc.); and on the other hand certain species (*D. willeyi*, *D. diaphana*) form cespitose and finally massive colonies by lateral or sub-basal budding. Stolonization is represented by the genus *Rhizopsammia*.

APOROSA. The Aporosa furnish no single family, the limits of which are undoubted, to illustrate the two lines of development in colony formation, but a fairly complete series may be found within the limits of the suborder as a whole.

COLONIES ARISING BY BUDDING. *Caryophyllia* is an example of imperforate solitary coral, and what has been said about *Balano-phyllia* applies also to *Caryophyllia*.

*Haplohelix*, an Oligocene genus in the family Oculinidæ, stands as an example of primitive dendroid colony, having gemmation from one side only. In *Oculina* the corallites are small and numerous, arranged spirally or scattered irregularly over the branches and imbedded in coenenchyma—obviously an advance over *Haplohelix* in colony-formation.

A reduction in size of corallites and filling in of coenenchyma is to be found in the family Orbicellidæ. *Galaxea* forms a sub-massive colony with exsert turbinate calices, while in *Orbicella* the calices are smaller and imbedded in coenenchyma; the latter condition must be interpreted as a marked advance over the former in colony-evolution.

COLONIES ARISING BY FISSION. *Lophohelia* is an example of a primitive dendroid colony. The geniculate branching indicates that the colony results from simple successive unequal fissions, the original turbinate shape typical of the solitary corals being retained by each calice. Other colony-formation by fission is illustrated by the three families *Eusmiliidae*, *Mussidae*, and *Favidae*. *Eusmilia* forms cespitose colonies by dichotomous or trichotomous fission, but the rapid separation of the corallites with upward growth is accompanied by withdrawal of soft parts, leaving the colony complex only as to skeleton. The soft parts are continuous between members of the last division, so as a rule the polyps are confluent in twos and threes. In *Dichocoenia* the same division into two or three calices occurs, but reduction in size of calices and filling of intercalicinal spaces with coenenchyma results in a massive colony in which all soft parts are continuous and the calices are confluent in small groups.

In *Mussa sinuosa* fission results in a meandrine form, but the walls of confluent groups are ununited, leaving the soft parts of the individual groups distinct. In *Diploria* the walls of the adjacent series of corallites are united by the peripheral ends of costae, which leaves a shallow trough, over which, however, the polyps are continuous. In *Meandrina* the fusion of the walls directly into a single colline brings about the highest union between the soft parts of an entire head that is to be found throughout the whole group Aporosa.

FUNGIDA. In the Fungida it was not found possible to follow out the two lines of colony formation because of incomplete data

as to the mode of asexual reproduction. However, in the study of hard parts there appears to be a series in increasing complexity, within the family *Fungidae*, exemplified by the genus *Fungia*, which is invariably solitary; and *Herpetolitha*, which has an axial series of calices with several peripheral parallel series of calices, the septocostae being continuous between calice and calice; and *Polyphyllia*, the last step in the series, having calices decreased in size, increased in number, and crowded together.

The genera of the *Agariciidae* are typically compound, but in the Tertiary simple forms appear to have been fairly common (*Microseris*, *Trochoseris*, *Palaeoseris*, etc.). *Cyathoseris*, from the Oligocene and Eocene, forms a massive colony by costal gemmation, the young corallites remaining permanently in a circle about the periphery of the mother polyp. Within the family *Agariciidae* it is possible to choose a graded series of genera and species from such forms as *Siderastraea*, in which a definite pericalicular wall interrupts communication between polyps, to certain species of *Agaricia* in which there is no definite pericalicular boundary, the septocostae and some of the mesenteries being continuous from polyp to polyp. The highest degree of sociality in the *Fungida* appears to be found in *Pachyseris*, in which the calices are disposed in parallel rows with continuous and parallel septocostae, with continuous columella, and showing no impression in the hard parts of distinct calices.

The most successful corals at the present time are undoubtedly those which have the most intimate union between the individual polyps; for example, *Porites* and *Acropora* in the Perforata, meandrine forms in the Imperforata, and in the *Fungida* those corals which have lost definite pericalicular boundaries, as for example the family *Agariciidae*. In modern reefs the world over these genera are found to be most numerous in individuals and often also in species and varieties. The communication between the visceral cavities of polyps in the Perforata is accomplished by perforations in the boundary walls, while in the Imperforata and the imperforate *Fungida* a similar result is brought about by the abolishment of the walls themselves in the line of confluence. In the one case the communication is intraskeletal; in the other, supraskelatal.

The unity and compactness of colonies of the *Hexacoralla* cannot be paralleled among the *Tetracoralla*, although the *Tetracoralla* shows some progress, from the diffuse *Diphyphyllum* to the compact *Strombodes* or *Acervularia*. Modern species have

fairly definite growth-forms; while such diffuse colonies as *Cyathophyllum calvini* and species of *Diphyphyllum* have apparently neither definite shape nor definite size, and one colony of *Cyathophyllum calvini* has been found which is reported as having probably had a diameter of fifty feet or more.

#### CONCLUSIONS

Two points seem clear: first, there has been progress throughout the geological history of corals from solitary to colonial, and within the colonial corals progress in compactness; second, the most successful of modern corals are those which have the highest degree of colonialism. Since this is so, there must be definite advantages in sociality.

In the animal kingdom there is always an advantage in numbers. The colonial condition supports a greater number of individuals in a favorable environment than is possible in the solitary condition. There is moreover an economy of skeletal tissue, for instance, epitheca. Then too, asexual multiplication, by budding and by fission, is more economical than sexual reproduction because in the former case the young inherit the same environment which has proven favorable for the parent and enjoy the protection of the parent polyp and of the colony. This is the same principle which in higher animals is called care of the young. These advantages are true not only of coral heads entirely covered with soft parts but also of colonies bearing only isolated polyps. In colonies where there is continuation of soft parts, and especially confluence of visceral chambers, there are the further advantages of equal distribution of food and transmission of nerve impulses. Where visceral chambers are continuous food ingested by one polyp will be transmitted to others; and continuity of soft parts means possibility of transmission of impulses from polyp to polyp, so that food and warning-stimuli call forth anticipatory reactions in neighboring polyps.

These advantages—community of food supply, economy of space, protection of young, transmission of warning stimuli, common action against enemies, and protection against extinction afforded by a large number of individuals—characteristic of all social groups in a certain stage of their evolution, are found to be present therefore even in the primitive sociality of the *Madreporaria*.

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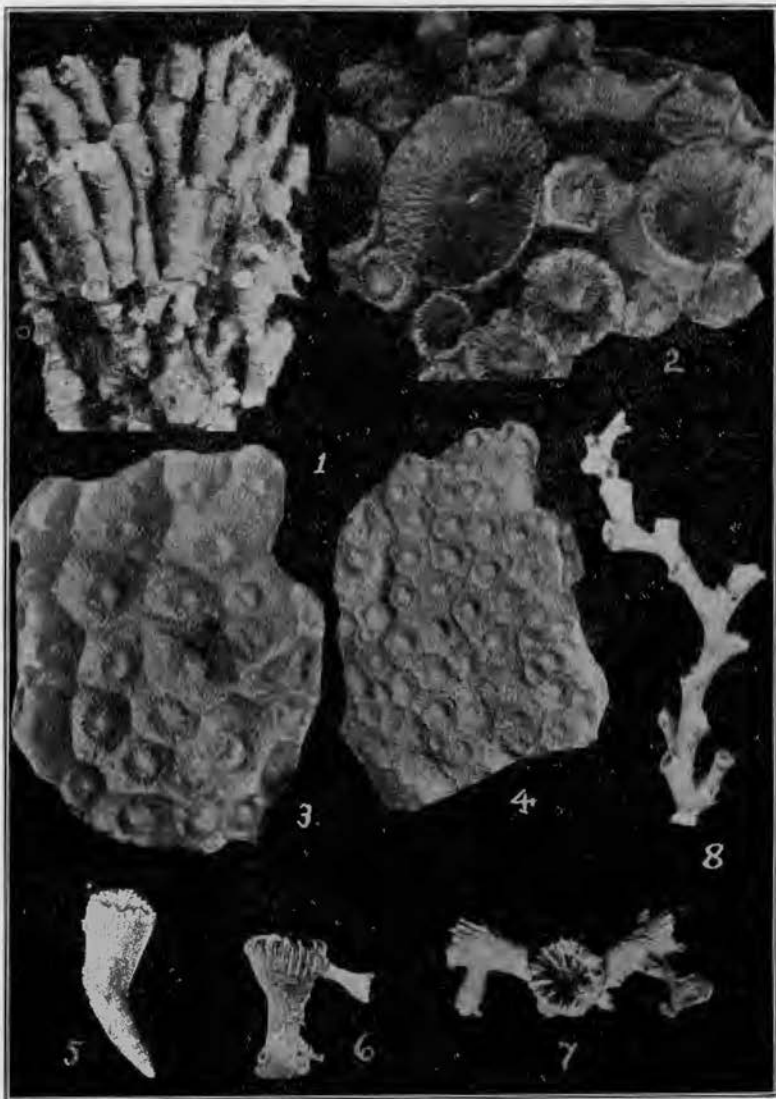
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PLATE III



## PLATE III

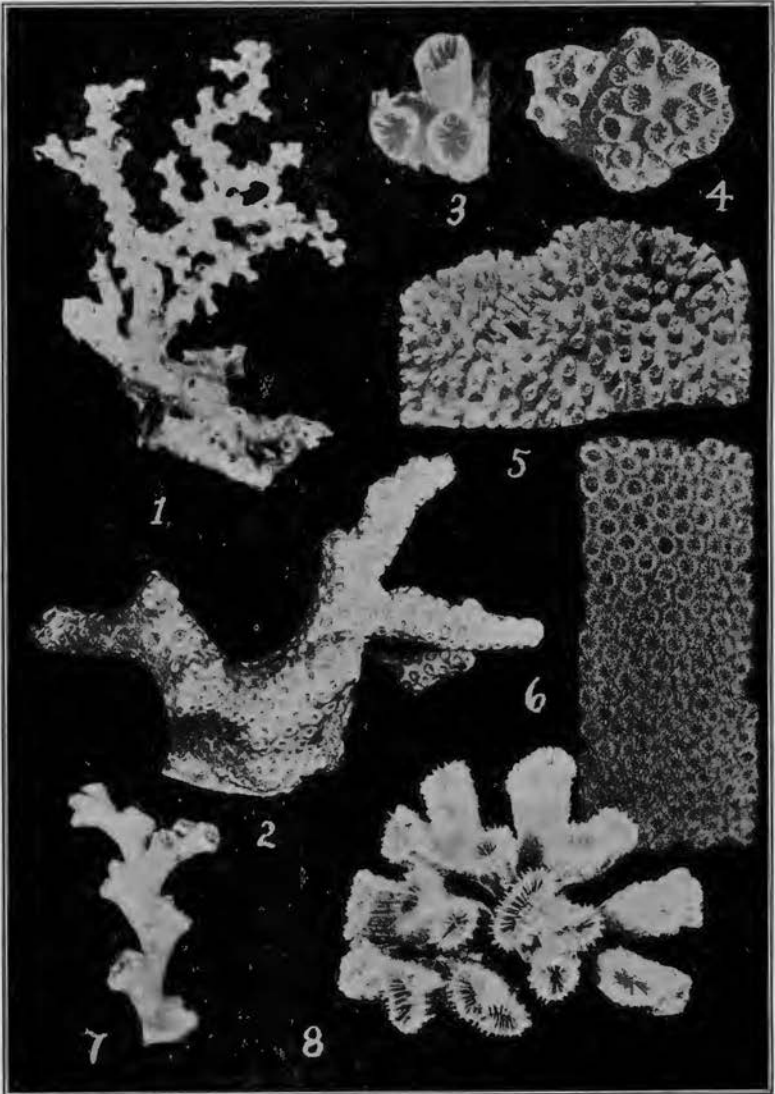
1. A small portion of a colony of *Diphyphyllum eruciforme*, x 1, showing multiple calicinal budding and intercolumnar braces. A diffuse type of colony. Specimen from the Iowa Silurian; furnished by the Geology Department, State University.
2. Portion of colony of *Lithostrotion canadense* var. *proliferum* Hall, x 1, top view. Also a diffuse type but with the columns contiguous and without intercolumnar braces. Specimen from Iowa Mississippian; negative furnished by Geology Department, State University.
3. Portion of colony of *Lithostrotion canadense* Castelnau, x 1. A more compact type which has assumed the polygonal shape of column due to crowding. The double nature of the intercolumnar walls is not apparent in the picture. Specimen from Iowa Mississippian; negative furnished by Geology Department, State University.
4. Portion of colony of *Acervularia inequalis* H. & W., x 1. A still more compact type, with single intercolumnar walls. Specimen from Iowa Devonian; negative furnished by Geology Department, State University.
5. *Balanophyllia socialis*. An example of solitary Hexacorallum. From Bourne (1905).
6. *Caryophyllia*, with undetached bud, x 1. Specimen from about sixty fathoms, off Barbados, British West Indies.
7. An unidentified specimen from Barbados, showing parent corallite and three generations of buds in place.
8. *Dendrophyllia profunda* Pourt., x ½, showing formation of a dendroid colony by successive lateral buds partly embedded in coenenchyma. Specimen from Florida, 230 to 400 fathoms.

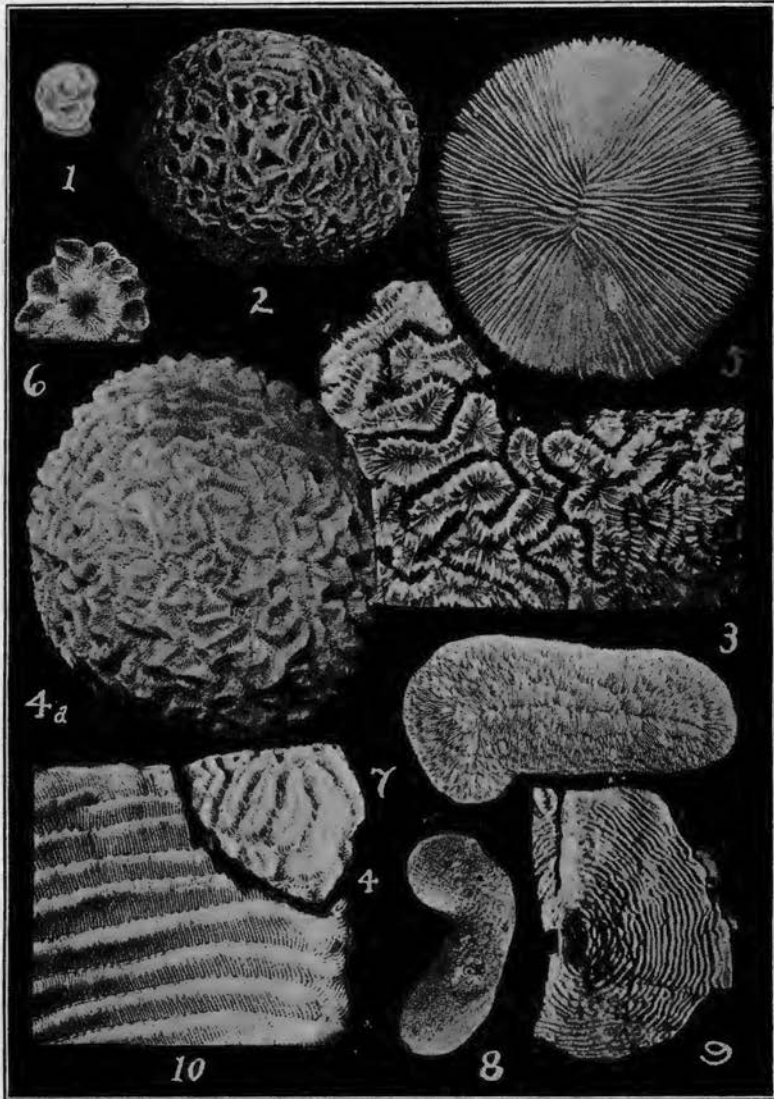
## PLATE IV

1. *Amphihelia*, x ¾. A more complex dendroid colony formed by alternate marginal budding, with dichotomous branching caused by twin-budding. The newly-formed calices have the original trumpet shape of solitary cup-corals but later become embedded in coenenchyma. Specimen from Barbados, 50 to 100 fathoms.
2. *Oculina robusta* Pourt., x ½. A further development of the coenenchyma idea. Deposition of coenenchyma keeps pace with the outward growth of the calices, and this, together with the greatly increased diameter and much more numerous calices per unit area, makes this one of the most compact of dendroid colonies. Specimen from Florida reefs.
3. *Dendrophyllia diaphana* Dana, x 1. The large size, trumpet shape, and comparative fewness of the calices, as well as the small amount of coenenchyma, mark this as a primitive type of colony. From Vaughan (1918, Plate 60, Fig. 3a).
4. *Dendrophyllia wileyi* (Gardiner), x ½. A slightly more advanced type than 3. From Vaughan (1918, Plate 60, Fig. 4).
5. *Galaxea fascicularis* (Linn.), x ½. A still more advanced type of spreading colony. The calices are reduced in size and increased

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PLATE IV





in number but the amount of coenenchyma is still small. From Vaughan (1918, Plate 34, Fig. 1).

6. Small portion of a head of *Orbicella annularis* Dana, x 1. A good example of a compact massive colony with small, numerous calices completely embedded in coenenchyma. Specimen from Florida reefs.
7. *Lophohelia prolifera* E. & H., x ½. A simple type of dendroid colony formed by unequal fission, with incomplete deposition of coenenchyma. Specimen from Florida, 230 to 400 fathoms.
8. *Eusmilia fasciculata* (Pallas), x ½. A cespitose colony formed by fission, without coenenchyma. Specimen from Barbados, about eight fathoms.

PLATE V

1. *Heteropsammia multilobata* Moseley, x ½. A primitive type of spreading colony arising by fission. The calices are few, relatively large, and exserted. From Moseley (1881, Plate XII).
2. *Dichocoenia*, x ½. A massive colony arising by fission. The fission-groups of calices are distinct but the spaces between them are completely filled with coenenchyma. Specimen taken from West Indian reef.
3. *Mussa sinuosa* (Lam.), x ½. An advance toward the meandrine type. The fission-groups are long and sinuous but the walls are distinct and separated by unbridged spaces. From Vaughan (1918, Plate 49, Fig. 3).
4. Small portion of colony of *Diploria*, x ½. The typical meandrine type. The walls between the fission-rows are still distinct at the summits but filled in at the base with coenenchyma and connected by costæ. Specimen from West Indian reefs.
- 4a. A colony of *Meandrina*, x ½. A very high type of meandrine coral. The separation between fission-rows is reduced to a single narrow column wall, Specimen from West Indian reefs.
5. *Fungia danae* E. & W., x ½. A typical solitary fungid. Specimen from Pacific ocean.
6. *Cyathoseris subregularis* Reuss, x ½, from the Oligocene of Italy. A primitive fungid colony formed by costal budding. From Zittel-Eastman's Textbook of Palaeontology, 1913, reproduced by permission of the publishers, Macmillan & Company.
7. *Herpetolitha crassa* Dana, x ¼. A comparatively low type of fungid colony. From Vaughan (1918, Plate 54, Fig. 1).
8. *Polyphyllia talpina* (Lam.), x ¼. The calices are crowded and less regularly arranged than in *Herpetolitha*. From Vaughan (1918, Plate 54, Fig. 2).
9. *Pachyseris speciosa* (Dana), x ½. A high type of agaricid colony, calices completely confluent in long parallel rows. From Vaughan (1918, Plate 54, Fig. 3).
10. *Pachyseris torresiana* Vaughan, x 2. Showing the continuous rows of calices. From Vaughan (1918, Plate 55, Fig. 1a).