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INDO-PACIFIC CORAL SPECIES BELONGING TO THE SUBFAMILY MONTASTREINAE VAUGHAN & WELLS, 1943 (SCLERACTINEA-COELENTERATA) PART I. THE GENERA *MONTASTREA* AND *PLESIASTREA*

by

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With two text-figures and four plates

Introduction

The results of this study are based on several collections mainly from the Pacific Ocean (New Caledonia, Great Barrier Reef, Australia) but also from the Indian Ocean (Indonesian Archipelago, Seychelles, Madagascar and the Mascarene Islands) and the Red Sea.

Apart from this material with the ecological data essentional in corals for a modern taxonomic approach, several other collections in different museums were examined in addition to the different type specimens as comparative material. Apart from the material from the Rijksmuseum of Natural History (RMNH) in Leiden and the Institute of Taxonomic Zoology (ITZ) in Amsterdam, specimens from the following museums and institutes were studied. British Museum of Natural History (BMNH), London; Musée National Histoire naturelle (MNHN), Paris; National Museum of Natural History (USNM), Washington, D.C.; Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Belgium; Australian Museum (AMS), Sydney; Queensland Museum (QMB), Brisbane; Australian Institute Marine Sciences (AIMS), Townsville, Queensland; National Museum Victoria (NMV), Melbourne; National Museum of South Australia (NMSA), Adelaïde; Station Marine d'Endoume (SME), Marseille, France; Institut d'Etude Supérieures Scientifiques de La Réunion (IESS); Ruhr Universität Bochum (RUB) F.R. Germany. Thanks also due to the keepers in charge of the coral collections of the different museums and institutes. This study was started as an identification of the collection made by Dr. H. Boschma

on board of the H.M. Willebrord Snellius (for further details on these collections see Wijsman-Best 1976) present in Leiden and the collection made by myself in New Caledonia (see Wijsman-Best 1972) present in Amsterdam.

History of the two genera

Whenever one works on the systematics of a group of reefbuilding corals one gets involved in a chaotic historical study. The genera *Montastrea* and *Plesiastrea* are no exception. A short exposition may be useful.

The presently described corals were historically reckoned to the large genus *Astraea*. In 1846, Dana divided this genus into several subgenera, *Orbicella, Plesiastrea, Diploastrea* and *Cyphastrea*. However, *Orbicella* needs no longer to be used since the older name *Montastrea* de Blainville, 1830, is available and for this genus as the type species of *Orbicella* is generally considered congeneric with the (fossil) type species of *Montastrea*. Other names available are *Heliastrea* M. Edwards & Haime, 1857 (including species of *Montastrea* and *Diploastrea*) and *Plesiastrea* M. Edwards & Haime, 1848. There has been much confusion as to the limits of the genera in this group. Klunzinger (1879) put several *Favia* species in *Orbicella;* Gardiner (1899, 1904) placed in the latter genus some species, belonging to *Diploastrea, Favia* and *Leptastrea*. Vaughan (1907, 1918) unfortunately included *Plesiastrea* in *Orbicella*. Matthai (1914) considered all species of *Montastrea* and *Plesiastrea* as belonging in one genus together with those of *Favia*.

These nomenclatorial confusions make literature after 1918 hardly understandable. What one author calls *Orbicella,* another calls *Plesiastrea*. The different authors understand something else under the name *Montastrea* or *Plesiastrea* or *Orbicella*.

To mention some of the more recent authors; the *Orbicella* specimens of Yabe et al. (1936) are corals belonging to *Plesiastrea,* some *Plesiastrea* species from Wells (1954) are corals belonging to *Montastrea*.

In view of the historical, ecological and geographical problems in the corals it is understandable that this confusion arose, and I prefer not to give a complete synonymy, but instead start at the species level. All data about names and types are given by Chevalier (1972). After having checked all type specimens I have come to the following conclusions:

There are two allied genera: *Montastrea* and *Plesiastrea*. To *Montastrea* belong: *M. curta* (Dana, 1846), *M. annuligera* (Milne Edwards & Haime, 1849), *M. magnistellata* (Chevalier, 1972), and cf. *M. forskaelana* (Milne Edwards & Haime, 1850). To *Plesiastrea* belonging; *P. versipora* (Lamarck, 1816).

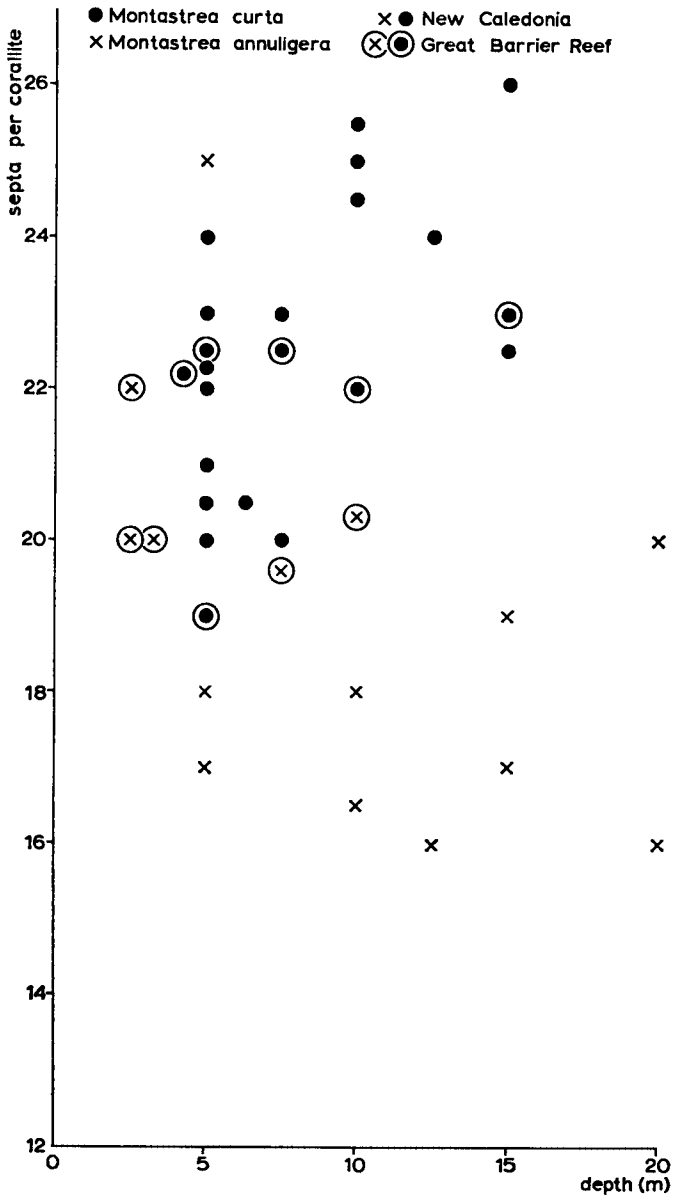

Fig. 1. Relation between number of septa per corallite and depth of collecting.

General taxonomy

Systematically *Montastrea* and *Plesiastrea* belong to the subfamily of the Montastreinae, viz., Faviidae with extratentacular budding. Other genera belonging to the same subfamily are *Leptastrea, Cyphastrea, Echinopora* and *Diploastrea,* which will be discussed in a following article (part II). Contrary to Wells (1956) *Plesiastrea* was included by Wijsman-Best (1972) in this subfamily. The main difference between *Montastrea* and *Plesiastrea* and the Faviinae is the dominant type of extratentacular budding; the other morphological characteristics of the two genera do resemble each other closely, which sufficiently explains the confusion with the Faviinae as described above. As with most coral species, the Montastreinae show an extensive degree of intraspecific variability due to the adaptional potentional (plasticity) of each colony with regard to the ecological conditions. Therefore, it is necessary to work with series of specimens, in which the intraspecific and intracolonial variability shows up.

General diagnosis of *Montastrea* de Blainville, 1830.

The colony is massive, incrusting or subfoliaceous. Colony formation by extratentacular budding, forming plocoid colonies. The corallites have a diameter ranging from 5 to 15 mm, the theca is septothecate, the septa are numerous with unequal dentated margins, often paliform. Lobes are present before the prominent septa, the columella is trabecular and well developed.

General diagnosis of *Plesiastrea* Milne Edwards & Haime, 1848.

The same description as given for *Montastrea* can be used for *Plesiastrea,* the only striking difference is the size of the corallites and the paliform structure. In *Plesiastrea* the corallites have a diameter ranging from 2 to 6 mm, and the paliform elements are much of each septum are present in each corallite.

Description of the species

Montastrea curta (Dana, 1846) (pl. 1 figs. 1-4)

Orbicella curta Dana, 1846: 209; holotype USNM no. 14 (pl. 1 fig. 1).[1])
Orbicella coronata Dana, 1846; USNM no. 57.
Astraea laperousiana Milne Edwards & Haime, 1849; MNHN.
Astraea solidior Milne Edwards & Haime, 1849; MNHN.
Astraea quadrangularis Milne Edwards & Haime, 1849; MNHN.
Orbicella wakayana Gardiner, 1899; BMNH no. 1927.5.12.122.
Orbicella rotumana Gardiner, 1899; BMNH no. 1927.5.4.202.
Orbicella funafutensis Gardiner, 1899; BMNH lost.

Material: 38 colonies. RMNH Coel. 9524 Ake Selaka, Halmahera, Indonesia. RMNH Coel. 9521 Karaton, Nenoesa Islands, Indonesia. RMNH Coel. 9888-9895 Togian Islands,

1) Synonyms with the location and if present, catalogue number of the type material.

Celebes, Indonesia. RMNH Coel. 10701-10711 Heron Island, Great Barrier Reef, Australia. RMNH Coel. 10712 Southern part, Great Barrier Reef, Australia. RMNH Coel. 9528 lagoon Noumea, New Caledonie. ITZ Coel. 6398 Passe Dumbéa, New Caledonia. ITZ Coel. 6400 Fausse Passe, New Caledonia. ITZ Coel. 6394 Passe Bulari, New Caledonia. ITZ Coel. 7658 Outer reef, New Caledonia. ITZ Coel. 6389, 6392 Tabu reef, New Caledonia. ITZ Coel. 6397 Tabu lagoon, New Caledonia. ITZ Coel. 6391, 6396, 6399, 6405 Forêt Snark lagoon, New Caledonia. ITZ Coel. 6385, 6393, 6395 Récif Ricaudy, New Caledonia.

Specimens in other collections: USNM (Washington) from Bikini, Tuamotu Islands, Great Barrier Reef; BMNH (London) from Great Barrier Reef; Collection G. Faure (La Réunion IESS) from the Mascarene Islands; Collection M. Pichon (Marseille SME) from Madagascar; AMS (Sydney) from One Tree Island, Great Barrier Reef.

Characters. — Corallum. The colony is plocoid, spherical flat or encrusting. The corallites are round, with a diameter ranging from 5 to 7 mm, the septa are variable in number (16 to 26) with an average of 22. They are sometimes regular with fine dentation, but the primary septa can be much more exsert and the dentation much more irregular. Only the major septa form a paliform lobe, they are not always so well developed. The costae are continuations of the septa on the coenosteum. The columella is round, well developed and consists of twisted trabeculae.

Polyp: The living tissue is in general brownish yellow with a green stomodaeum. The intensity of the colour is very variable.

Variability. — Although the morphological variability of this species is extensive, the intracolonial and also the intrapopulational variability is of the same range as that of the interpopulational variability. This may be due to the fact that this species has a restricted habitat preference.

It does not occur in extreme habitats (deep or muddy water). The differences in morphology are therefore mainly due to water movements (dentation, form of corallum) and competition with other corals.

The varieties of Chevalier (1972: 279) all fall within the range of variability to be seen in the present series, with the exception of var. ***annuligera,*** which in my opinion is a valid species.

A tendency is present towards a relation between the amount of skeleton formation (expressed as corallites per square unit and number of septa per corallite) and to light intensity, but very vaguely so (see graphs 1 and 2). As stated by Chevalier (1972) there are two extremes in the growth form series of this species, the one with small corallites and a deep fossa (*curta* ecomorph [1]) and one with much larger corallites with shallower calices.

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[1]) The term "ecomorph" has been accepted in this paper (viz. Veron & Pichon, 1977 in press) as a better word for "ecotype", as used by me in former publications.

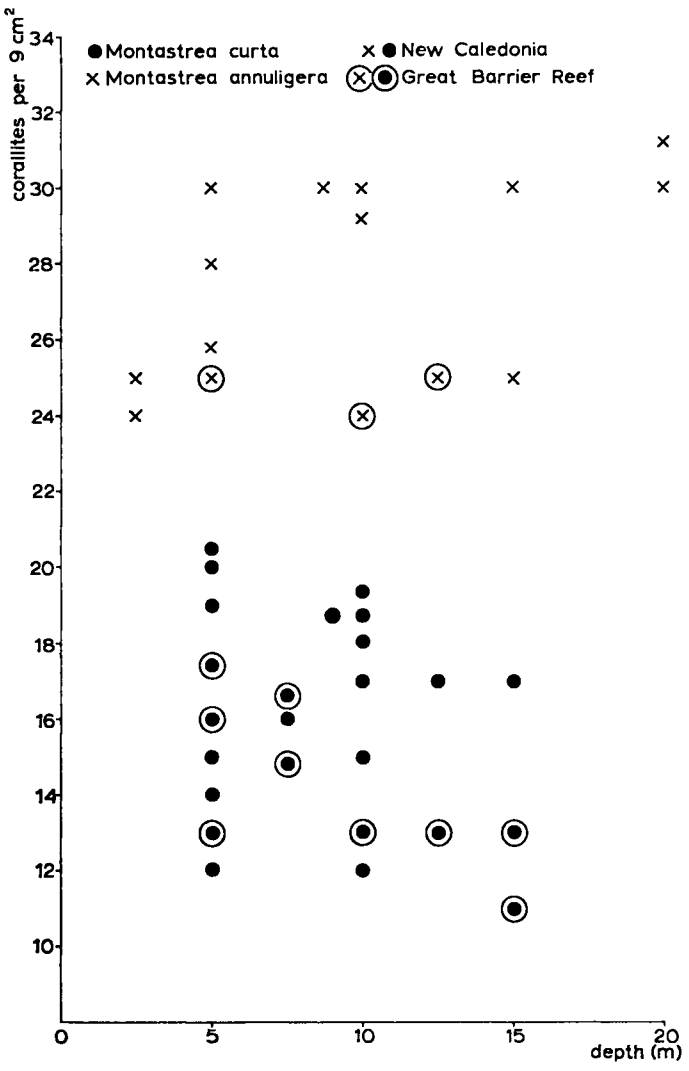

Fig. 2. Relation between number of corallites per cm² and depth of collecting.

Chevalier calls the last one "*lamarckiana*" variety, but the types of *A. lamarckiana* of Milne Edwards & Haime (from an unknown locality) can very well be worn specimens of *M. cavernosa* of the Atlantic. Anyway this ecomorph with large corallites is the most abundant one in the present series. Of the first ecomorph (*curta*), ITZ Coel. 6385 from the fringing reef of New Caledonia and ITZ Coel. 6397 from the lagoon of southern

New Caledonia are good representatives; of the other ecomorph (cf. *lamarckiana*) ITZ Coel. 7658 from the exposed reef of New Caledonia and RMNH Coel. 10703 from the outer reef of Heron Island (G.B.R. of Australia) are fairly typical.

These examples are indicative that ecomorphs are involved, rather than simple varieties, but with the present series and data nothing more difinite can be said. I agree with Chevalier that all transitional forms between the two extremes are present.

Discussion. — The types of *Montastrea curta* (holotype USNM no. 14, paratype USNM no. 22) come from the Fiji Islands, both small colonies built up by small corallites (5-6 mm) with a deep calyx. The general appearance is a regular built corallum from a sheltered habitat. The type of *M. coronata* (syntype USNM no. 57 from Tahiti and syntype USNM no. 58 from Wake Island) do resemble the growth-form of *M. curta,* there is a slight difference in the thickness of the theca and the number of septa, these characters are both less developed in *M. coronata.* The three synonyms of this species described by Milne Edwards & Haime are: *Heliastrea laperousiana* from Vanikoro, its holotype, a specimen fixed on the anchor of the wreck of Laperouse's "Astrolabe", shows a regularly developed encrusting colony. The holotype of *Heliastrea solidior* from Tongatabu is figured by Matthai (1914, pl. 25 fig. 8). That of *Heliastrea quadrangularis* from an unknown locality is a small worn specimen of the present species.

Two species described by Gardiner in 1899, *Orbicella rotumana* (Gardiner, 1899: pl. 49 fig. 3) and *O. wakayana* (Gardiner, 1899: pl. 49 fig. 2), are also synonyms of *M. curta,* as both fall within the range of variability of the present species. The sibling species *M. annuligera* has indeed been confused with *M. curta* by most authors. One of the few authors who has mentioned the species is Gardiner (1905), his record is based on specimens from Minikoi (Maldive Archipelago); Vaughan (1907) mentioned the species from French Somaliland. This last record is erroneous (see p. 91). My own conclusion to separate *M. curta* and *M. annuligera* is based on museum collections as well as on field material. After the discussion of *M. annuligera* the reasons for the separation will be given. *M. curta* is very common in the Pacific; as far as my field experience goes, it is more abundant than *M. annuligera* on the reefs of New Caledonia and on the Great Barrier Reef. As judged by its representation in museum collections it is quite rare in the Western Indian Ocean and in the Red Sea. Three specimens are known to me from these localities, one from Madagascar one from La Réunion (Mascarenes) and one from the Seychelles.

When it is assumed that *M. curta* is an ecomorph of more quiet water and cf. *lamarckiana* of more exposed sites, the morphological modifications are in accordance with the general pattern as described for the intratentacularly budding Faviinae (Wijsman-Best, 1974).

Montastrea annuligera Milne Edwards & Haime, 1849 (pl. 2 figs. 1-4)

Heliastrea annuligera Milne Edwards & Haime, 1849; holotype MNHN (pl. 2 fig. 1).
Orbicella vacua Crossland, 1952; BMNH no. 1934.5.14.129.

Material: 20 colonies. 9518, 9519, 9523 Karaton, Nenoesa Isl., Indonesia. RMNH Coel. 9522 Bay of Beo, Talaud Isl., Indonesia. RMNH Coel. 9520 Binongko, Toekang Besi Isl., Indonesia. RMNH Coel. 10713, 10714 Heron Island, Great Barrier Reef, Australia. RMNH Coel. 10715 Lizard Island, G.B.R. Australia. RMNH Coel. 10716-10718 Heron Island, reef flat, G.B.R. Australia. RMNH Coel. 9529 Snark, inside Barrier Reef, New Caledonia. ITZ Coel. 6406 Passe Dumbéa, outside Barrier Reef, New Caledonia. ITZ Coel. 6390, 6401, 6402 Fausse Passe, outside Barrier Reef, New Caledonia. ITZ Coel. 6388, 6403, 6404 Tabu inside Barrier Reef, New Caledonia. ITZ Coel. 6384 Snark, inside Barrier Reef, New Caledonia.

Specimens in other collections: USNM (Washington) from American Samoa; BMNH (London) from Maldives and Laccadives; IESS (La Réunion) from the Mascarenes, collection G. Faure; AIMS (Townsville, Australia) from the Great Barrier Reef and Norfolk Isl., RUB (Bochum, Germany) from the Red Sea, collection H. Schuhmacher. MRAC (Tervuren) from the Seychelles.

Characters. — Corallum: The colony is plocoid, spherical, flat or encrusting. The corallites are round, with a diameter ranging from 3 to 5 mm; the septa are variable in numner (16 to 20) in general quite regular, the septal edges are finely dentated. All the primary septa have a paliform lobe in the fossa, forming a crown. This very distinct skeleton structure is regular especially in the shallow water colonies. Finely formed costae are present on the coenosteum. The columella is trabecular, small and round.

Polyp: The living tissue is light brown.

Variability. — The uniformity of the species is apparent. The thickness of the theca is quite variable; the theca can be rather protruding and thick (*vacua* ecomorph) or hardly developed in height and thin (more like the holotype, the *annuligera* ecomorph). The first ecomorph is found in more exposed waters, the latter in a more sheltered habitat, but because so few ecological data are known no more can be said about the influence of the environment on the growth. The *vacua* ecomorph has in general deeper calices and poorer developed paliform lobes, in contrast to the *annuligera* ecomorph, with shallow fossa and a better developed pali crown.

The variability in other morphological characters, like number of septa, degree of dentation and corallites per square unit, is of the same scale as described in *M. curta*. Moreover the present species seems to be more limited in habitat choice.

Discussion. — The holotype of *M. annuligera* Milne Edwards & Haime (pl. 2 fig. 1) is a well preserved flat colony from "Australia" in which the characters, in regard to the present knowledge of variability, are clear. There are several colonies in the present series which resemble the type (see pl. 2 fig. 4). The holotype of *M. vacua* Crossland (pl. 2 fig. 2) is a rounded colony, which I identified with some doubt with the present species. It differs mainly from *M. annuligera* by its deep calices, in which the paliform lobes are not very distinct (hence the name). But I agree with Chevalier (1972: 291) that the paliform lobes are not altogether absent, but present in several corallites.

The two above described species *M. curta* and *M. annuligera* do overlap in at random collected series. For instance when we compare Coel. 6384 *M. annuligera* (a colony from a sandy bottom in the lagoon, with corallites with a shallow fossa, few developed paliform lobes and comparatively large corallites), with Coel. 6385 *M. curta* (a colony from a shallow reef habitat, with comparatively small corallites, few septa and rather much paliform lobe formation), we see that the two colonies resemble each other closely. But within one biotope the differences are very apparent. There are six localities where they could be separated from each other by their specific characters:

1. In the Station "forêt Snark" on the barrier reef of New Caledonia, ITZ Coel. 6405-6396-6399-6391 and 6328 are *M. curta* and ITZ Coel. 6384 and TMNH Coel. 9529 are *M. annuligera.*
2. In the station Karaton, Nenoesa Isl. in Indonesia, RMNH Coel. 9521 is *M. curta* and RMNH Coel. 9523-9519-9518 are *M. annuligera.*
3. In the station Fausse Passe on the barrier reef of New Caledonia ITZ Coel. 6400 is *M. curta,* ITZ Coel. 6402-6401-6390 is *M. annuligera.*
4. In the station Tabu, in the lagoon of New Caledonia ITZ Coel. 6392, 6397, 6398 are *M. curta*; Coel. 6404, 6388, 6403 are *M. annuligera.*
5. In the station Heron Island (Great Barrier Reef, Australia) on the reef flat RMNH Coel. 10701 to 10711 are *M. curta*; RMNH Coel. 10716 to 10718 are *M. annuligera.* In transect across the reef flat no differences in habitat between the two species were apparent.
6. In the station NossiBé (Madagascar) Coll. M. Pichon (Marseille) no. 1275.69 is *M. curta*; no. 454-67 is *M. annuligera.*

Here we find again the difficulty of distinguishing two sibling species, because in the same biotope the same morphological adaptation (to be seen, e.g., in regularity of skeleton structure, dentation and form of colony) has

its effect on the different coral colonies. So the pliable specific characters become less distinct. In the graph (fig. 1) the specific character provided by number of septa per corallite has been plotted against the depth. The separation is not clear, mainly because we are dealing here with two characters: size of the corallite and the number of septa. When we take one character into account only, e.g. the number of corallites per square unit, the separation is undeniable. In these graphs there is no correlation to be seen with depth, mainly because the species show a definite preference to a certain habitat. The two species show a different preference to their optimal habitat: *M. annuligera* occurs more often in shallow water, while *M. curta* has a more wide-spread distribution on the reef. In this respect it is remarkable that in the Western Atlantic a parallel evolutionary development has taken place. We find in the West Indies also two species of *Montastrea,* one with larger corallites (*M. cavernosa*) and one with smaller corallites (*M. annularis*). The first occurs in a much broader range of biotopes than the latter. This is deduced from the study by Laborel in 1969 in Brasil (Laborel, 1969: 180).

As already mentioned, two ecomorphs can be distinguished in the present species. If we look at the collection zoogeographically, from the central Pacific westwards towards the Indian Ocean a gradual change is apparent. A small collection from American Samoa collected by A. Lamberts and present in the Smithsonian Institution in Washington, D.C. (USNM) consists of five specimens of the *vacua* ecomorph. Most of the New Caledonian specimens belong to the *vacua* ecomorph, although Coel. 6406 shows more the *annuligera* ecomorph. One specimen from Norfolk Island also shows the *annuligera* ecomorph. On the Great Barrier Reef of Australia the two forms are present, from field data it is concluded that the *annuligera* ecomorph is dominant. The specimens from the Snellius expedition (Indonesian archipelago) have in general larger corallites and resemble the *annuligera* ecomorph. Gardiner (1899) described the species from the Maldives and Laccadives, these specimens are present in the BMNH (London); no. 1976.1.11.1. They and the photograph (Gardiner, 1899: pl. 63 fig. 32), show the *annuligera* form. From the Western Indian Ocean nine specimens from the Mascarenes (La Réunion and Mauritius) collected by G. Faure and present in the Centre Universitaire de la Réunion are all close to the *annuligera* ecomorph, although they are said to be collected in different habitats. The same holds for the specimen from Nossi Bé (Madagascar) collected by M. Pichon, and present in Marseille (SME). From these data it could also be concluded that we are dealing here with two sibling species overlapping geographically in the Coral Sea area: "*M. vacua*" with a geo-

graphical distribution eastwards in the Pacific and *M. annuligera* reaching westwards towards the Indian Ocean. But because no specific differences can be distinguished in the area where both ecomophs occur, and because the ecological preference of the two forms can as yet not be discussed for the dearth of data, it is best to describe them as one species. When *annuligera* and *vacua* are ecomorphs from more exposed and more sheltered habitats, respectively their morphological modification is in accordance with the general pattern of variation as described for the subfamily Faviinae (Wijsman-Best, 1972).

The record by Vaughan, 1907 of *M. annuligera* from French Somaliland is not correct. Vaughan's specimen (USNM no. 21966) which I examined in the Smithsonian Institution, Washington, D.C. is not *M. annuligera* but a *Plesiastrea versipora,* Vaughan (1918: 86) discussed this misidentification himself, he dropped the name *O. annuligera* for his specimens from Djibouti and created a new name *O. gravieri* for them. However, *O. gravieri* can now be placed in the synonym of *Plesiastrea versipora.*

Montastrea magnistellata Chevalier, 1972 (pl. 3 figs. 1, 2)

Mantastrea magnistellata Chevalier, 1972; holotype MNHN.

Material: 4 colonies. RMNH Coel. 9526 Tanah Djampea, Indonesia. RMNH Coel. 9527 Tanah Djampea, Indonesia. RMNH Coel. 8525 Wotap, Tanimber Isl., Indonesia. ITZ Coel. 6386 Passe Dumbéa, New Caledonia.

Specimens in other collections: AIMS (Townsville, Australian) from the Great Barrier Reef. MRAC (Tervuren) from the Seychelles.

Characters. — Corallum: The colony is plocoid, spherical, flat or encrusting. The corallites are rounded and large, the average diameter is 12 mm, the septa are in general very regular and numerous (30 to 35) hardly exsert and form outside the theca wall regular costal ridges. The dentation on the skeleton elements is regular, on the septal edges they can form irregular teeth. There is a crown of paliform lobes placed around the columella, which consists of thin trabeculae.

It is the only *Montastrea* with such large corallites, and can be easily distinguished by this character from the *Montastrea* species, previously described in this article.

Polyp: There are no data available about the living animal.

Variability. — The three specimens from the Indonesian archipelago Coel. 9526-9527 and 8525 resemble each other closely, and do not deviate much from the original description by Chevalier of specimens of New Caledonia. Coel. 6386 (pl. 3 fig. 2), however, is a flattened colony with very light texture. The corallites, although of the same large size, have fewer

septa (20 to 25). This can be due to the fact that the specimen comes from a depth of 25 m outside the barrier reef. Although it is likely that we are dealing here with an ecomorph there is a possibility that another species is involved, because no intermediate specimens are known.

Discussion. — The holotype of *Montastrea magnistellata* is present in the MNHN and is well described and figured by Chevalier (1972: 293, pl. 9 fig. 3, pl. 3 fig. 2). The species is probably not common in the Indo-Pacific region, because it has not been recognized before and I did not come across specimens in collections of other musea. The species has been recorded from New Caledonia and Indonesia; however, it is also present on the Great Barrier Reef (Veron, Pichon & Wijsman-Best, in prep.).

Montastrea forskaelana (Milne Edwards & Haime, 1850) (pl. 3 figs. 3, 4)

Heliastrea forskaelana Milne Edwards & Haime 1850; holotype MNHN (pl. 3 fig. 3).
Material: 2 colonies. RMNH Coel. 9197 "Red Sea". RMNH Coel. 9798 Aqaba, Red Sea.

Characters. — Corallum: the colony is plocoid, spherical. The corallites are rounded and always protruding, the average diameter is 5 mm: in general the septa are equally and regularly developed, varying from 20 to 24 in number. The dentation on the septa as well as on the costae is strong, which gives the colony a spiny appearance. The paliform lobes are little developed, the columella consists of many twisted trabeculae. The species is distinguished from the other *Montastrea* species by the protruding corallites and the strong dentation on the skeleton elements.

Variability. — The type series consists of a few large colonies in which the corallites are in general larger in diameter than in the specimens collected by H. Schuhmacher in Aqaba. For the rest they resemble the type series closely, except in size. The latter colonies as well as the corallites are smaller. Because so little material is present, not much more can be said about the intraspecific variability.

Discussion. — After having examined the type series in Paris I accept with some doubt the present species as a valid *Montastrea* species, differing mainly from the ones previously described by the protruding corallites and strong dentation. Dr. H. Schuhmacher collected several specimens in Aqaba, Red Sea in shallow water. One of these specimens he kindly offered to our museum, the other ones were studied. More collecting and fieldwork has to be carried out before the species can be fully treated as to its variability and distribution. It may very well be possible that it is a geographical growth

form of the well known Indo-Pacific species *Echinopora lamellosa* (Esper). This problem of intraspecific variability and geographical growth forms will be treated again in the second part of my paper on the Montastreinae, in which the genus *Echinopora* will be discussed. *Orbicella mamillosa* Klunzinger, 1879 described from the Red Sea might be a synonym of the present species, but because the type specimen is lost, no definite decision has been taken.

Plesiastrea versipora (Lamarck, 1816) (pl. 4, figs. 1-4)

Astraea versipora Lamarck, 1816; holotype MNHN.
Plesiastrea urvillei Milne Edwards & Haime, 1849; MNHN.
Plesiastrea quatrefagiana Milne Edwards & Haime, 1849; MNHN.
Plesiastrea proximans Dennant, 1904; type lost.
Orbicella gravieri Vaughan, 1918; USNM no. 21966 (new name for *O. annuligera* sensu Vaughan, 1907).
Favia ingolfi Crossland 1931; BMNH lost.
Plesiastrea salebrosa Nemenzo, 1959.

Material: 27 colonies. RMNH Coel. 10719 Innisfail G.B.R. Australia. RMNH Coel. 10722 Heron Island, Australia. RMNH Coel. 9996 Togian Reef, Celebes, Indonesia. ITZ Coel. 6413 Tabu, New Caledonia. ITZ Coel. 6407, 6410, 6411 Ile Nou, New Caledonia. ITZ Coel. 6408, 6414 Récif Ricaudy, New Caledonia. ITZ Coel. 6412 Baie de Dumbéa, New Caledonia. ITZ Coel. 6409 Baie de Citron, New Caledonia. ITZ Coel. 6686 Ambon Indonesia. ITZ Coel. 6688 Riouw Archipelago Indonesia. ITZ Coel. 6685 Timor Indonesia. ITZ Coel. 6687 Hangsisi, Indonesia.

Specimens in other collections: MNV (Melbourne), 8 colonies from different localities in S. Australia; QMB (Brisbane) G. 7262 Flinders reef, N.S.W.; AMS (Sydney) G. 13103, 14347 Port Jackson, N.S.W.; AMS (Sydney) G. 14345 Batemains Bay, N.S.W.; AIMS (Townsville) Coll. Veron nos. 1204, 1524 Queensland; SME (Marseille) Coll. Pichon NB 80 Nossi Bé Madagascar; IESS (La Réunion) Coll. Faure Reu 218, 240, 293, 309, 458 La Réunion; IESS (La Réunion) Coll. Faure Mau 256, 315 Mauritius; IESS (La Réunion) Coll. Faure Ro 297 Rodriguez; MRAC (Tervuren) from Mozambique.

Characters. — Corallum: The colony is plocoid, rounded, flat or encrusting. The corallites are small, average diameter 3 mm, but ranging from 2.5 mm to 5 mm. In general the corallites are closely set, although in deep water specimens they can be widely separated. The septa are numerous, about 35 in number but can vary according to the width of the theca. The most striking character is provided by the paliform lobes in front of all major septa, which form two crowns in most corallites. The costae are present in front of all major septa, numerous and continue on the coenosteum. The dentation is fine and very regular. The columella is small and round, consisting of fine trabeculae. The corallites may be rather protuberant, especially in specimens found in turbid water.

Polyps: the living tissue is light to dark brown.

Variability. — *Plesiastrea versipora* is of an extreme variability. Not only the habit of the colony, the size of the corallites, the number of septa and the height of the theca wall (adaptive characters changing as a result of major ecological factors) are variable interpopulationally, but within one population the characters can also vary considerably. The holotype of *P. versipora* (Pl. 4 fig. 1) represents a common ecomorph from a shallow reef habitat, the type of *P. urvillei* (Pl. 4 fig. 2) is a flat colony in which the corallites have a shallow fossa and much less strongly protruding corallites, this ecomorph represents specimens from calmer or deeper water. The ecomorph *urvillei* can be found in very muddy water, the corallites are more widely placed (see Pl. 4 fig. 4). Another extreme in the range of variability shows the specimen figured in Pl. 4 fig. 3, with closely set strongly protruding corallites. Even the numerous paliform lobes set in the characteristic two crowns can disappear in some colonies.

Discussion. — This very widely distributed coral species occurs all over the Indo-West Pacific and is present even as a very common species in the colder waters of southern Australia and more turbid water in western Australia. It is often mixed up in museum collections with *Favia stelligera* (viz. Q.M.B. G. 7262 from Flinders Reef) and is in generally called *Plesiastrea urvillei* in the southern Australian museums. After examining the type in Paris and the collection in Melbourne (MNV). I agree with Chevalier's conclusion that we are dealing here with a single species. The type of *P. urvillei* (Pl. 1) is a small colony from "Port du Roi Georges" (Australia) which differs from *P. versipora* by the less protuberant corallites with shallower calices. In general the specimens of the South Australian *P. versipora* resembles this variety or subspecies *urvillei*. The holotype of *P. versipora* from the "Indian Ocean" is a small colony with rather closely set corallites. The type of *P. quatrefagiana* corresponds closely with the holotype of the present species, the slightly different appearances still fall easily within the range of variability of the species. Although the type of *P. salebrosa* has not been examined, the description and figure as given by Nemenso (1959: 92) gave me the impression of dealing here with *P. versipora*. The type of *F. ingolfi* Crossland, 1931 is lost, but we are dealing here as Crossland stated himself with a "closely allied" growth form of *F. versipora* with much larger and very distinctive perithecae. The type material of *P. proximans* of Dennant could not be traced anywhere in the Southern Australia museums (Melbourne-Adelaide) but the description revealed that it is merely a deep water form (dredged from 22 fathoms) of the common *urvillei* ecomorph

of S. Australian waters. *P. gravieri,* is a synonym of *O. annuligera*; this conclusion has been taken after examination of the type in the USNM (Washington). In my opinion the species *Favia irregularis* Chevalier, also falls within the range of variability of *P. versipora.*

The specimens of the collections of the Amsterdam and Leiden museums do not give me any clue as to the pattern in the variability of the species. There are four major varieties, to be distinguished:

— corallites closely set; not protuberant (*versipora* ecomorph)
— corallites closely set; protuberant (Pl. 4 fig. 3)
— corallites rather large and shallow fossa (var. or subspec. *urvillei*)
— corallites widely separated (Pl. 4 fig. 4) generally from darker or deeper sites.

But as Chevalier (1972: 293) remarked there are many transitional forms between *P. versipora* and *M. curta.* A collection from the Mascarene Islands (la Réunion, Mauritius, Rodriguez) made by G. Faure, shows the same aspect of variability. The different groups of growth forms can be recognized without throwing more light on a significant ecological factor. Only an extensive ecological study can show, in how far the growth forms or ecomorph can be explained. With our present knowledge we can only indicate the great variability of *P. versipora* which, also is caused by the enormous geographical distribution.

In some specimens, e.g. a colony from Nossi-Bé (collection M. Pichon) and ITZ Coel. 6687 from the Indonesian archipelago, the most characteristic features (the double crown of paliform lobes and the small regular corallites) start fading. These colonies might even be considered as transitional forms between the present species and *Montastrea annuligera.* But here again we are probably dealing with extreme forms of two series which superficially show a certain degree of overlap, but with due considerations of the habitats of the various specimens probably are separated by a wide gap.

General discussion

The two genera of the Montastreinae (a subfamily which includes a total of six Indo-Pacific genera) dealt with in these pages are *Montastrea* and *Plesiastrea.* Within the family of the Faviidae the subfamily the Montastreinae is distinguished from the Faviinae by the occurrence of extratentacular budding. This is largely a quantitative difference, as extratentacular budding also occurs in certain species of *Favia* (see Wijsman-Best, 1972). Therefore the distinction between the Montastreinae and Faviinae may be an artificial one. *Montastrea* is a common genus on reefs, represented by seven species of which two, *M. cavernosa* and *M. annularis*

occur in the Atlantic Ocean. *M. forskaelana* is limited to the Red Sea, the three remaining species *M. curta, M. annuligera* and *M. magnistellata* occur in the Indo-Pacific. *M. curta* is by far the most common species of the genus in the Pacific Ocean. As discussed, in the Pacific it is more frequent than *M. annuligera,* with which it may occur in the same habitat. Although a more detailed quantitative study has to be carried out before stating anything definite about ecological preference of the two species, it seems likely that *M. curta* has the broader range of biotopes (also a broader range of intraspecific variability) than *M. annuligera,* which seems to have a preference for shallow reef sites. The same phenomenon has been observed in the two Atlantic *Montastrea* species, *M. cavernosa* and *M. annularis*; this apparently is a parallel evolutionary development. Material in the Western Indian Ocean in museum collections shows that *M. annuligera* is more frequent than *M. curta.* From *M. magnistellata* only very little material is recorded; this may indicate that the species is a rare one. *Plesiastrea russelli* Wells, 1954, known from the holotype only, has been recognized as a synonym of *Favites rufa* Wijsman-Best, 1972, now that more ecological fieldwork has been carried out in the Great Barrier Reef. The evidence will be treated in Veron, Pichon & Wijsman-Best, in prep.

Of the genus *Plesiastrea* several species have been described, but after an extensive study of the variability of the widely distributed *Plesiastrea* species, not any definite character could be distinguished, on which more than one species in this genus could be recognized. With the acceptance of the monospecific genus *Plesiastrea* the question arises whether the differences with the most closely allied species of the genus *Montastrea* (*M. annuligera*) are sufficiently important to maintain a separate genus for *P. versipora.* Chevalier, 1972, also discussed the characters of the two genera. I agree with his conclusions, and basing myself on the available material I do not see new arguments asking for a change in the present separation of the two genera. The representatives from other coral taxa, to which the specimens belonging to *Montastrea* and *Plesiastrea* come closest, are the rounded solid coral colonies with a plocoid growth form belonging to the genus *Favia.* Judged by their similar structure and growth form they probably have the same function on the reef but there is a significant difference in their quantitative appearance on the reef and therefore their success in the competition in the complex reef ecosystem. The genus *Favia* is much more abundant and more speciation has taken place (*Favia* has more than ten Indo-Pacific species). This may be a result of the different way of asexual reproduction. *Favia* has mainly intratentacular budding, *Montastrea, Plesiastrea* have mainly extratentacular budding. The hypothesis could be formulated that extra-

tentacular budding imposes an important limit to the adaptional plasticity of the coral colony. To this opinion I shall have to refer again after having treated the other Montastreine genera.

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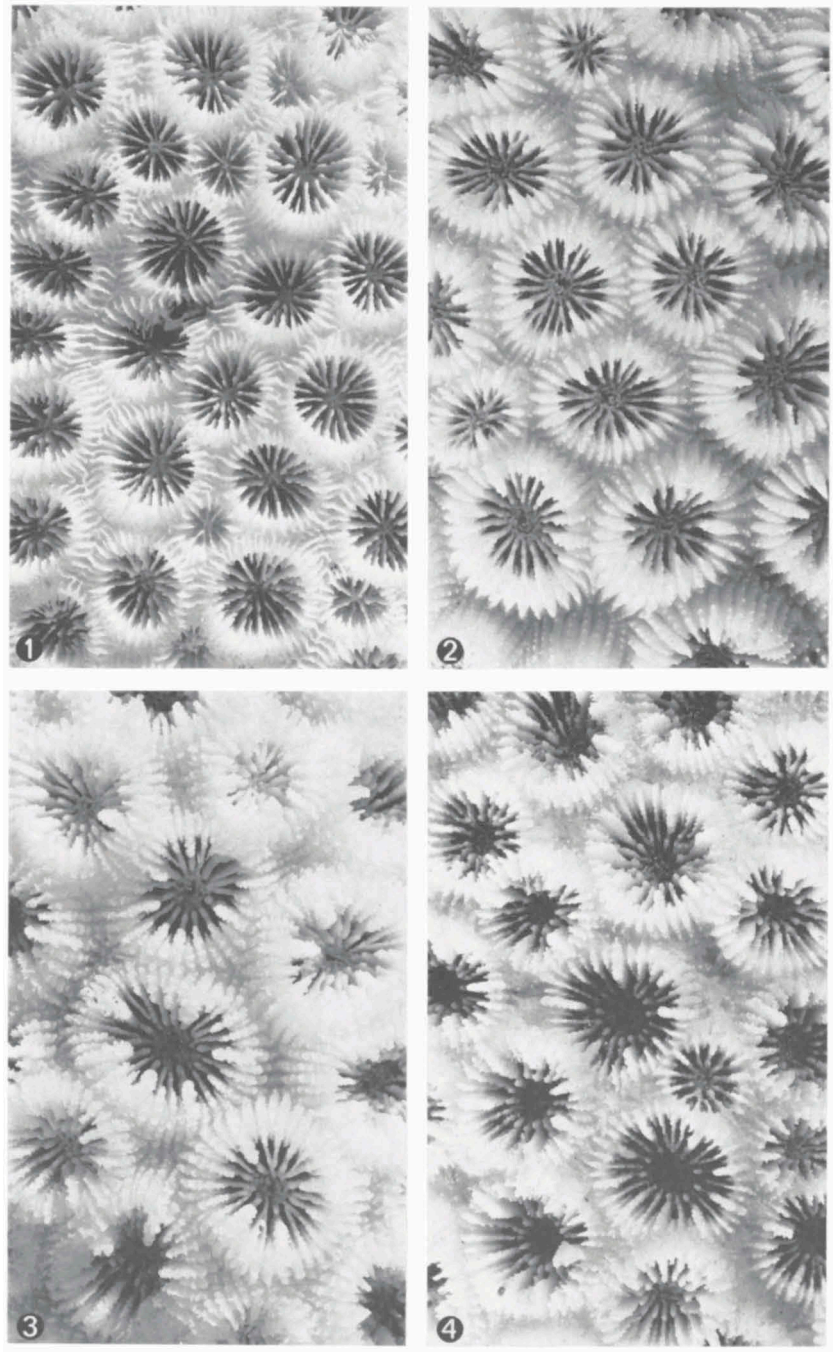
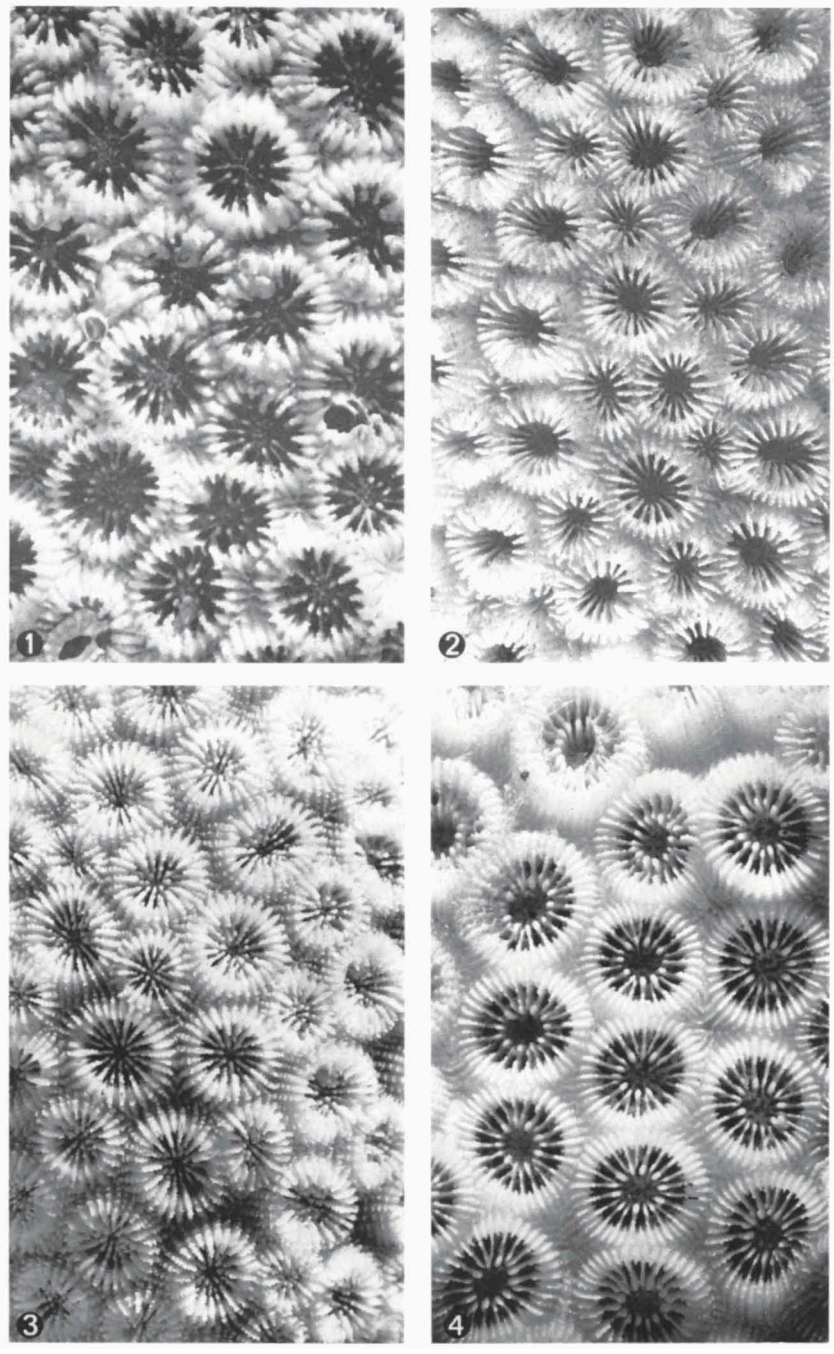
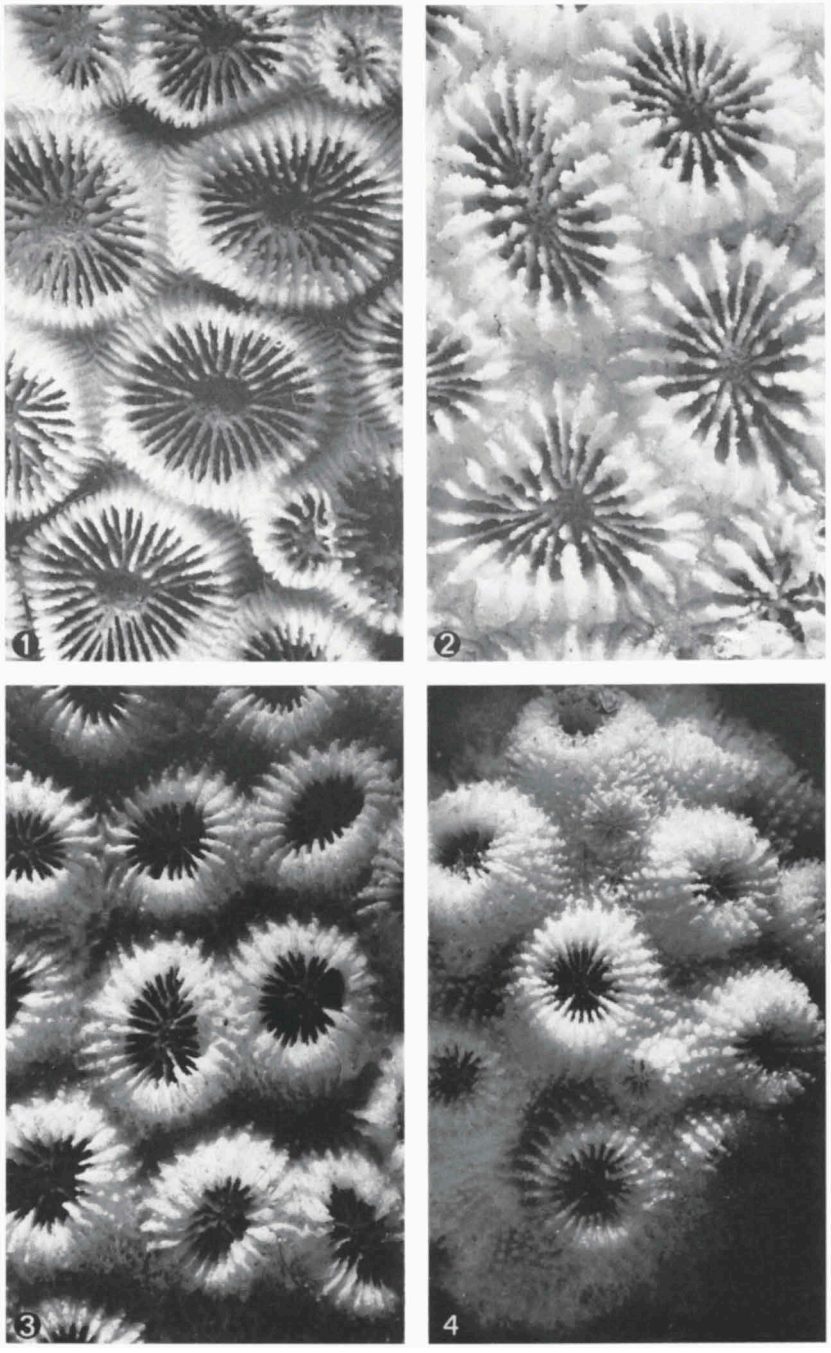


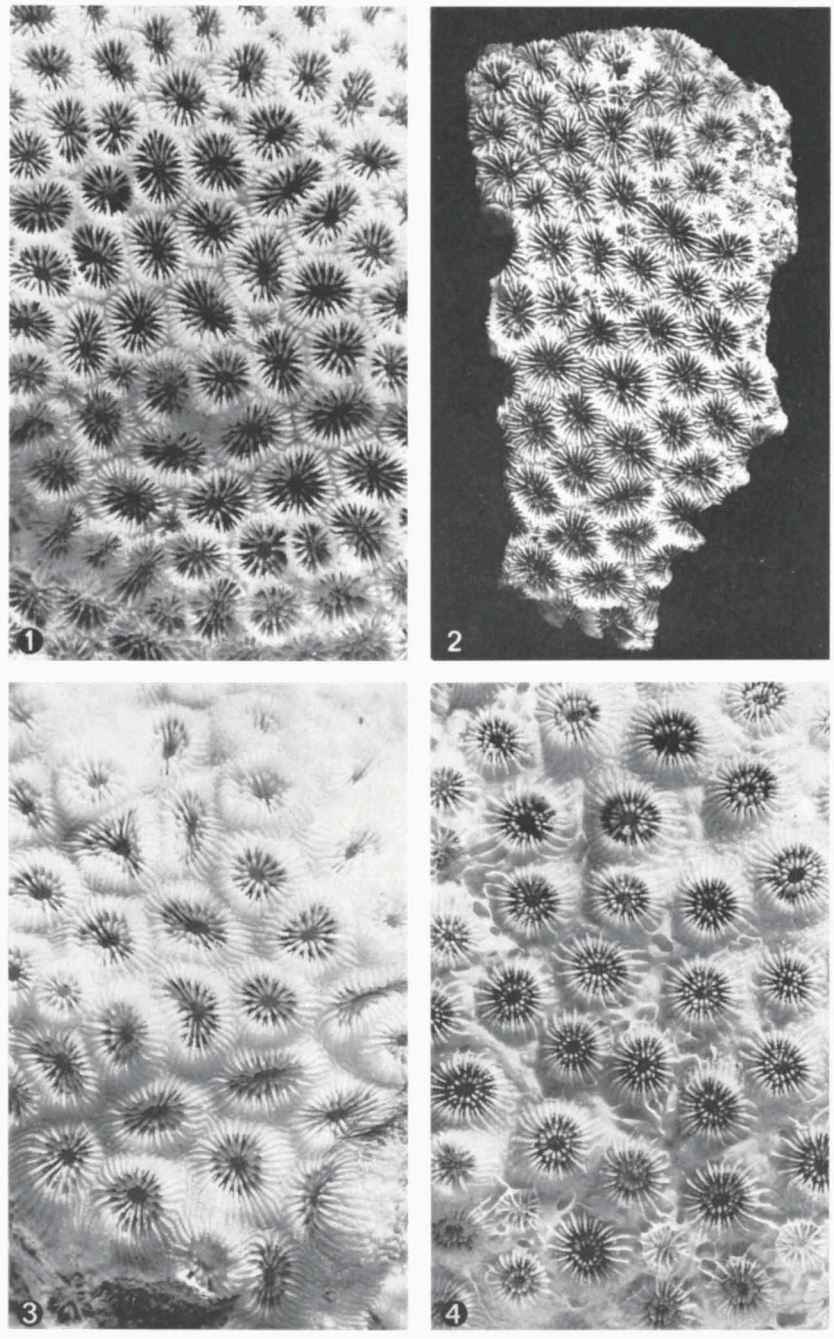
Figs. 1-4. *Montastrea curta* (Dana). 1, holotype, USNM no 14; 2, from New Caledonia, ITZ, Coel. 6400; 3, from New Caledonia, RMNH Coel. 9528; 4, from New Caledonia, ITZ Coel. 6396. × 3.



Figs. 1, 3, 4. *Montastrea annuligera* (Milne Edwards & Haime). 1, holotype, MNHN; 3, from New Caledonia, RMNH Coel. 9529; 4, from Australia, RMNH Coel. 10718. × 3.
Fig. 2. *Montastrea vacua* (Crossland). Holotype, BMNH no. 1934 5.14.129. × 3.



Figs. 1, 2. *Montastrea magnistellata* Chevalier. 1, from Indonesia, RMNH Coel. 9526; 2, from New Caledonia, ITZ Coel 6386. × 3. Figs. 3, 4. *Montastrea forskaclana* (Milne Edwards & Haime). 3, holotype, MNHN; 4, from Red Sea, RMNH 9798. × 3.



Figs. 1, 3, 4. *Plesiastrea versipora* (Lamarck). 1, holotype, MNHN; 3, from New Caledonia, ITZ Coel. 6410; 4, from New Caledonia, ITZ Coel. 6413. × 3. Fig. 2. *Plesiastrea urvillei* (Milne Edwards & Haime). Holotype, MNHN. × 2.5.