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INDO-PACIFIC CORAL SPECIES BELONGING TO THE SUBFAMILY MONTASTREINAE VAUGHAN & WELLS, 1943 (SCLERACTINEA-COELENTERATA) PART II. THE GENERA *CYPHASTREA*, *LEPTASTREA*, *ECHINOPORA* AND *DIPLOASTREA*

by

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With five plates

INTRODUCTION

In the first part of the study on the Montastreinae (Wijzman-Best, 1977) I have dealt with the genera *Montrastrea* and *Plesiastrea* on the basis of material from a wide range of localities in the Indo-Pacific ocean. In the present paper dealing with the remaining genera of the Montastreinae the geographical approach has been extended. This study is based upon collections from Hawaii, Enewetak (Marshall Islands), New Caledonia, Eastern Australia, Indonesia, Western Thailand, the Mascarenes, the Seychelles and the Red Sea (Gulf of Aqaba). In most of these areas locally available collections have been examined as well as material collected by myself, with ecological data. Material from Western Thailand has kindly been given to me on a loan by H. Ditlev; material from the Seychelles has been studied in the Musée Royal de l'Afrique centrale (MRAC), Tervuren, Belgium. Collections from the Red Sea examined are those of Dr. H. Schuhmacher in the Ruhr Universität in Bochum, and of Dr. G. Scheer in the Hessisches Landesmuseum in Darmstadt. ¹⁾

The type material studied is housed in the Museum für Naturkunde der Humboldt Universität in Berlin (ZMB), the British Museum of Natural History, London (BMNH), the Muséum National d'Histoire Naturelle,

¹⁾ The trip to Israel and fieldstudies in Elat have been financed by the Royal Dutch Academy of Sciences at Amsterdam.

Paris (MNHN), the National Museum of Natural History, Washington D.C. (USNM), the Universitetets Zoologiske Museum, Copenhagen (UZMC), the Tokohu Imperial University, Sendai, Japan (TIU), the Yale Peabody Museum, New Haven (YPM), University of Glasgow (GI). Thanks are due to the keepers in charge of the coral collections of the different museums and institutes.

Most of the material on which this paper is based is in the Rijksmuseum van Natuurlijke Historie in Leiden. The collections from Indonesia made by Dr. H. Boschma on board of the H.M. Willebrord Snellius have been added to by material from all localities in the Indo-Pacific mentioned above made either by myself or given to the Museum by my collaborators in the field (Hawaii, Enewetak, Great Barrier Reef, Mascarenes). As a result of assistance in identifying specimens (Seychelles, W. Thailand) some material has been added as well. The collection from New Caledonia made by myself in 1972 is in the Institute of Taxonomical Zoology (ITZ) at Amsterdam; material collected later on (1976) is also in Leiden.

In order to make the geographical variation study of the various coral species as complete as possible I have studied the large coral collections from all over the Indo-Pacific in London (BMNH) and Washington D.C. (USNM).

HISTORY OF THE FOUR GENERA

As stated in the first part of the study of the Montastreinae one gets involved in a complex taxonomic history whenever one works on a group of reefbuilding corals. The two genera of this subfamily dealt with in Wijsman-Best (1977) have given most confusion in the literature because they closely resemble some of the Faviinae species. In the genera dealt with in the present paper (*Cyphastrea*, *Leptastrea*, *Echinopora* and *Diploastrea*) the confusion is less because the generic characteristics are more clear-cut.

The genus *Cyphastrea* already recognized by Milne Edwards & Haime in 1848, split off from the genus *Astrea* Lamarck (which included various genera), has been correctly used by all later authors. (Forskål (1775), still used the name *Madrepora*). As stated in Veron, Pichon & Wijsman-Best (1977) there are approximately twenty-six *Cyphastrea* species. In the present paper five species are recognized and described three of which occur throughout the Indo-Pacific (*C. serailia*, *C. chalcidicum*, *C. microphthalma*) whereas two are more restricted geographically (*C. japonica*, *C. ocellina*).

Chevalier (1975: 9) brings up the problem with the Atlantic genus *Solenastrea* of Milne Edwards & Haime. I agree that if *S. hemprichiana* Milne Edwards & Haime, 1850, is the genotype the name *Solenastrea* has to

be dropped. Recent investigations in the Caribbean region showed that *Plesiastrea* Milne Edwards & Haime, 1848 (= *Solenastrea bournoni* Milne Edwards & Haime, 1950) as well as *Cyphastrea* Milne Edwards & Haime, 1848 (= *Astrea Orbicella excelsa* Dana, 1846) are present. A Miocene reef found in Baixo, Madeira Archipelago, shows fossil specimens of both genera. But more work has to be carried out on the recent corals in the Western Atlantic region before we may conclude how closely the species of these genera correspond with those known in the Red Sea at the moment.

The genus *Leptastrea* was also recognized by Milne Edwards & Haime in 1848, split off from the heterogenous genus *Astrea*. These authors further recognized a genus *Baryastrea*, which was correctly synonymized with *Leptastrea* by Matthai in 1914. Because the variability in specific characters is very great the various species described in the literature are often placed in different genera (*Prionastrea*, *Cyphastrea*, *Orbicella*). There are about twenty *Leptastrea* species; in the present paper five species are recognized and described three of which have an Indo-Pacific distribution (*L. bottae*, *L. purpurea*, *L. transversa*), and two are more limited geographically (*L. pruinosa*, *L. bewickensis*). *Leptastrea* has often been confused with *Montastrea* to which it is closely related as stated by Wells in 1956. However, once we know the variation within the different species, the genus is easy to recognize. In modern coral literature, therefore, there is little confusion.

The genus *Echinopora* was already recognized by Lamarck in 1816, but because the variability in growth forms within the genus and species is so great, several generic names have been used later on, such as *Explanaria* (Ehrenberg, 1834), *Echinastrea* (de Blainville, 1830), *Stephanocora* (Ehrenberg, 1834), *Acanthopora* (Verrill, 1864) and *Acanthelia* (Wells, 1937). In the first part of the study of the Montastreinae (Wijsman-Best, 1977: 92) I described *Montastrea forskaelana* from the Red Sea. After a detailed field study I came to the conclusion that one is dealing here with a *Echinopora* species the range of variability of which overlaps with that of a *Montastrea*. Six *Echinopora* species are recognized in the present study; more than twenty five species names are known. Most of them were already synonymized in the extensive study by Matthai (1914).

The genus *Diploastrea* was recognized by Matthai in 1914. Up to that moment the only and easy to recognize species of this genus had been placed in *Astrea* by Lamarck, in *Heliastraea* by Milne Edwards & Haime, and in *Orbicella* by Gardiner. No authors after Matthai changed or doubted the genus *Diploastrea*. The only living species is *D. heliopora* (Lamarck, 1816), and it occurs throughout the Indo-Pacific.

GENERAL TAXONOMY

As stated in the first part of the present study I do hold on to view that the two subfamilies Faviinae and Montastreinae are separate (in contrast to the view as given in Veron, Pichon & Wijsman-Best, 1977), although admittedly the distinction appears to be artificial. The Montastreinae consist only of genera the species of which reproduce asexually, mainly by extratentacular budding. In Wijsman-Best (1977) four species of *Montastrea* were described one of which in this paper is replaced in the genus *Echinopora*. One species only is known of *Plesiastrea*.

Montastrea is known from the Jurassic or Cretaceous. During the cenozoic the genus had an Atlantic and Indo-Pacific distribution. The five species living at the present time are rather well defined, the Atlantic being very different from those of the Indo-Pacific. *Plesiastrea* is known from the Eocene of Indonesia. During the Miocene the genus had a Tethys distribution. According to Chevalier (1971) the genus is extinct in Europe and the Atlantic since the Pliocene. It is suggested here that the so called genus *Solenastrea* is the Atlantic *Plesiastrea*, but this still has to be substantiated. The seventeen species dealt with in this paper all show intraspecific variability to a greater or less degree due to the adaptational potential (plasticity) of each colony with regard to the ecological conditions.

Because this study is based on collections from many places throughout the Indo-Pacific not only intra- or interpopulational variation will be discussed but also the geographical variation. This varies significantly among the different species discussed. Mostly the ranges of variation of the different geographical areas fall within the interpopulational variation ranges. This is directly connected with the stage in the speciation process the species have reached.

According to the New Systematics, the species "consists of a group of populations which replace each other geographically or ecologically and of which the neighbouring ones intergrade or interbreed whenever they are in contact or which are potentially capable of doing so" (Mayr 1963: 120). I shall return to this polytypic species concept in the general discussion (p. 260).

Of the genera treated here *Diploastrea* is known from the Cretaceous of the whole Atlantic and Indo-Pacific area (Tethys distribution). The only recent species, *D. heliopora*, is present throughout the Indo-Pacific and is very homogeneous as far as variation is concerned. The species is extinct in the Caribbean region. It has not been found in Miocene reefs (Frost, 1977).

The much younger genus *Cyphastrea* is not mentioned by Frost (1977) as a fossil in the American region but has possibly been mixed up with the

genus *Solenastrea*. It is rare in the Caribbean region at the present time as already stated above. It is concluded here that five Indo-Pacific species are known three of which occur throughout the Indo-Pacific, while two have a more limited geographical distribution. Especially *C. serailia* shows a great amount of geographical variation, the reason of much confusion in the literature, a possible result of its still being in the full speciation process. The species of the Atlantic genus *Solenastrea*, *S. bournoni* and *S. hyades* as discussed by Frost, range from the beginning of the Miocene up to the Recent and will have to be examined taxonomically and ecologically before we shall know whether we are dealing here with *Plesiastrea* or with a distinct genus (vide Chevalier, 1975: 9). The two genera *Echinopora* and *Leptastrea* both are known only from the Indo-Pacific region *Leptastrea* from the Oligocene and *Echinopora* from the Miocene onwards. Of the six species belonging to *Leptastrea* three have an Indo-Pacific distribution. In these (*L. purpurea*, *L. transversa*, *L. bottae*) the geographical variation extends beyond the inter-population variation and therefore they may be regarded as dynamically evolving species. In this case one may consider the use of subspecies. *L. pruinosa* and *L. bewickensis* are known only from the Western Pacific, but this may be due to lack of data. Of the six species belonging to *Echinopora*, two have an Indo-Pacific distribution (*E. lamellosa*, *E. hirsutissima*); two occur only in the West Indian Ocean (*E. gemmacea*, *E. forskaliana*), one is found only in the N.W. Pacific (*E. mammiformis*), and one (*E. horrida*) only in the Pacific. The hypothesis as discussed in Veron, Pichon & Wijsman-Best (1977), viz., that the two species of *Echinopora* involved (*E. lamellosa*, *E. hirsutissima*) are more distinct in the Indian Ocean than in the S.W. Pacific but display each a much greater intraspecific variability, will be dealt with again in the general discussion section of the present paper.

General diagnosis of *Cyphastrea* Milne Edwards & Haime, 1848. — The colony is massive, encrusting or branching; the growth form is plocoid. The corallites have a diameter ranging from 1-5 mm. The costae rarely extend over the coenosteum the surface of which is spinose (the main characteristic in which the genus may be distinguished from the other Montastreinae). The septal and thecal formation varies in each species.

General diagnosis of *Leptastrea* Milne Edwards & Haime, 1848. — The colony is massive or encrusting; the growth form is sub-ceriod to ceriod. The corallites have a diameter ranging from 2-15 mm. The septal arrangement and dentation vary in the different species. The costae are hardly developed. In case any coenosteum is present, it is dense.

General diagnosis of *Echinopora* Lamarck, 1816. — The colony is sub-

massive to foliaceous or ramose; the growth form is plocoid. The corallites have a diameter ranging from 3-6 mm. The coenosteum is dense or vesicular, the costae are reduced to spines or are absent.

General diagnosis of *Diploastrea* Matthai, 1914. — The colony is massive; the growth form is plocoid. Only one Indo-Pacific species is known, which shows little intraspecific variation. The calices are approximately 4 mm in diameter, the walls are septothecate. The septa are regular in form, giving a characteristic star-like appearance.

DESCRIPTION OF THE SPECIES

Cyphastrea serailia (Forskål, 1775) (pl. I figs. 1, 2)

Madrepora serailia Forskål, 1775; lectotype UZMC no. 4 (coll. Forskål).

Solenastrea hemprichiana Milne Edwards & Haime, 1890; MNHN.

Solenastrea gibbosa Milne Edwards & Haime, 1890; MNHN.

Solenastrea forskaeliana Milne Edwards & Haime, 1890; MNHN.

Solenastrea sarcinula Milne Edwards & Haime, 1890; MNHN.

Cyphastrea bruggemanni Quelch, 1886; BMNH no. 86.12.9.155.

Cyphastrea suwadivae Gardiner, 1904; BMNH no. 1927.5.4.33.

Cyphastrea conferta Nemenzo 1959; ? Philippines.

Material: 60 colonies. RMNH: Indonesia: Coel. 9188, 9189, 9303, 12803, 12806, Bay of Jakarta; Coel. 12801, Poeloe Toesa; Coel. 12802, 12804, Paternoster Isl.; Coel. 12805, Kelapa. Australia: Coel. 12186, Bushy Isl.; Coel. 12188, 12685, Lizard Isl.; Coel. 12692, 12693, 12694, 12696, 12697, 12698, Great Barrier Reef; Coel. 12699, Heron Isl. New Caledonia: Coel. 12654, Baie de Prony; Coel. 12656, Récif Ricaudy; Coel. 12657 (2x), 12700, Banc Gail. Marshall Isl.: Coel. 12798, 12810, 12811, 12812, Enewetak. Thailand: Coel. 12807, 12808, 12809, Phuket. Red Sea: Coel. 12688, 12690, Gulf of Aqaba; Coel. 12689, Mukebla. Coel. 12800, la Réunion. Coel. 12799, Seychelles.

ITZ: New Caledonia: Coel. 6081, 6091, Baie Uméo; Coel. 6107, Ile Nou; Coel. 6090, 6106, Magenta; Coel. 6097, Banc Gail, Coel. 6079, Baie Prony; Coel. 6092, 6093, 6094, 6096, Forêt Snark; Coel. 6084, 6088, 6089, 6101, 6103, Récif Ricaudy; Coel. 6078, Ile Maître; Coel. 6086, Baie Dumbea; Coel. 6100, Tabu; Coel. 6104, Passe Bulari. Indonesia: Coel. 6479, Haingsisi; Coel. 6478, Timor; Coel. 6475, Rotti Isl., Coel. 6479, Saleyer.

Specimens in other collections: Phuket, Western Thailand, collection H. Ditlev. Gulf of Aqaba, collection Y. Loya. Red Sea, collection H. Schuhmacher.

Characters. — Corallum. This species mostly forms massive to submassive colonies. The corallites are rounded, with a diameter of about 2,5 mm, the theca is very variable in height, probably due to environmental factors, because it differs only slightly intracolony. The most characteristic feature is the septal formation; there are two cycles of 12 septa. The first and second order septa are equally developed, and have a granulated surface, reaching up to the columella and often ending in a paliform rod. The columella is small and trabecular. The costae are thin and continue over the coenosteum. The coenosteum is often composed of disseptimental blisters; it is always covered

with exothecal spines. The species is common in all reef biotopes and it shows a considerable range of variation.

Polyp. The colour of the living tissue is ranging from pale to dark brown depending on light intensities.

Variability. — Looking at the variability of the species interpopulationally, we arrived at recognizing four ecomorphs (see Veron, Pichon & Wijsman-Best, 1977: 172). In view of the geographical variation as treated in this paper the collection can be divided into the same categories:

1. Ecomorph *hemprichiana* from exposed biotopes. In the Red Sea this form is described as a valid species and already regarded as a possible synonym in Veron, Pichon & Wijsman-Best. Fieldstudy in 1978 in the Gulf of Aqaba showed indeed that *hemprichiana* is only a form restricted to exposed biotopes.

2. The form as described from sub-temperate zones (Solitary islands) is the more normal form in the Red Sea from deeper water. Also in the series upon which the present data are based this form does not differ much from the ones found in tropical regions.

3. Ecomorph *suvadivae* is an extreme adaptation of this species to dark biotopes. In New Caledonia this form is common in the bay biotopes and agrees completely with the general trend of variation as found in other plocoid Faviidae. The coenosteum becomes blistered, the corallites are far apart, the amount of skeleton formation (viz., number of septa, thickness of thecae etc.) decreases and the polyp becomes more developed to be able to clean itself from sedimentation.

4. A more or less intermediate form is the most common one, showing clearly the skeleton features, but with rather widely separated corallites. A large collection, all from the environment of Phuket (W. Thailand) shows this ecomorph.

Discussion. — The type series of this species, present in the Zoological museum in Copenhagen, consists of six coralla No. 4 has been chosen as lectotype. It represents the last growth form as discussed above, and comes from the Red Sea. *C. hemprichiana* is regarded here as a synonym of *C. serailia*; the other changes as discussed in Veron, Pichon & Wijsman-Best (1977) especially in view of the treatment by Chevalier (1975) are accepted. *Cyphastrea serailia* is probably the most common Indo-Pacific *Cyphastrea* species. Because it is an extremely adaptable one it occurs in all biotopes and on the different reefs. This may be the reason why the intra-population variation hardly exceeds the geographical variation. It is true that the species is more abundant in the Pacific than in the Indian ocean.

Distribution. — Widely distributed from the Red Sea, West Indian Ocean,

Thailand and in the Pacific as far east as the Marshall Islands. Also from the Solitary Islands, Philippine Islands up to the Japanese archipelago.

Cyphastrea chalcidicum (Forskål, 1775) (pl. I fig. 3)

Madrepora chalcidicum Forskål, 1775; neotype BMNH no. 19.78.1.1.4.

Cyphastrea capitata Studer, 1878; ZMB lost.

Material: 36 colonies. RMNH: Indonesia: Coel. 9186, Togian Isl.; Coel. 12776, Tanah Djampea; Coel. 12777 (2x), Kera, Timor; Coel. 12778, Bay of Jakarta. Australia: Coel. 12766, 12773, 12774, Heron Isl.; Coel. 12185, Swain Reefs; Coel. 12187, Bushy Isl. New Caledonia: Coel. 12775, Baie de Prony; Coel. 12767, 12770, 12771, Passe Dumbea; Coel. 12768, 12769, New Caledonia. Marshall Isl.: Coel. 12779, 12780, Enewetak. Thailand: Coel. 12781, Phuket. Coel. 12783 Mauritius. Coel. 12782, 12784, St. Gille, la Réunion. Red Sea: Coel. 12785 (4x), 12786, 12787, 12788, Gulf of Aqaba.

ITZ: New Caledonia: Coel. 6082, Snark; Coel. 6080, 6087, 6109, 7902, Baie Dumbea; Coel. 7901, Baie de Prony.

Specimens in other collections: Phuket, Western Thailand, collection H. Ditlev. Gulf of Elat, collection Y. Loya. Réunion, collection G. Faure.

Characters. — Corallum. The species mostly forms massive colonies, they are sometimes encrusting. The large corallites, which are often protuberant, are characteristic for this species. Well-developed costae that give the corallite a "star-like" appearance are often present. There are twelve septa of the first order, which are mostly exsert. The second order septa are less developed and do not reach the columella. All septa and costae are dentate and granulated. Paliform lobes are hardly present or can be distinguished from the long dentations near the columella. The columella itself is not well-developed and consists of a few trabeculae.

Polyp. The colour of the living tissue is extremely variable, intra-populationally as well as geographically. In general we find beige to dark brown with grey or green pigmentation.

Variability. — The species is less abundant than *C. serailia*, especially in the Pacific region and more restricted to certain biotopes. It does not occur in very exposed areas and it does not adapt easily to sedimentation. As a result the species does not show a great range of variation, but within its limits the same as found in other plocoid Faviidae. In the Red Sea *C. chalcidicum* is common and easily to be distinguished under water from the other two, *C. serailia* and *C. microphthalma*, with which it is so often confused in the literature and collections which are based on material collected at random.

Discussion. The type species having been reported lost by Matthai in 1914, a neotype has been designated (BMNH Coel. no. 1978.1.1.4) and figured in Veron, Pichon & Wijsman-Best (1977: fig. 347). Chevalier (1975) regards this species as a synonym of *C. serailia* with which I do not agree.

Especially in the W. Indian Ocean there two species are very distinct and easy to separate from each other. Veron, Pichon & Wijisman-Best (1977) discussed the possibility of synonymizing *C. ocellina* (Dana) with *C. chalcidicum*. It may be true that the specimen described by Nemenzo in 1959 from the Philippines as a *C. ocellina* is a *C. chalcidicum*, but in this geographically unlimited study I came to the conclusion that *C. ocellina* is a valid species with a Northern Pacific distribution.

Distribution. — Throughout the Indo-Pacific from the Red Sea to the Marshall Isl., but more abundant in the Red Sea and Western Indian Ocean than in the Pacific.

Cyphastrea micropthalma (Lamarck, 1816) (pl. I fig. 4)

Astrea micropthalma Lamarck, 1816; holotype MNHN.

Cyphastrea savigny, Milne Edwards & Haime, 1851; MNHN.

Cyphastrea muellere Milne Edwards & Haime, 1851; BMNH no. 86.12.9.151.

Cyphastrea aspera Quelch, 1886; BMNH no. 86.12.9.154.

Cyphastrea gardineri Matthai, 1914; BMNH no. 1927.5.4.151.

Material: 60 colonies. RMNH: Indonesia: Coel. 12745, 12747, 12748, 12752, 12753, Bay of Jakarta; Coel. 12746, 12747, Binongko, Toekang Besi; Coel. 12744, 12750, Kera, Timor; Coel. 12751, Poeloe Toesa, Obi Latoe; Coel. 12755 Karaton, Nenoesa Isl.; Coel. 10781, 12754, Makassar; Coel. 9190-9195, Togian Isalnds; Coel. 12757 (8x), Beo, Talaud Isl.; Coel. 12756 (8x), Ake Selaka, Halmahera; Coel. 10762, Ambon. Australia: Coel. 12739, 12740, 12741, Heron Island; Coel. 12189, Pompey complex. New Caledonia: Coel. 10720, Forêt Snark; Coel. 12742, Baie de Prony; Coel. 12743, Baie de Dumbea. Marshall Isl.: Coel. 12759, 12759, 12760, Enewetak. Thailand: Coel. 12761, 12762, Phuket, Coel. 9187. Red Sea: Coel. 12763, 12764, Gulf of Elat. Coel. 12765, Mauritius. ITZ: New Caledonia: Coel. 6083, 6102, Baie de Pronny; Coel. 6108, Récif Ricaudy; Coel. 6077, 6085, 6098, 6105, Forêt Snark; Coel. 6095, Ile de l'Arrenière; Coel. 6099, Baie Uémo.

Specimens in other collections: Phuket, Western Thailand, collection H. Ditlev. Gulf of Elat, collection Y. Loya. Reunion, collection G. Faure.

Characters. — Corallum. The colony is mostly encrusting but also sub-massive; rounded colonies often are bulbous. The corallites are small, with a diameter of 1-2 mm. The most characteristic skeleton feature is the septal arrangement. The first order septa nearly always number ten, which are equal in size, are regularly granulated and leads up to the columella. Paliform lobes are usually present, forming a crown around the small columella. The second order septa are smaller; both cycli of septa are hardly exsert. In some corallites, however, especially in parts of the colony that are not very well illuminated, the first order septa can be very exsert. Costae are present bearing elongated spines and granulations that continue on the coenosteum.

Polyp. The colour of the living tissue is variable, ranging from pale brown to dark brown or green.

Variability. — *Cyphastrea microphthalmia* is a widely spread species; it does occur in all biotopes from very shallow ones where hardly any coral growth is present down to deeper water biotopes and in muddy environments. The skeleton characters of the corallites remain unusually stable. As for the range of variation in the colony the same trend is found as described for *C. serailia* and found in other plocoid Faviidae. When growing up in optimal conditions the colonies are massive and the corallites closely packed and well built; when conditions are less good especially when light diminishes the corals become thin and flat, the corallites shallow and far apart. The skeleton elements are minimally developed in that case.

Discussion. — The type-specimen of this species is a large colony present in the Lamarck collection in Paris, and comes from Australia. It is a typical specimen from a shallow reef facies, and shows the specific characters very well. *Cyphastrea savignyi* and *C. mulleri* both described by Milne Edwards & Haime were already recognized as synonyms by Matthai in 1914. The first one is a specimen present in Paris and comes from the Red Sea. The other one is not found in Paris, but it is possible that the specimen in London, (n° 47.I.I.8) is the type *Cyphastrea aspera* described by Quelch and comes from the New Hebrides. The only synonym of this species that has given trouble in the literature is the one described by Matthai (1914: 48) as *C. gardeneri*. It comes from the Red Sea and after by field study in the Gulf of Aqaba I came to the conclusion that we are dealing here with a growth form of an exposed reef facies as found in the Red Sea. Especially the deeper calices and heavier dentation make this growth form rather atypical — that explains why we still had our doubts about the synonym of this species in Veron, Pichon & Wijnsman-Best (1977).

Distribution. — Widely distributed from the Red Sea to the Hawaiian Islands. It is not so common in the Red Sea, and neither in the Mascarenes or Seychelles, but it is common in Thailand and Coral sea area.

***Cyphastrea japonica* Yabe & Sugiyama, 1932 (pl. 1 fig. 5)**

Cyphastrea japonica Yabe & Sugiyama; holotype TIU, Japan.

Material. 2 colonies. RMNH Australia: Coel. 12784, Palm Isl. Great Barrier Reef; Coel. 12790, Northern Great Barrier Reef.

Specimens in other collections: Australia G.B.R. collection Veron.

Characters. — Corallum. The species forms fructicose colonies, very unlike other *Cyphastrea*. There are axial corallites that can extend up to 8 mm beyond the secondary lateral corallites. The calices are small with an average diameter of 22 mm. The septa are arranged in two major cycles and one that is not always developed. The six primary septa are thicker and more

exsert than the other; pali are not well developed; the columella consists of small styliform rods. The most striking feature apart from the branching growth form are the heavily granulated costae. Also the coenosteum is ornamented with perithecal spines.

Polyp. The colour of the living tissue is dull green or brown, the axial corallites are much paler.

Variability. — The series of specimens known and examined of this species all are found in the Great Barrier Reef. Apart from the type locality (Misahi, Japan) the species has not been found elsewhere. Therefore the intraspecific variability is probably much larger than as described by Veron, Pichon & Wijsman-Best (1977: 179). More collecting and field work has to be done before one can say more about the pliability and adaptation possibility of this species. So far we can only say that the species forms encrusting colonies, supporting short branches that anastomose with each other, of which the type specimen is a good example.

Discussion. — The type specimen in Japan has not been examined but good photographs (Yabe & Sugiyama, 1932 pl. XVII 4-6) and the small collection of the G.B.R. show the species to be a valid one, and not, as often stated, a mere growth form of an allied species. Yabe (1932: 25) mentions that the species approached *Cyphastrea ocellina* Dana. They are certainly not synonyms, this conclusion was made after more material was collected and studied of the latter, this will be dealt with in the discussion of *C. ocellina*.

Distribution. — At the present time only known from Japan and the Great Barrier Reef. It is certainly not present in New Caledonia or eastwards in the Pacific, but it is likely that it will be found one day in the Indonesian archipelago.

Cyphastrea ocellina (Dana, 1846) (pl. I fig. 6)

Astrea Orbicella ocellina Dana, 1846; holotype lost, neotypes BBM SC 662, RMNH Coel. 12791.

Material: 11 colonies. RMNH: Indonesia: Coel. 9196, Togian Isl.; Coel. 10788, Ujung Pandang. Marshall Islands: Coel. 12792, 12793, 12794, 12795, 12796, 12797, Enewetak. Hawaii: Coel. 12691, 12786, 12791, Ohao Isl.

Characters. — The corallum is massive or encrusting, older colonies often become lobed and glomerate. The corallites are small, with a diameter of 1-2 mm. The septal structure is the most characteristic feature of the species. The six septa of the first cycle are in general exsert and irregularly granulated, then are thin and fall steeply down into the fossa; the six septa of the second cycle are of the same structure but always lower and smaller in size. A third cycle is present but not always completed. The species resembles

C. microphthalmalma at first sight (as already remarked by Dana in his original description) but the two exsert unequal major septa constitutes the most remarkable difference from *C. microphthalmalma* that has only ten first order septa. Paliform lobes are small or absent; they can hardly be distinguished from the septal trabeculae that form the columella. The columella is moderately developed and always granulated. Costae are rarely present, only some irregularly placed granulations on the smooth or blistered coenosteum.

Polyp. The colour of the living tissue is pale to darker pinkish brown.

Variability. — The species has at the present day only been found in the Northern Pacific, and the variability seen within the series is not very great. It does not extend the interpopulational variability of the species as found in Enewetak at various habitats. The size of the corallites, the thickness of the thecal and especially the development of the various skeleton elements are different as seen in so many species of this family, as a result of the various ecological circumstances.

Discussion. — The type specimen of this species is lost, and therefore a neotype is indicated and chosen from the type locality. This specimen agrees completely with the description of Dana, Milne Edwards & Haime recognized the species as a valid one and placed it in the genus *Cyphastrea* with doubt. Verrill (1866) and Studer (1900) mention the species from Hawaii. Vaughan (1907: 103) saw the species extensively from the collections in Washington D.C. and Yale (New Heaven) all from the Hawaiian Islands. Lately the species is often regarded as a possible synonym of *C. serailia* (viz., Chevalier 1975: 18) or *C. chalcidicum* (viz., Veron, Pichon & Wijsman-Best 1977: 173), but *C. ocellina* does not occur in the Southern Pacific.

Distribution. — This species has only been found in Celebes, Enewetak and the Hawaiian Islands, but it is likely that it has a wider distribution. Much field work in New Caledonia and the Great Barrier reef has so far failed to provide evidence as to its occurrence in this area.

Leptastrea bottae (Milne Edwards & Haime, 1849) (pl. 2 figs. 3-6)

Cyphastrea bottae Milne Edwards & Haime, 1849; holotype MNHN.

Baryastrea solida Milne Edwards & Haime, 1850; MNHN lost.

Leptastrea inaequalis Klunzinger, 1879; ZMB.

Lepastrea agassizi Vaughan, 1907; USNM no. 21633.

Lepastrea hawaiiensis Vaughan, 1907; USNM no. 61632.

Material: 13 colonies. RMNH: Australia: Coel. 12194, Lizard Isl.; Coel. 12195, Great Detached Reef; Coel. 12732, Heron Isl. New Caledonia: Coel. 12730, 12731, Nouméa. Red Sea: Coel. 12672, 12673, 12680, 12687, Gulf of Aqaba. Mascarenes: Coel. 12733, Réunion.

ITZ: New Caledonia: Coel. 6198, Fausse Passe; Coel. 6199, 6200, Tabu.

Specimens in other collections: Réunion, Mauritius, collection G. Faure. Gulf of Aqaba, collection H. Schuhmacher. Hawaiian Isl., collection Bishop Museum Honolulu.

Characters. — The corallum is massive, forming flat encrusting or rounded colonies. The growthform is plocoid. The corallites in general are small and equal in size (about 3 mm in diameters) but in some places they are pressed together and much smaller; a single giant calyx is not rare. This species is different from other *Leptastrea* species because of the thick or thickened thecae, which gives the appearance of protuberant calices. The primary cycle of septa is more developed and more exsert than the other ones. Two smaller cycles of septa are present. Paliform lobes before the first two cycles of septa fuse with the small trabecular columella, forming a rounded columellar structure. In many populations the intercalicular groove described by Rosen as “groove and tubercle” structure is present; in others, however, it lacks completely, so it is not a specific character as it often has been accepted, nor of pathologic origin (see Randall, 1971).

Polyp. The living tissue of this so easily recognisable species is pale to darker brown, depending on the amount of light the polyp receives, so it differs strikingly within one colony as well between different populations.

Variability. — *Leptastrea bottae* is widely distributed in the Indo-Pacific, from the Red Sea to the Hawaiian Islands. Although the interpopulational variation is great, the whole geographical variation does not extend this range of variation within the species, the closely situated areas do overlap in intra-specific variation only populations from widely separated areas vary significantly. It is probably a local factor that influences the variable thickness of the theca wall and the intercalicular ridges that gives the species such a characteristic appearance. Further study on the origin and effectiveness of these commensal organisms is necessary before any further conclusions are warranted.

Discussion. — In the collection in Paris there are two type specimens of *Leptastrea bottae* from the Red Sea, the smaller one (see Veron, Pichon & Wijsman-Best, 1977 figs. 298-299) however is the closely allied species *Leptastrea transversa* Klunzinger. The larger colony (see pl. 2 fig. 4) represents well *Leptastrea bottae* without the groove and holes. The main difference between these closely allied species is the septal arrangement: *L. bottae* has a distinct first cycle of septa whereas *L. transversa* has almost equally developed first and second cycles of septa. In the fieldwork carried out in the Gulf of Aqaba *L. bottae* of the type locality could be examined and the problem around the type series (viz., Vaughan 1918: 94 and Veron, Pichon & Wijsman-Best 1977: 155) could be solved. The two species are still mixed up in several collections examined. *L. solida* has been recognized by Matthai (1914) as a synonym. Now that the validity of the name “*bottae*” has been restored, *solida* can be regarded as more synonym. *L. inaequalis* is a

good specimen of *L. bottae* showing the grooves around the calices clearly. *L. hawaiiensis* and *L. agassiz* both of Vaughan and from the Hawaiian Isl. show extreme forms very irregular and more plocoid than those of the type locality but still falling within the range of variation as known in the other parts in the Indo-Pacific.

Distribution. — The species is present throughout the Indo-Pacific from the Red Sea to the Hawaiian Islands. It occurs in all biotopes of the different reef types, but is never common. It is remarkable that there are no records of this species from Indonesia or Japan; it certainly is not present in the Marshall Islands.

***Leptastrea purpurea* (Dana, 1846) (pl. 3 figs. 1, 2)**

Astrea purpurea Dana, 1846; holotype USNM no. 75.

Astrea pulchra Dana, 1846; USNM. no. 74.

Leptastrea ehrenbergiana Milne Edwards & Haime, 1850; MNHN.

Leptastrea stellulata Verrill, 1867; YPM lost.

Orbicella klunzingeri Gardiner, 1899; BMNH lost.

Favia hawaiiensis Vaughan, 1907; USNM no. 21635.

Material: 29 colonies. RMNH: Indonesia: Coel. 10755, Ujung Pandang; Coel. 9331, 9768 Bay of Jakarta; Coel. 12701, Kera, Timor; Coel. 12702, Beo, Talaud Isl. Australia: Coel. 12191, Whitsundays; Coel. 12710-12712, Heron Isl.; Coel. 12713, Hayman Isl. New Caledonia: Coel. 6202, 6205, 6213, 6214, Récif Ricaudy; Coel. 6204, Ile Nou; Coel. 6209, 6210, Baie de Citron. Marshall Isl.: Coel. 62703-62708, Enewetak. Thailand: Coel. 12709, Phuket. Red Sea: Coel. 12675, 12676, 12684, 12685, 12686, Gulf of Aqaba.

ITZ: New Caledonia: Coel. 6202, 6205, 6213, 6214, Récif Ricaudy; Coel. 6204, Ile Nou; Coel. 6209, 6210, Baie de Citron.

Specimens in other collections: Phuket, Western Thailand, collection H. Ditlev. Gulf of Aqaba, collection Y. Loya, H. Schuhmacher. Mascarenes, collection G. Faure.

Characters. — Corallum. The colony is encrusting or massive, the growth form is cerioid to subcerioid. The diameters of the calices are characteristically variable in size (2-11 mm). The primary septa are well developed and irregular. Lower cycles of septa often fuse with the higher ones. In general the fossa is clear and there is hardly any development of paliform lobes; when the fossa is shallow the paliform lobes are more distinct. The columella consists of a few twisted trabecular pinnacles, the dentation in general is fine.

Polyp. The color of the living tissue is pale to darker brown, depending on the part of the colony.

Variability. — As discussed in Veron, Pichon & Wijsman-Best (1977) this widespread species is extremely variable intracolony as well as interpopulationally. Comparing the intrapopulation variation within the whole geographical area of the species, there is little difference. This is not the case in the closely allied species *L. transversa*, with which the present species is often confused. According to the general trend for the growth form

in relation to ecological conditions in the Faviidae, this species shows well-developed, rounded colonies in well-illuminated sites; when the specimen grows in darker water the colony is flatter, the growthform is more plocoid.

Discussion. — The type of *L. purpurea* is from the Fiji Islands and a representable species. Because the range of variation within the species is so great, many nominal species names are known in literature that by now are recognized as synonyms. *L. pulchra* also comes from the type locality; it differs only slightly, *L. stellulata* Verrill and *L. hawaiiensis* (Vaughan) both come from the Hawaiian Islands. In 1918 Vaughan gave an extensive discussion on the variability of *L. purpurea* and synonymizes *L. hawaiiensis*.

Distribution. — *L. purpurea* is a widespread species throughout the Indo-Pacific. In the Coral sea area it is by far the most common *Leptastrea*. More westwards in the Indian Ocean it becomes less abundant, in the Red Sea the species is rather rare and is dominated by *L. transversa*.

***Leptastrea transversa* Klunzinger, 1897 (pl. 3 figs. 3, 4)**

Leptastrea transversa Klunzinger, 1879; holotype ZMB.

Leptastrea immersa Klunzinger, 1879; ZMB.

Leptastrea roissyana Edwards & Haime, 1850; MNHN.

Material: 29 colonies. RMNH: Australia: Coel. 12190, Swain Reefs, Great Barrier Reef, Coel. 12714, Palu Isl., Great Barrier Reef, Coel. 12715, Lizard Isl., Great Barrier Reef, Marshall Isl.: Coel. 12718-12728, Enewetak. W. Thailand: Coel. 12729, Phuket. Red Sea: Coel. 12674, 12677, 12678, 12679, 12681, 12683, Gulf of Aqaba. Mascarenes: Coel. 12716, Mauritius; Coel. 12717, Cap Homard; Réunion, Coel. 12240; St. Gilles, Réunion.

ITZ: New Caledonia: Coel. 6203, 6207, 6216, Récif Ricaudy; Coel. 6206, Fausse Passe, Coel. 6211, Baie Prony.

Specimens in other collections: W. Thailand, Phuket, collection H. Ditlev. Mascarenes, collection G. Faure. Gulf of Aqaba, Red Sea, collection Y. Loya.

Characters. — Corallum. The colony is massive or encrusting. The corallites are normally rounded, giving the appearance of a plocoid growthform. When the thecae are thinner the calices are polygonal and therefore the growth form becomes more subcerioid. The first two cycles of septa are equally developed and regularly dentated; this is the best characteristic by which it distinguishes itself from *L. purpurea*. The secondary cycle is much smaller, often ending in a well developed paliform lobe. The columella consists of a few trabeculae that are often fused forming a small elongated rod. This is clearly seen in the type of Klunzinger from the Red Sea, but in other areas it is not always so clear.

Polyp. The colour of the living tissue, that is light green or yellow, makes it easy to separate the species under water from *L. purpurea*.

Variability. — The species is widely distributed, but most common in the

W. Indian Ocean. In the Red Sea (the type locality) *L. transversa* is the most common *Leptastrea*; in the literature and collections it is often mixed up with *L. bottae*. Only after an extensive field study in the Gulf of Aqaba it was possible to solve the confusion of the three *Leptastrea* species. The results have already been explained under *L. purpurea*. In the Coral Sea area *L. bottae* and *L. transversa* often loses its plocoid appearance and comes close to *L. purpurea*. This explains the confusion in literature about these two species *L. transversa* however is definitely a valid species with a different geographical distribution than *L. purpurea*.

Discussion. — The type of this species is a typical example of the subcerioid growthform from the Red Sea. *L. immersa* of Klunzinger represents the more plocoid growthform that resembles *L. bottae*. These two forms can be seen as ecomorphs, *transversa* ecomorph from deeper and calmer water, *immersa* ecomorph from shallower, more turbid water. However, the distinction is not always very clear, so more ecological detailed study has to be carried out before we can say more about the factors influencing these growthforms. The type of *L. roissyana* is from an locality but falls within the intraspecific variation of *L. transversa*. In Veron, Pichon & Wijsman-Best (1977: 158) it is regarded as a synonym of *L. purpurea*, but at that time the whole range of variation of these three closely allied species was not yet known.

Distribution. — From the Red Sea to the Pacific as far East as the Marshall Isl. More common in the Western Indian Ocean, becoming more rare in the Pacific.

***Leptastrea pruinosa* Crossland, 1954 (pl. 2 fig. 1)**

Leptastrea pruinosa Crossland, 1954; holotype BMNH no. 1934.5.14.630.

Material: 13 colonies. RMNH: Indonesia: Coel. 12734, Thousand Isl.; Coel. 6949, Togian Isl., Celebes; Coel. 10770, Makai Isl., Spermonde Reef, Celebes. Australia: Coel. 12192, 12193, Lizard Isl., Great Barrier Reef; Coel. 12735, Palu Isl., Great Barrier Reef. New Caledonia: Coel. 12736, 12737, Nouméa. Marshall Isl.: Coel. 12726, 12738, Enewetak. ITZ: New Caledonia: Coel. 6212, 6215, 6218, Tabu; Coel. 6208, Baie Dumbea.

Characters. — The colonies of this species are in general small and encrusting. The corallites are small with an average diameter of 5 mm; they are often polygonal. The septa are numerous; the first two cycli are equal in length, not exsert and reach as far as the columella, sometimes ending in a small paliform rod. The third, fourth and occasionally fifth order of septa are shorter, all septa are strongly dentated and granulated. This last phenomenon is most characteristic for the species. The columella is small and trabecular. The skeleton features show a remarkable resemblance to *L.*

transversa, the dentated septa is the best character to use for separation of the two species. Under water, however, they are easily recognized, firstly because the polyps of the present species are often expanded during the day and secondly their polyps are very different in colour in comparison with those of the closely allied species *L. transversa* and *L. purpurea*.

Polyp. The colour of the living tissue is in general dark brown, the stomodaeum is green.

Variability. — The intraspecific variability is not great. Although the species is rather common in the Great Barrier Reef and New Caledonia it is rather rare in Museum collections. This is probably due to the fact that the colonies are in general small and difficult to collect.

Discussion. — The type of the present species is a small specimen collected by Crossland in the Great Barrier Reef and after long hesitation (according to the author himself) described as a new species. It is a good example of a species problem we often meet in reef corals. A genus with several intergrading species, where only a more detailed field and geographical study can prove whether we are dealing with one or more species.

Distribution. — The species does not have a wide distribution. It has only been found in the Indonesian archipelago, Great Barrier Reef and New Caledonia. It is certainly absent in the Red Sea and Western Indian Ocean, and also does not occur in the Marshall Island. That leaves the distribution rather restricted.

***Leptastrea bewickensis* Veron, Pichon & Wijsman-Best, 1977**

(pl. 2 fig. 2)

Leptastrea bewickensis Veron, Pichon & Wijsman-Best, 1977; holotype BMNH no. 1977.I.1.5.

Material: 1 colony. RMNH. Coel. 13327 Great Barrier Reef. Australia.

Specimens in other collections: Great Barrier Reef, collection Veron. BMNH London, Coel. 1963.12.11.5. van Tahiti.

Characters. — The colony is massive. The corallites are uniform in size, with an average diameter of 2.5 mm. The septa are arranged in three cycles, the primaries are exsert and distinctive. Very characteristic is the nearby absence of dentation. The secondary and tertiary septa are much less distinct. I refer to the original description for further details.

Polyp. The colour of the living tissue is pale brown and white.

Variability. — Not much can be said about the variability of this probably rare species because so little material is available. In the BMNH I studied a specimen collected by Crossland in Tahiti that belongs to the present species and is very similar to the ones found in the Great Barrier Reef.

Discussion. — *L. bewickensis* is a good example in modern coral systematics of recognizing a new species in the field. First the different species of the genus have to be known with their whole intraspecific variability and field characters; then new species may be established that before only were seen as variations of already described species.

Distribution. — The species is known from the Great Barrier Reef and more eastwards into the Pacific Ocean towards Tahiti. It has not as yet been recorded from other areas, which is probably only the result of not recognizing the species.

***Echinopora lamellosa* (Esper, 1797) (pl. 3 figs. 5, 6)**

Madrepora lamellosa Esper, 1797; holotype Hessisches Landesmuseum Darmstadt.

Echinopora rosularia Lamarck, 1816; MNHN.

Echinopora undulata Dana, 1846; USNM no. 126.

Echinopora reflexa Dana, 1846; USNM no. 164.

Echinopora flexuosa Verrill, 1864; YPM no. 1829.

Echinopora concinna Verrill, 1901; YPM no. 6182.

Echinopora elegans Verrill, 1901; YPM no. 6180.

Material: 42 colonies. RMNH: Indonesia: Coel. 9255, 9257, 9258, 9259, 9262, 9264, 12350 (2x), Ambon; Coel. 9247, 9260, 9263, Togian Isl., Celebes; Coel. 9304, 9311, 12352, 21357, Bay of Jakarta; Coel. 9254, Str. Sunda; Coel. 12348, 12353, Poeloe Toesa; Coel. 12349, Bone Tamboeng; Coel. 12351, Kera, Timor; Coel. 12354, Banda; Coel. 12355, 12356, Key Isl.; Coel. 12358, Talaud Isl. Australia: Coel. 12196, Tjouw reef; Coel. 12197, 12198, Palm Isl., Great Barrier Reef. New Caledonia: Coel. 12359, 12365, Nouméa. Marshall Isl.: Coel. 12366, 12367, 12368, Enewetak. W. Thailand: Coel. 12347, Phuket. Red Sea: Coel. 12665, 12666, Gulf of Aqaba. Seychelles: Coel. 12067, Mahé.

ITZ: Indonesia: Coel. 289, Bay of Jakarta; Coel. 293, 6449, Banda. New Caledonia: Coel. 6130, Passe Dumbéa; Coel. 6134, 6135, Foret Snark.

Specimens in other collections: Western Thailand. Phuket, collection H. Ditlev. Gulf of Aqaba. Red Sea, collection Y. Loya. Mascarenes, collection G. Faure. Red Sea and Ceylon, collection G. Scheer.

Characters. — Corallum. The colony is laminar, foliate, cyathyform, sometimes encrusting. The encrusting ones are in general thicker than the foliate ones. The corallites are small (3-5 mm diameter) and cylindrical. When the theca is hardly developed the primary septa are very exsert. A ring of paliform lobes in front of the first two cycles of septa and the generally well developed spines on the costae give the characteristic spiny appearance of the *Echinopora* species. The columella is well developed and spongy. The types of budding described from specimens collected by Boschma and Verwey in Indonesia were also observed in other parts of the Pacific (e.g. Great Barrier Reef). This "unusual manner of budding" (Boschma, 1928) gives rise to a second layer of calices (see pl. 3 fig. 6).

Polyp. The colour of the living tissue is uniform light to darker brown.

Variability. — Although intracolony large colonies can be very variable

in structure from thin foliate to thicker encrusting or highly funnel-shaped, the general structure of the corallites remains remarkably stable. This statement counts also intrapopulationally and zoogeographically. A specimen from the Red Sea is very much the same as one from Indonesia or the Marshall Islands. Probably the species is rather stenotypic — restricted to certain ecological conditions, viz., protected deeper water. As said a wide range of intraspecific variation can already be observed in one colony, this concerns mainly the development of septa and pali, the space in between corallites and the different granulation on the skeletal elements.

Discussion. — The type of Esper is well figured (Esper, 1797 pl. 58 figs. 1, 2). The specimen was present in Erlangen but has been transferred to the Hessisches Landes Museum in Darmstadt. All later synonyms from various localities: *E. rosularia* from the Seychelles, *E. undulata* from the Sulu Sea, *E. reflexa* from the Fiji Isl., *E. flexuosa* from Singapore and *E. concinna* from Palau Isl., have long been recognized as such. This is due to the fact that the species remains rather uniform throughout the Indo-Pacific.

Distribution. — As already mentioned *E. lamellosa* is a widely spread species in the whole Indo-Pacific. Nevertheless it is abundant in the Indo Australian region, relatively rare in the Western Indian Ocean and rare in The Red Sea.

***Echinopora gemmacea* (Lamarck, 1816) (pl. 4 figs. 1, 2)**

Explanaria gemmacea Lamarck, 1816; holotype MNHN.

Stephanocora hemprichii Ehrenberg, 1834; ZMB. lost.

Explanaria hemprichii Ehrenberg, 1834; ZMB lost.

Echinopora rousseaui Milne Edwards & Haime, 1849; MNHN lost.

Echinopora solidior Milne Edwards & Haime, 1849; MNHN lost.

Echinopora ehrenbergi Milne Edwards & Haime, 1849; MNHN.

Orbicella mammillosa Klunzinger, 1879; ZMB lost.

Echinopora fructiculosa Klunzinger, 1879; MNHN.

Echinopora carduus Klunzinger, 1879; MNHN.

Material: 17 colonies. RMNH: Red Sea: Coel. 9240, 9241, 9242, 9243, 9244, Red Sea (old collection); Coel. 12658, 12659, 12660, Gulf of Aqaba, Mascarenes: Coel. 12371, Rodriguez; Coel. 12370, 12371, 12372, 12373, Mauritius. Mozambique: Coel. 12100, Inhaca.

ITZ: Madagascar: Coel. 1699, 1717 Nosi Bé.

Specimens in other collections: Red Sea. Gulf of Aqaba, collection Y. Loya, collection H. Schuhmacher. Mascarenes, collection G. Faure. Great Barrier Reef, collection J. Veron.

Characters. — The species is most abundant in the Red Sea, where it occurs in either large plocoid colonies or sub-dendroid ones, or colonies showing both growth forms. The corallites are much larger than in the former species with an average diameter of 6 mm, they are in general protruding,

often only from one side according to the direction of the light. The three cycli of septa are well developed, of the first cycle they are very exsert, these lobes are often divided into two parts. The costal dentations are unequal and strongly developed. These strongly dentated costal ridges are characteristic for the species. Paliform lobes are poorly developed, the columella is large and spongy.

Polyp. The living tissue is from pale to darker brown, some colonies in the Red Sea are greyish brown (a striking contrast to the yellowish brown colour of *E. hirsutissima*, a closely allied species with which it has often been confused).

Variability. — As discussed in Chevalier (1975: 86) and Veron, Pichon & Wijsman-Best (1977: 191) the species is rare in the Western Pacific and eastern Indian Ocean and morphologically it comes close to *E. lamellosa* and *E. hirsutissima*. This is the reason why in many collections of this area these three species are mixed up. Intrapopulationally the intraspecific variation is not great, but on geographical level there are significant differences. Chevalier remarks that it is well possible that *E. gemmacea* is differently evaluated in the Pacific than in the Western Indian Ocean. It is true that in the Red Sea I did not have any trouble separating the three valid species. Mostly they show a fruticose growth, but sometimes the growth form is more plocoid. The skeleton features of the corallites remain remarkably stable. Another problem about *E. gemmacea* and its closely allied species is the relationship of *Orbicella mammillosa* Klunzinger and the present species. The field work carried out in the Gulf of Aqaba solved this problem. *O. mammillosa* is a later synonym of *Astrea forskaliana* Milne Edwards & Haime. *A. forskaliana* has by now correctly been recognized as a valid *Echinopora* species that occurs only in the Red Sea and nearby seen possibly up to the Mascarenes. *E. forskaliana* has never been recognized in literature apart from *O. mammillosa* by Klunzinger, later on called *Plesiastrea mammillosa* by Loya & Slobodkin (1971) and the doubtful recognition by myself of *Montastrea forskaelana* in part of the present coral studies. Veron, Pichon & Wijsman-Best (1977) concluded only that synonymy with *E. gemmacea* is a possibility. Further details of this confusing problem will be discussed under *E. forskaliana*.

Discussion. — The type locality of *E. gemmacea* is the Red Sea, and all other synonyms as mentioned above are from that area or Western Indian Ocean. They all fall within the range of intrapopulationally variation as known at the present time. It is not remarkable that in modern literature the species is rarely mentioned from Pacific localities, Umbgrove describes the species from Indonesia, Chevalier from New Caledonia and Veron, Pichon & Wijs-

man-Best from the Great Barrier Reef. Several specimens present in the collection in Leiden and other musea are identified as *E. gemmacea* but are either *E. lamellosa* or *E. hirsutissima*. It has never been recorded from the eastern part of the Indian Ocean.

Distribution. — Although the geographical distribution ranges from the Red Sea as far East as New Caledonia, it is abundant especially in the Red Sea and Western Indian Ocean.

Echinopora hirsutissima Milne Edwards & Haime, 1849 (pl. 4 figs. 3, 4)

Echinopora hirsutissima Edwards & Haime, 1849; holotype MNHN.

Echinopora helli Rousseau, 1854; MNHN.

Echinopora solidior Gardiner, 1904; BMNH lost.

Echinopora tertia Gardiner, 1904; BMNH lost.

Material: 18 colonies. RMNH: Indonesia: Coel. 9248, Ambon; Coel. 12374, Poeloe Toesa, Obi Latoe; Coel. 12427, 12428, Bay of Batavia. Australia, Great Barrier Reef: Coel. 12199, Swain reef; Coel. 12200, Tyou reef; Coel. 12201, Low Island. New Caledonia: Coel. 12429, 12430, Récif Ricaudy, Nouméa. W. Thailand: Coel. 12369, Ko Surion. Red Sea: Coel. 12661, 12663, 12664, Gulf of Aqaba; Coel. 9245, Red Sea.

ITZ: Mascarenes: Coel. 1872, Mauritius. New Caledonia: Coel. 6131, 6133, Récif Ricaudy; Coel. 6132, Baie de Prony.

Specimens in other collections: Western Thailand, collection H. Ditlev. Mascarenes, collection G. Faure.

Characters. — Corallum. The colony is laminar, explanate, very often rising up forming lobated masses. The corallites are round, the thecae are little developed. The septa are in three cycles, of which the primary one can be very distinctly developed. The granulation and dentation are well developed especially on the exsert septa and on the costae. The last two features give the species its characteristic spiny appearance. The columella consists of some trabeculae.

Polyp. The colour of the living tissue is light yellow brown.

Variability. — The species shows a great intraspecific variability, especially when looking at the geographical variation. The development of the primary septa and the rate of dentation is extremely variable. This is the reason why this species may easily be confused with closely allied species like *E. lamellosa* and *E. gemmacea*, Chevalier (1975: 86) discusses this extensively, formulating his doubts about the validity of this species in a hypothesis that the *Echinopora* species are less quickly developed evolutionary in the Pacific than in the Western Indian Ocean. Veron, Pichon & Wijsman-Best (1978: 193) also state that the differences between *E. lamellosa*, *E. hirsutissima* and *E. gemmacea* are less conspicuous in the Western Pacific than in the Indian Ocean.

A recent field study in the Red Sea (Gulf of Aqaba) carried out by myself

in 1978 showed clearly the distinction of the three species. The confusion in literature and collections are even more understandable in view of the two colony forms of *E. gemmacea* (plocoid and subdendroid) and by adding another closely allied species *E. forskaliana* to the group. The last one is the most abundant and easiest to recognize species with a limited geographical distribution to the Western Indian Ocean, but throughout the years always confused with the others (see under *E. forskaliana*). Although all four allied species show overlap in their characteristics, after a thorough fieldstudy one is able to separate them distinctly from each other in the Red Sea. It is true that the distinction is less clear in the Indonesian Archipelago and Australia. But I doubt whether this has anything to do with the tempo of evolution; it is more likely that the more distinct species are a result of the peripheral position of this area, so to isolation and the much less strong competition because the Red Sea reefs consist of approximately 40% of the coral species in the optimal coral reef area (Indonesia and the Coral Sea).

Discussion. — The type locality of the present species is unknown. *E. helli* is described from the Seychelles. Although the species shows a great intra-specific variability and is widely distributed in the Indo-Pacific there are only a few nominal species names available. This is the result of its being so often mixed up with closely allied species — and in literature and museum collection being described under wrong names.

Distribution. — Widely distributed from the Red Sea to New Caledonia. It has not been found in the Marshall Islands.

***Echinopora horrida* Dana, 1846 (pl. 5 fig. 1)**

Echinopora horrida Dana, 1846; holotype USNM no. 162.

Material: 22 colonies. RMNH: Indonesia: Coel. 9249, 9250, 9251, Togian Isl.; Celebes, Coel. 9305, 9306, 9307, 9308, 9309, 9310, 12381, 12383, 12384, 12386, Bay of Batavia; Coel. 9252, 9253, 12376-12378, Bay of Ambon, Coel. 12380 Binongko, Toekang Besi Isl., Coel. 12379, Wotap, Tanimber Isl., Coel. 12382, Tanah Djampea; Australia: Coel. 12204, Palm Isl., Great Barrier Reef, Coel. 12205, Hope Isl., Great Barrier Reef.

Specimens in other collections. Western Thailand, collection, H. Ditlev.

Characters. — Corallum. The colony is dendroid. The main branches can be rather thick (up to 4 diameter) but the side branches are in general thin and very spiny, as a result of the well developed spines on costae and the exsert septa. The end of a branch is often flattened and thin. These are the main characteristics of the species with which it separates itself from the other *Echinopora* species. The corallites are circular and small (up to 4 mm in diameter). The first two cycli of septa reach up to the columella. A spongy columella and some paliform dentations are present. The in the periphery

clockwise directed trabeculae are not always so clear in the specimens from Indonesia as in the ones from Australia (vide, Veron, Pichon & Wijsman-Best, 1977: 196).

Polyp. The living tissue is pale to dark brown.

Variability. — There is not so much interpopulational variation in this species, although intracoloniaally seen the base of the corallum can be flat, the older branches thick and the younger ones very thin. Parts of three extreme sites of the colony can be very unlike each other. But this is often the case in branching Scleractinian corals especially with small corallites. At a closer look the structure of the corallites are very much the same. In short it can be stated that the geographical variation of this species falls within the intracoloniaal variation.

The only species with which it can be confused in the field is *E. mammiformis*, but the latter has much smoother costal ridges.

In literature the affinity with *E. gemmacea* has been discussed but in view of the geographical distribution there is no problem. *E. horrida* does not occur in the Red Sea or Western Indian Ocean, so there is no point in confusing it with the dendroid form of *E. gemmacea*. As already said *E. gemmacea* is hardly dendroid in the Pacific.

Discussion. — The type is a large colony from the Fiji Islands. There are no nominal species names because the species is rather rare and limited in its distribution. Faustino (1927) and Nemenzo (1959) mention the species from the Philippines, Umbgrove (1939) from the Indonesian archipelago but not much doubts are expressed as to its identification.

Distribution. — The species is known in the Pacific from W. Thailand up to the Fiji Isl. In the Northern Pacific it is known from the Philippines but it is not present in the Marshall Islands.

Echinopora mammiformis (Nemenzo, 1959) (pl. 4 figs. 5, 6)

Leptastrea mammiformis Nemenzo, 1959; holotype Philippines.

Echinopora glabra Chevalier, 1975; MNHN.

Material: 3 colonies. RMNH: Australia: Coel. 12202 Palu Isl., Great Barrier Reef; Coel. 12203 Nara Inlet, Whitsundays, Great Barrier Reef, Coel. 12206 Pompey Reef, Great Barrier Reef.

Characters. — Corallum. The colony can be massive, explanate or branching. The corallites are round with an average diameter of 3-4 mm. They are "mammiform" and rather regular. The septa are in three or four cycles, the primary ones are well exsert. The long dentations in the center form pali and columellar structure. The clockwise direction of these skeletal structure is rather clear. Most characteristic of this species is the well developed and

smooth costae by which it distinguishes itself from the other *Echinopora* species.

Polyp. The living tissue is uniformly light brown.

Variability. — Because this species is known from three areas and since 1954 has been mentioned only by three authors, it is probably a rare species, also because it is not easily confused with other allied species as so often happens. There is as far as we know now not so much intra- or interpopulational variability and the geographical area is comparatively small. The growth form of the corallum comes closest to *Echinopora horrida*, but the lack of prominent dentation makes it a valid species.

Discussion. — The type of *Leptastrea mammiformis* of Nemenzo is a explanate colony, the type of Chevalier, *Echinopora glabra*, is a branching colony. Further field study in the Great Barrier Reef revealed that both forms are possible in this species (Veron, Pichon & Wijsman-Best 1977). The same phenomenon occurs in *Echinopora gemmacea* in the Red Sea, which also gave a lot of confusion in literature.

Distribution. — So far it has only been recorded from New Caledonia, the Philippines and the Great Barrier Reef, but it has probably a much wider distribution.

Echinopora forskaliana (Milne Edwards & Haime, 1850) (pl. 5 figs. 2, 3)

Astrea forskaliana Milne Edwards & Haime, 1850; holotype MNHN.

Material: 12 colonies. RMNH: Red Sea: Coel. 9798, Aqaba, Coel. 9197 Red Sea; Coel. 12667, 12669 (4x) Elat, Coel. 12668, Na'Ama, Southern Sinai, Coel. 12670 South of Elat, Coel. 12671 (2x), 12682, Mukebla.

Specimens in other collections: Rodriguez Mascarenes, collection G. Faure.

Characters. — Corallum. The colony is flat to rounded and plocoid. The corallites are rounded and very often protruding, the diameter may be from 3 to 6 mm. The type specimen has extreme large corallites (see Wijsman-Best 1977 pl. 3 fig. 3); in general the species has smaller corallites. The septa are equally and regularly developed, varying from 18 to 24 in number. The paliform lobes are little developed, the columella consists of many twisted trabeculae often arranged in a clockwise direction as seen in other *Echinopora* species. The costae are distinct, the dentation is regular and strongly developed.

Polyp. The colour of the living tissue is beige to greyish brown. This light colour makes that the species is easy to recognize under water.

Variability. — The growth form as well as the structure of the corallites are rather stable. The rate of protruding only may be very different. In the first part of the Montastreinae study it was stated that more field work

should be carried out to find out what "*Montastrea forskaelana*" exactly is. This was realized in 1978 in the Gulf of Aqaba (Red Sea) where the species is very abundant and as said above easy to recognize under water. It is amazing therefore that the species for such a long time not has been mentioned in literature or confused with others in collections. This is due to the fact that the last century more coral research has been done in the Eastern Indian Ocean and Western Pacific (the optimal area for coral growth) in the form of local coral reef studies. This gave rise to several mistakes made in systematical studies. About this approach of the geographical unlimited species variation more will be said in the general discussion.

Discussion. — As already said under *Montastrea forskaelana* in the first part of this Montastreae paper the type series as present in Paris showed specimens that were difficult to recognize in this group and very different from other Pacific material. Because it is proved now that this *Echinopora* species is limited to the Western Indian Ocean no synonyms are described. The confusion with *E. gemmacea* is easy to understand, but has been solved now.

Distribution. — As far as known the species is limited to the Red Sea and possibly Western Indian Ocean. The last statement is based on one doubtful specimen from the Mascarenes.

Diploastrea heliopora (Lamarck, 1816) (pl. 5 fig. 4)

Astraea heliopora Lamarck, 1816; holotype MNHN.

Orbicella minikoiensis Gardiner, 1904; BMNH no. 27.5.4.153.

Astraea Orbicella glaucopsis Dana, 1846; USNM no. 3.

Astraea Orbicella patula Dana, 1846; USNM no. 16.

Material: 12 colonies. RMNH: Indonesia: Coel. 12870 (4x), Binongko, Toekang Besi; Coel. 12871, Bay of Jakarta; Coel. 12872 (2x), Poeloe Toesa, Obilatoe; Coel. 12873 (2x), Kara Kelong, Talaud Isl. Australia: Coel. 12173, Lizard Island, G.B.R.

ITZ: New Caledonia: Coel. 6123, le Sournois, Passe Bulari. Madagascar: Coel. 6191, Nosî Bé.

Specimens in other collections: Western Thailand, collection H. Ditlev. Red Sea, collection G. Scheer.

Characters. — Corallum. The colony is round and forms huge coral masses — (2 m high and several meters in diameter). The corallites are characteristically symmetrical in shape, and round. The septa are arranged in three nearby equally developed septa, often ending in a small paliform rod. The dentation is also regular and strong. Costae are in between the septa arranged in a regular row opposite the ones from the neighbouring corallite. This monotypic species of the genus *Diploastrea* is easy to recognize and has since

Gardiner never been mentioned in literature under another name or confused with other species.

Polyp. The colour of the living tissue is uniform pale cream.

Variability. — There is little variability as well intercolonial as inter-geographically. The only interspecific variability I have observed is the normal rate of calcification in relation to depth as is known in other Faviidae. Specimens from habitats from deeper water are smaller, flatter, with thinner skeleton elements.

Discussion. — The type specimen from this species comes from Australian waters and is a well representative colony. Both synonyms as described by Dana originate from the Fiji Islands. *Orbicella minikoiensis* of Gardiner is the first record of *D. heliopora* from the Indian Ocean. Although the geographical distribution of this old species is large I have noticed myself that it is very rare in the Red Sea and Faure (1977) does not mention the species from the Mascarenes. As stated by Veron, Pichon & Wijsman-Best (1977: 155) the species is abundant in East Australia.

Distribution. — Widely distributed from the Red Sea to Samoa, but common in the Coral see area and much more rare towards the Western Indian Ocean.

GENERAL DISCUSSION

In this second part of the study of the Montastreinae the four genera *Cyphastrea*, *Leptastrea*, *Echinopora* and *Diploastrea* are dealt with. In the chapter General Taxonomy these genera and their 17 species are treated geologically as well as geographically.

Because this group of reefbuilding corals is well worked out especially ecologically in several areas, it has been possible to compare the intra- and interpopulational variability with the geographical variability, and this has resulted in better understanding of the geographical distribution of some of the species, especially those that are intrapopulationally very variable and therefore give rise to problems in their identification in other areas. These are in full speciation, and consequently we cannot speak any more of ecomorphs but we are dealing either with "geomorphs" or with subspecies. Because this is as yet quite a new and difficult subject to treat in coral taxonomy, I shall give some examples resulting from the species studied in the present paper.

In the genus *Leptastrea*, only known from the Indo-Pacific since the Oligocene, the species *L. bottae* and *L. transversa* have a distribution from the Red Sea to far into the Eastern Pacific. The geomorphs of these species from the extreme areas do vary, but the different intrapopulational variation

range in connecting areas do overlap, so although the differences have given a lot of confusion in the literature we are not dealing here with subspecies but more with geomorphs of one species.

In the genus *Echinopora* the species *E. hirsutissima* is common in the Red Sea and Western Indian ocean; the geomorph in the Pacific is very different and closely resembles *E. gemmacea*. In the Red Sea these two species are very easy to separate; a third closely allied but valid species has developed in the Red Sea: *E. forskaliana*. These intergrading forms or geomorphs are products of genera that are in full speciation, so whether we are dealing with subspecies or extreme geomorphs of already established species is irrelevant.

On p. 238 I already mentioned the polytypic species concept of the New Systematics. These categories lower than the species are called "sub-groups" by Simpson (1961: 172) and discussed as follows: "Those sub-groups are commonly recognized as subspecies and they are "real" in that they correspond with groupings in nature and not solely in the taxonomists mind. In many other species, however, no such relatively nonarbitrary or semiarbitrary subgroups are evident". Because we still have so much difficulty in separating coral species as a result of their intraspecific variability it is better not to use the term subspecies as long as we have not found a stable specific character. That is why I have introduced here the term geo-morph for those species in which the geographical variation exceeds the interpopulational variation.

Cyphastrea is an older genus, possibly already existing in the Atlantic in the beginning of the Oligocene. The recent species in the Indo Pacific that have a wide distribution show a great interpopulational variability (especially *C. serailia*) but it does not exceed the geographical variability. I regard the genus as more stabilized and no geomorphs have to be recognized. The present study shows that the solution of the limitation of the species in intergrading species of a given genus can only be found with field study of the intra- and interpopulational variability (ecomorphs) and geographical variability (geomorphs or subspecies).

In the first part of the study of the subfamily Montastreinae I discussed the hypothesis that extratentacular budding imposes an important limit to the adaptional plasticity of the coral colony. After further quantitative study I still can state that the intratentacular budding Faviidae are more abundant and form larger colonies than the extratentacular Montastreinae. As further worked out in Wijsman-Best (1977a) the Montastreinae are less abundant in the reef and they form in general smaller colonies; and the meandroid colony structure (the fastest growing species in the Faviinae) is not possible. They appear to be most successful apart from the plocoid *Montastrea* and *Diploastrea* in fast growing branching species of the genus *Echinopora*.

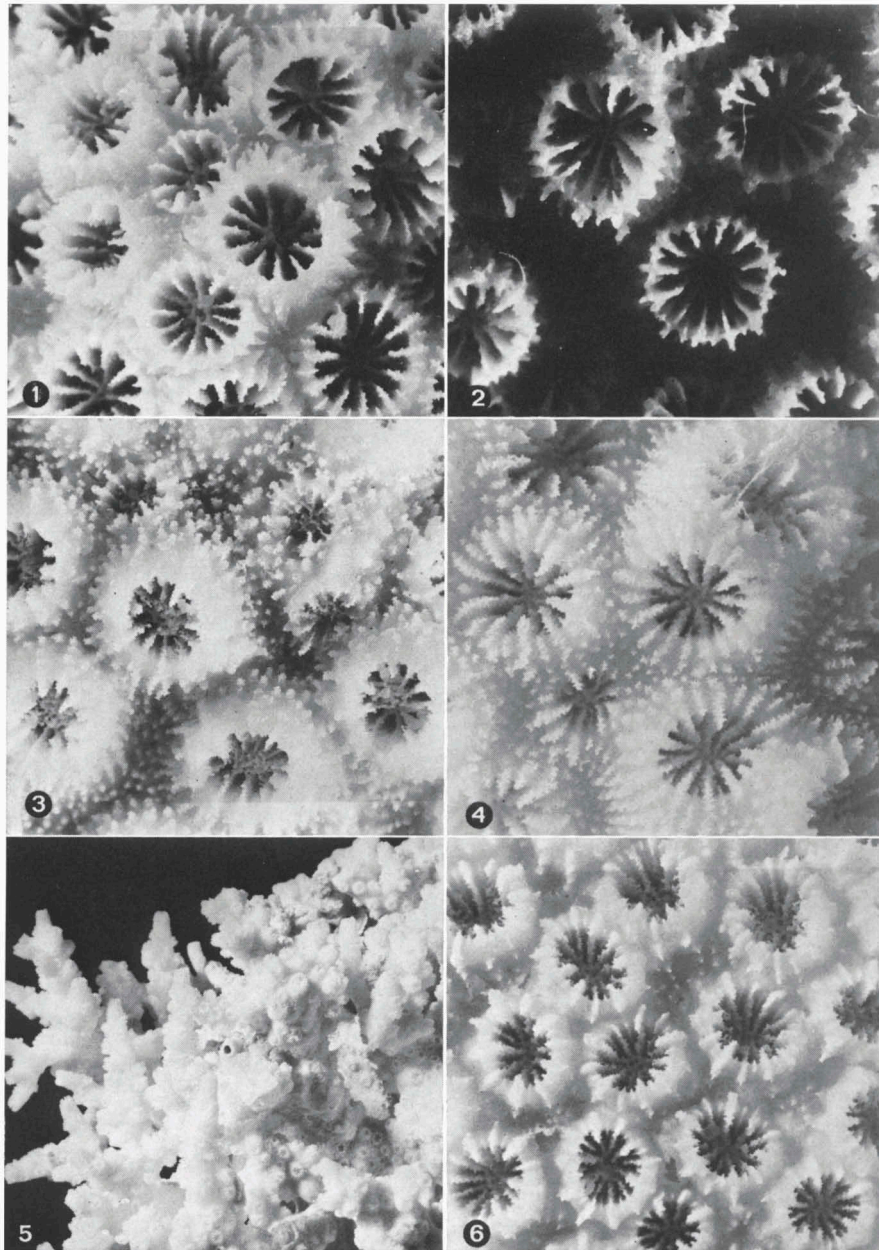
It has to be added here that in the Atlantic reefs *Montastrea* is an extremely abundant and important genus in fossil as well as in recent reefs. The Faviinae are hardly developed or of quantitative importance in the Atlantic. But as already remarked on p. 239 about the fossil records of the Montastreaeinae (concerning genera like *Cyphastrea*, *Solenastrea*, *Tarbellastrea*, *Plesiastrea* etc.) vide Chevalier (1961) and Frost (1977), a lot of work still has to be done before one can give a correlated development of the coralreefs in the Atlantic and in the Indian Ocean.

In stead of having tried to present a historical review and revision of this group of corals, I have aimed at giving a better description of the biological species belonging to the present genera especially in view of their geographical distribution.

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Figs. 1, 2. *Cyphastrea serailia* (Forskål, 1775). 1, Red Sea, RMNH Coel. 12590, $\times 7.5$; 2, holotype, MNHN, $\times 10$. Fig. 3. *Cyphastrea chalcidicum* (Forskål, 1775), Australia, RMNH Coel. 12185, $\times 5$. Fig. 4. *Cyphastrea microphthalma* (Lamarck, 1816), New Caledonia, RMNH Coel. 10720, $\times 10$. Fig. 5. *Cyphastrea japonica* Yabe & Sugiyama, 1932, Australia, RMNH Coel. 12184, $\times 0.8$. Fig. 6. *Cyphastrea ocellina* (Dana, 1846), Marshall Isl., RMNH Coel. 12793, $\times 7.5$.

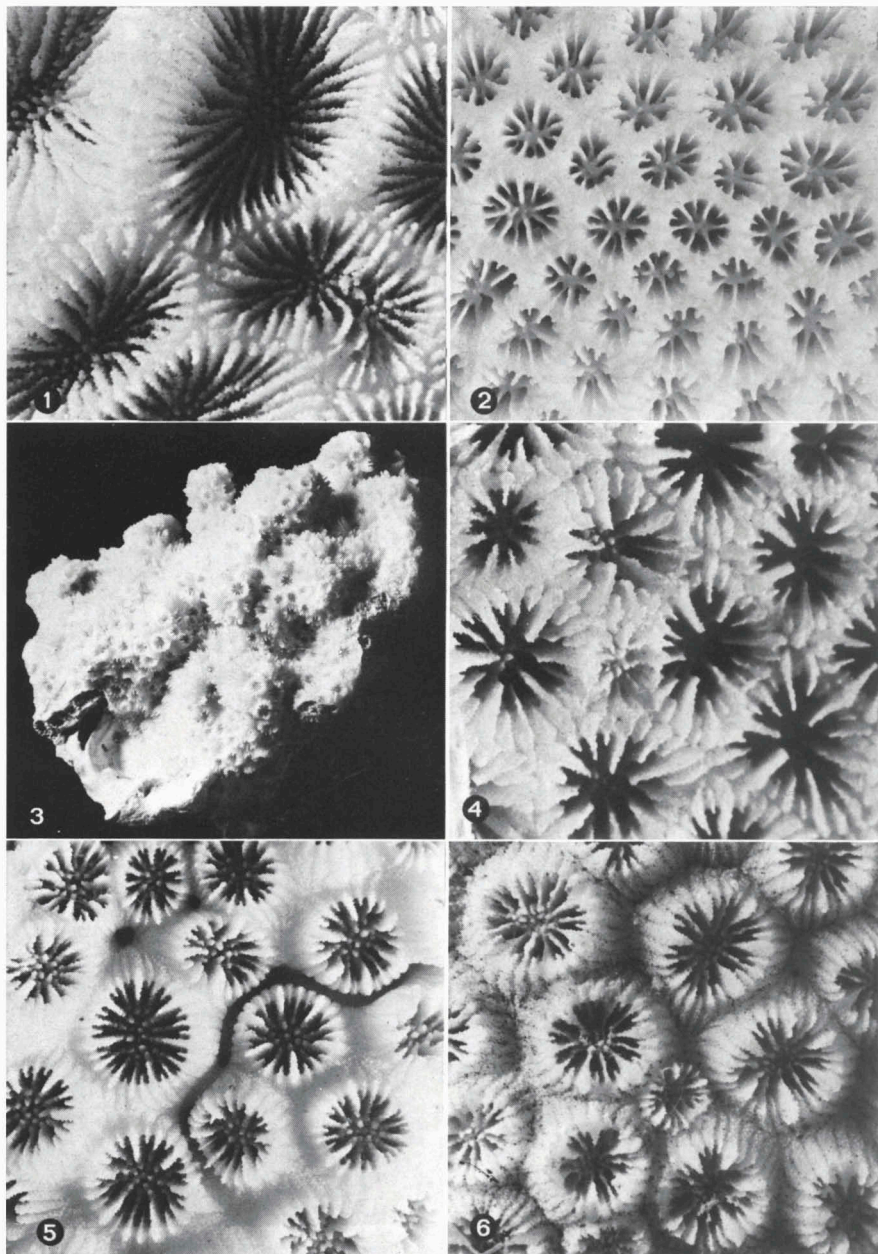
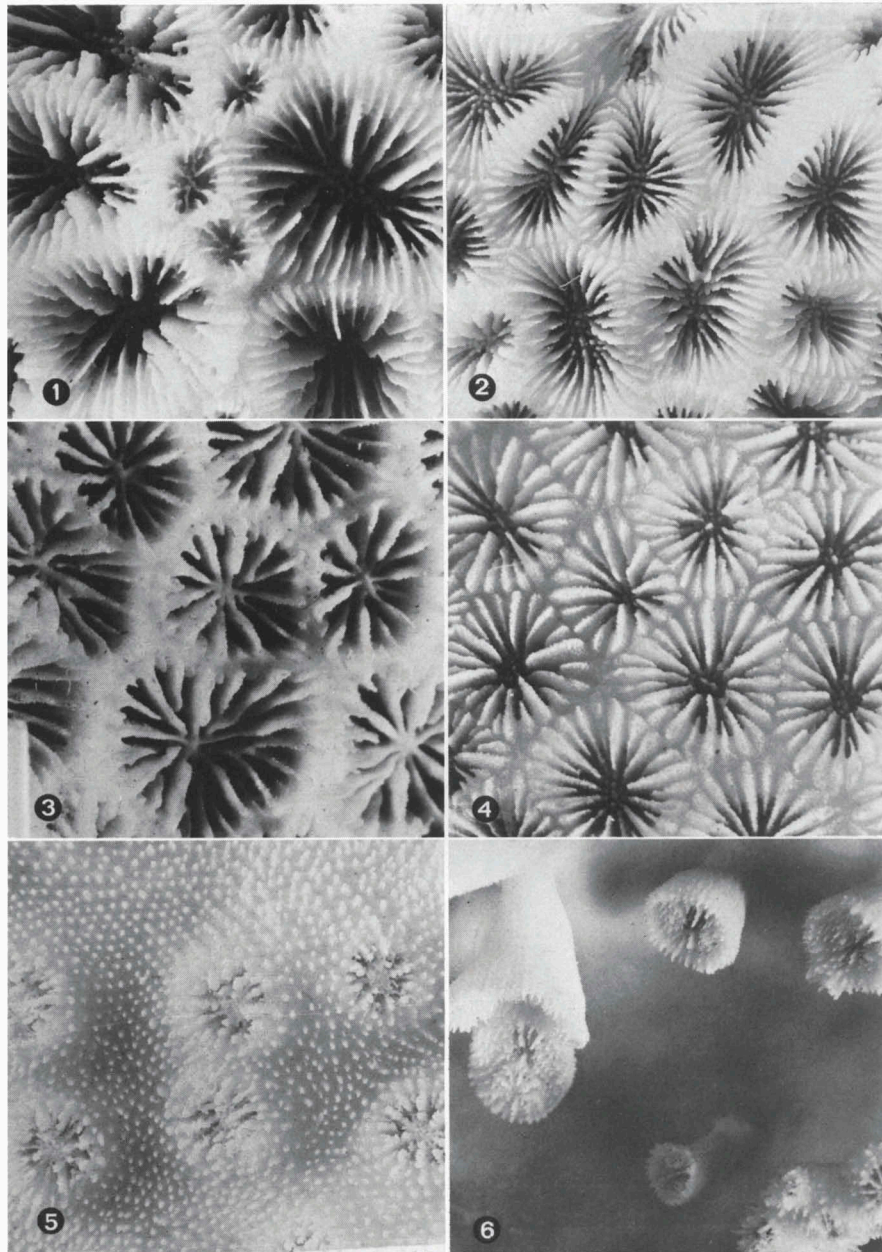
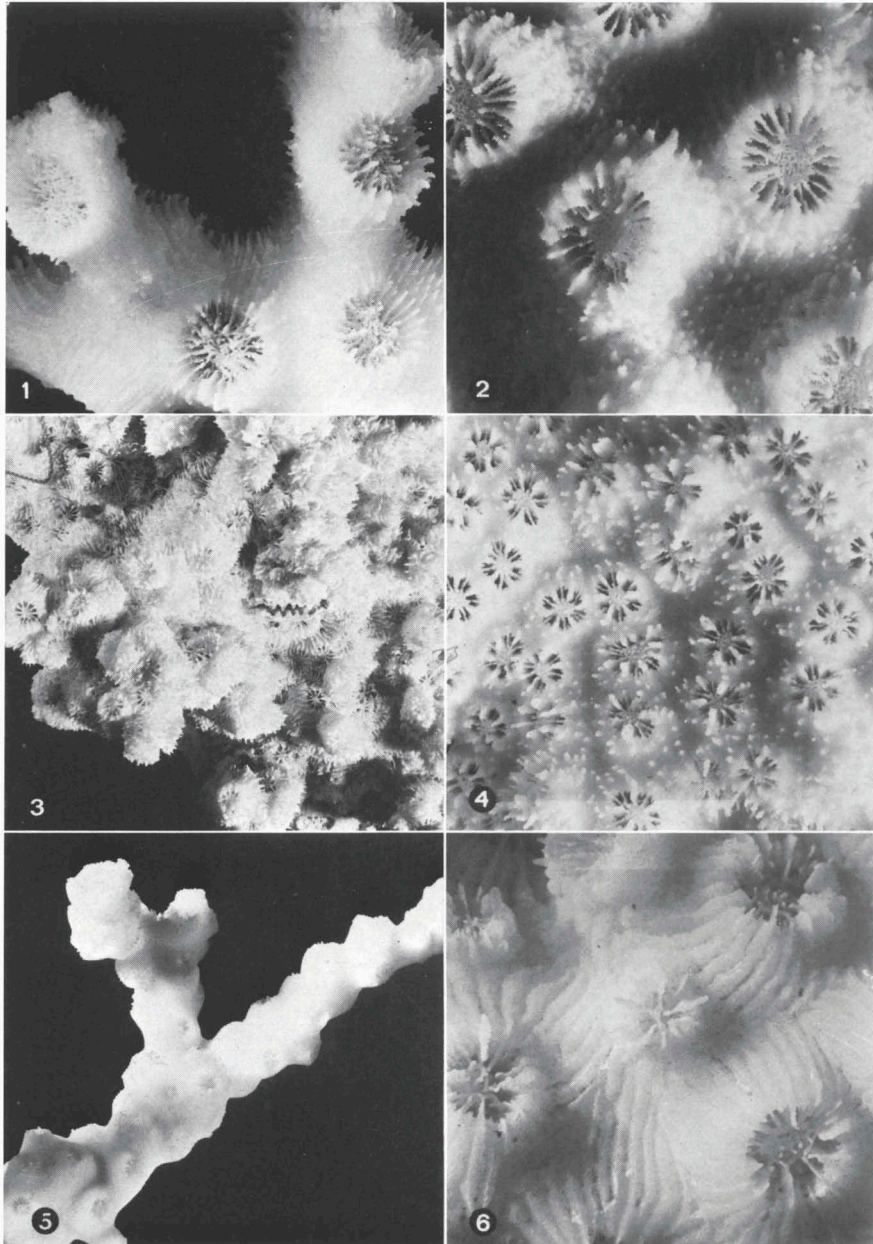


Fig. 1. *Leptastrea pruinosa* Crossland, 1954, New Caledonia, ITZ Coel. 6218, $\times 9$. Fig. 2. *Leptastrea bewickensis* Veron, Pichon & Wijsman-Best, 1977, holotype, BMNH no. 1977.1.1.5, $\times 4$. Figs. 3-6. *Leptastrea bottae* (Milne Edwards & Haime, 1849). 3, New Caledonia, ITZ Coel. 6199, $\times 0.8$; 4, holotype, MNHN, $\times 7.5$; 5, Red Sea, RMNH Coel. 12687, $\times 5$; 6, Hawaii, BBM, Honolulu, $\times 5$.



Figs. 1, 2. *Leptastrea purpurea* (Dana, 1846). 1, Indonesia, RMNH Coel. 107755, $\times 5$; 2, Red Sea, RMNH Coel. 12676, $\times 4$. Figs. 3, 4. *Leptastrea transversa* Klunzinger, 1879. 3, holotype ZMB, $\times 7.5$; 4, Red Sea, RMNH Coel. 12678, $\times 5$. Figs. 5, 6. *Echinopora lamellosa* (Esper, 1779). 5, New Caledonia, ITZ Coel. 6135, $\times 4$; 6, Indonesia, RMNH Coel. 12351, $\times 2.5$.



Figs. 1, 2. *Echinopora gemmacea* (Lamarck, 1816). 1, Red Sea, RMNH Coel. 12660, $\times 2$; 2, Red Sea, RMNH Coel. 12372, $\times 2.5$. Figs. 3, 4. *Echinopora hirsutissima* Milne Edwards & Haime, 1849. 3, W. Thailand, RMNH Coel. 12369, $\times 0.8$; 4, Australia, RMNH Coel. 12200, $\times 2$. Figs. 5, 6. *Echinopora mammiformis* (Nemenzo, 1959). 5, Australia, RMNH Coel. 12202, $\times 0.8$; 6, Australia, RMNH Coel. 12202, $\times 4$.

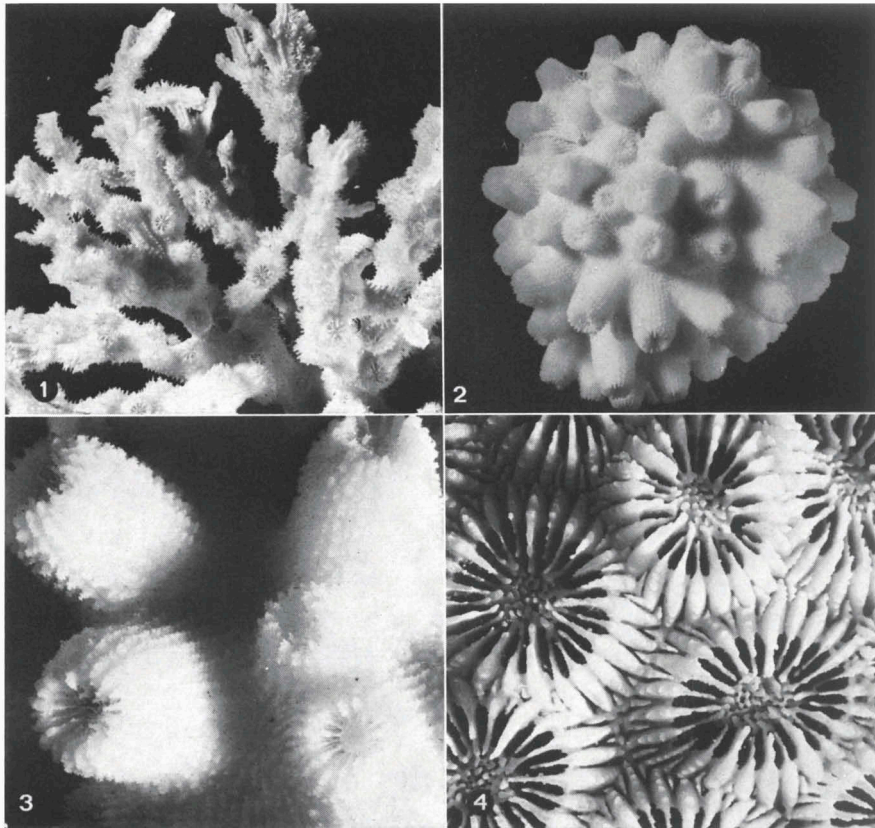


Fig. 1. *Echinopora horrida* Dana, 1846, Indonesia, RMNH Coel. 12377, $\times 0.5$. Figs. 2, 3. *Echinopora forskaliana* (Milne Edwards & Haime, 1850). 2, Red Sea, collection H. Schuhmacher, $\times 0.8$; 3, Red Sea, collection H. Schuhmacher, $\times 2.5$. Fig. 4. *Diploastrea heliopora* (Lamarck, 1816), Australia, RMNH Coel. 12173, $\times 3.5$.