

# Historical biogeography of *Fungia* (*Pleuractis*) spp. (Scleractinia: Fungiidae), including a new species from the Seychelles

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An update of the phylogeny and biogeography of mushroom coral species belonging to *Fungia* (*Pleuractis*) is presented. Among the five species of this monophyletic group, one is described as new to science. This species, *Fungia seychellensis* spec. nov., was discovered during the Netherlands Seychelles Expedition (1992-1993) in the framework of the Netherlands Indian Ocean Programme 1990/1995.

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## Introduction

During the Netherlands Seychelles Expedition (1992-1993) of the Netherlands Indian Ocean Programme 1990/1995, a survey was made of the stony coral fauna (Scleractinia, hydrocorals and octocorals) of the Seychelles. Among the approximately 150 species of stony corals encountered during the expedition, a new mushroom coral species of the genus *Fungia* (Scleractinia: Fungiidae) was found.

This new species, which is described in the present paper, is classified with the subgenus *Pleuractis* (see below). Another species of this subgenus was recently described as new to science from Taiwan (Hoeksema & Dai, 1991). With these two taxa, the total number of species belonging to *Pleuractis* amounts to five. *Fungia scutaria* Lamarck, 1801, which was previously classified with the same subgenus, is now classified with the monotypic subgenus *Lobactis* (see Hoeksema, 1989, 1990).

Because of this recent increase in our knowledge since the taxonomic revision of the Fungiidae was published (Hoeksema, 1989), a short update is presented of the phylogeny and biogeography of *Fungia* (*Pleuractis*). In an earlier study (Hoeksema, 1991), the phylogenetic position of the recently described species from Taiwan, *F. taiwanensis*, as sister-species of *F. moluccensis*, was already established, but not in combination with an extensive phylogenetic analysis. Therefore, in the present study, all five species will be taken into account.

## The research area

The reefs visited during the Netherlands Seychelles Expedition (fig. 1) consist of fringing reefs on the higher granitic islands of the Seychelles Bank and of atolls on

the Amirantes Bank, and the isolated atoll of Platte Island. As a result of earlier expeditions, much is already known about the geological history of the islands and the structure and development of their reefs (Braithwaite, 1971, 1984; Rosen, 1971b; Stoddart, 1984; Wells, 1988).

The reef coral study of the Netherlands Seychelles Expedition was performed during a land-based survey of the fringing reefs around Mahé and Sainte Anne Island (5.xii.1992 - 15.xii.1992), and of a cruise along islands of the Seychelles Bank and the outer atolls of the Amirante Bank and Platte Island on board R/V Tyro (15.xii.1992 - 8.i.1993). Corals were sampled using snorkel equipment, SCUBA, rectangular dredges, Agassiz trawls, and a Van Veen grab. Specimens of the new species were only found by SCUBA-diving.

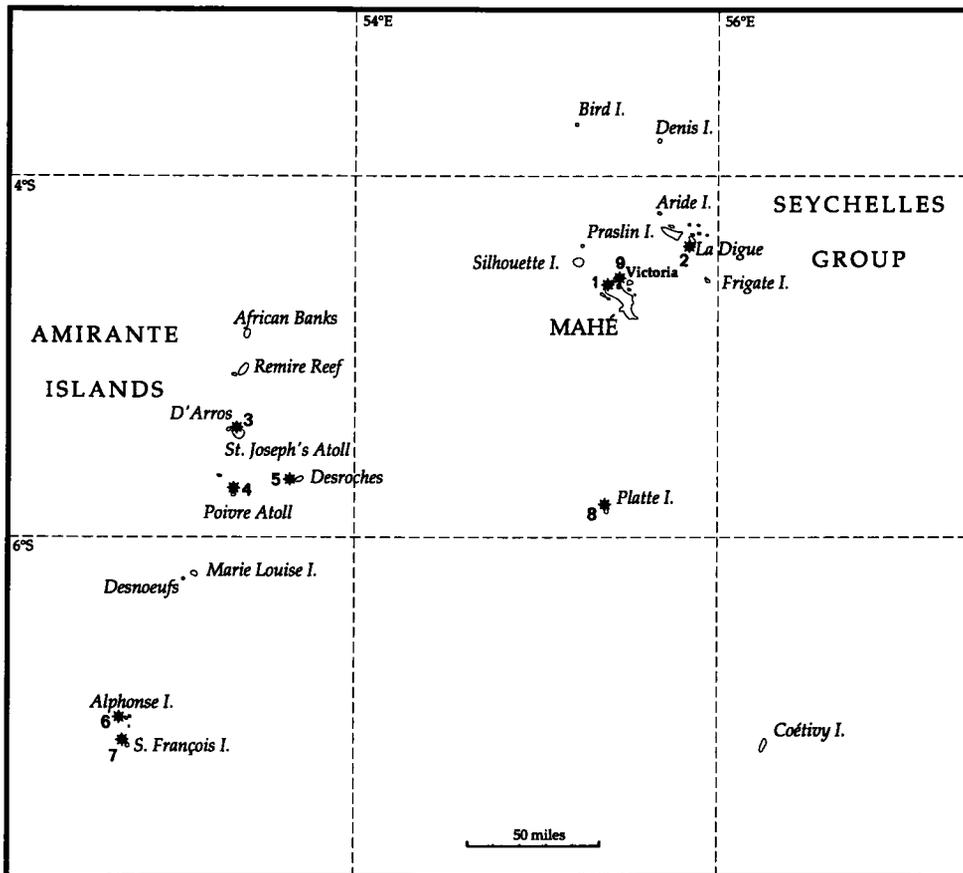


Fig. 1. Localities where specimens of *Fungia (Pleuractis) seychellensis* were collected during the Netherlands Seychelles Expedition (localities 1-8, 4.xii.1992 - 9.i.1993) and by A.J. Bruce (locality 9, 24.iii.1966). 1. Sta. 619, NW Mahé, Baie Beau Vallon, Hotel "Auberge Club des Seychelles". 2. Sta. 737, SW La Digue Island. 3. Sta. 753, NW St. Joseph's Atoll, southern slope of passage. 4. Sta. 767, N Poivre Island. 5. Sta. 772, W Desroches Atoll. 6. Sta. 786, NW Alphonse Island. 7. Sta. 792, NW St. François Atoll, bay near entrance of lagoon. 8. Sta. 796, N of Platte Island. 9. A.J. Bruce coll., NE Mahé, Anse Étoile.

### Systematics

Order Scleractinia Bourne, 1900  
 Suborder Fungiina Verrill, 1856  
 Superfamily Fungiicae Dana, 1846  
 Family Fungiidae Dana, 1846  
 Genus *Fungia* Lamarck, 1801  
 Subgenus *Pleuractis* Verrill, 1864

Type species.— *Fungia paumotensis* Stutchbury, 1833, designated by I.C.Z.N. (1991), as proposed by Hoeksema (1990).

Diagnosis.— Oval-elongate mushroom corals, either monostomatous (usually with a single, large mouth) or polystomatous (with a large central mouth surrounded by smaller ones). Oral surface humped (convex around the mouth) or not so. Septa straight or sinuous. Septal dentations granular or angular. Arrangement of granulations on septal sides even or irregular, or arranged in rows or ridges parallel to the septal margin. Corallum wall perforated in adult specimens. Costal spines blunt, simple and granulate, or laterally compressed.

#### *Fungia* (*Pleuractis*) *paumotensis* Stutchbury, 1833

*Fungia* (*Pleuractis*) *paumotensis*; Hoeksema, 1989 (synonymy): 143-148, figs. 23, 372-385, 646-647; Veron & Hodgson, 1989: 262; Veron, 1990: 63; Hoeksema & Dai, 1991: 221, figs. 67-70; Sheppard & Sheppard, 1991: 103, fig. 104; Hoeksema, 1993: 8.

*Fungia paumotensis*; Veron, 1992: 132; 1993: 215.

New records since Hoeksema (1989).— Yanbu, Saudi Arabia, Central Red Sea (Sheppard & Sheppard, 1991); S Red Sea (Zoological Museum Berlin: 1 specimen); Comoro Islands (ZMB: 1 specimen); S Taiwan (Hoeksema & Dai, 1991); Madang, N Papua New Guinea (ZMB 4997: 1 specimen; Hoeksema, 1993); Vanuatu (Veron, 1990); Onotoa, Gilbert Islands (National Museum of Natural Sciences, Canada, NMCI 1989-0665: 1 specimen).

Diagnosis.— Coral outline regularly oval. Oral surface not humped. Septa straight. Tentacular lobes absent. Septal dentations relatively large and distinctly angular. Granulations on septal sides fused in ridges parallel to septal margin. Aboral surface smooth. Detachment scar disappearing. Costae nearly equal in size. Costal spines fused in pairs or groups and laterally compressed.

Distribution.— From the western Indian Ocean and the Red Sea to the Tuamotu Archipelago (= Paumoto Islands), Society Islands (fig. 17).

#### *Fungia* (*Pleuractis*) *moluccensis* Van der Horst, 1919

*Fungia* (*Pleuractis*) *moluccensis*; Nishihira, 1988, 1991: 120; Hoeksema, 1989 (synonymy): 135-139, figs. 21, 349-358, 642-643; Veron & Hodgson, 1989: 262; Hoeksema & Dai, 1991: 216, figs. 43-47; Sheppard & Sheppard, 1991: 103, fig. 105; Hoeksema, 1993: 8.

*Fungia moluccensis*; Veron, 1992: 132; 1993: 215.

New records since Hoeksema (1989).— Sinai, Egypt (Sheppard & Sheppard, 1991); S Yemen (Coll. Dr. W. Wranik, Wilhelm-Pieck-Universität, Rostock, Germany: 1 specimen); Seychelles (Coll. Seychelles Fishing Authority, Victoria, Mahé, Seychelles: 1 specimen); S Taiwan (see Hoeksema & Dai, 1991); S Japan (Nishihira, 1991; Veron, 1992); Society Islands (California Academy of Sciences: 1 specimen).

**Diagnosis.**— Coral outline irregularly oval. Oral surface strongly humped. Septa straight. Tentacular lobes usually absent. Septal dentations fine and sharp, or varying from granular to ravel-shaped. Granulations on septal sides fine and evenly distributed. Aboral surface uneven. Detachment scar remaining in adult stage, or at least distinctly discernible. Costae irregularly shaped and unequal in size. Costal spines blunt and granular.

**Distribution.**— From the Red Sea to the Society Islands (fig. 18).

### ***Fungia (Pleuractis) gravis* Nemenzo, 1955**

*Fungia (Pleuractis) gravis*; Hoeksema, 1989 (synonymy): 140-143 (partim: not USNM 78293 from the Seychelles), figs. 22, 360-370, 644-645; Hoeksema & Dai, 1991: 221, figs. 63-66; Hoeksema, 1993: 8.

New records since Hoeksema (1989).— Ambon, Indonesia (Rumphius Biohistorical Expedition, 1991; RMNH Coel. 18424); S Taiwan (see Hoeksema & Dai, 1991); Madang, N Papua New Guinea (see Hoeksema, 1993). The previous record from the Seychelles (Hoeksema, 1989) was based on a misidentification.

**Diagnosis.**— Coral outline usually regularly oval. Oral surface usually humped in adult specimens. Septa usually straight. Tentacular lobes occasionally present. Septal dentations relatively small and angular or granular. Granulations on septal sides evenly distributed. Aboral surface even. Detachment scar disappearing. Costae nearly equal in size. Costal spines fused and laterally compressed.

**Distribution.**— From the Andaman Islands to the Society Islands (fig. 19).

### ***Fungia (Pleuractis) taiwanensis* Hoeksema & Dai, 1991**

*Fungia (Pleuractis) taiwanensis* Hoeksema & Dai, 1991: 216, figs. 43-47.

**Diagnosis.**— Coral outline irregularly oval. Oral surface strongly humped. Septa more or less straight, except around secondary mouths. Tentacular lobes usually absent. Septal dentations fine and sharp, or varying from slightly lobate to ravel-shaped. Granulations on septal sides fine and evenly distributed. Aboral surface uneven. Detachment scar disappearing in adult stage. Costae irregularly shaped and unequal in size. Costal spines blunt and granular.

**Distribution.**— SW and S Taiwan (fig. 20).

### ***Fungia (Pleuractis) seychellensis* spec. nov. (figs. 2-15)**

*Fungia (Pleuractis) gravis*; Hoeksema, 1989: 140 (partim).

Type material.— Holotype: RMNH Coel. 18303, Netherlands Seychelles Exped. Sta. 619, NW Mahé, Baie Beau Vallon, off Hotel "Auberge Club des Seychelles". Paratypes: RMNH Coel. 18304 (1 specimen), Sta. 737, SW La Digue Island; RMNH Coel. 18305 (1 specimen containing *Leptoconchus* spec.), same locality; RMNH Coel. 18306 (8 specimens), Sta. 753, NW St. Joseph's Atoll, southern slope of passage; RMNH Coel. 18307 (27 specimens), Sta. 767, N of Poivre Island; RMNH Coel. 18308 (1 specimen), Sta. 772, W Desroches Atoll; RMNH Coel. 18309 (3 specimens), Sta. 786, NW of Alphonse Island; RMNH Coel. 18310 (4 specimens), Sta. 792, NW St. François Atoll, bay near entrance of lagoon; RMNH Coel. 18311 (11 specimens), Sta. 796, N of Platte Island; USNM 78293 (1 specimen), NE Mahé, Anse Étoile, coll. A.J. Bruce (24.iii.1966, see Bruce, 1984).

Description.— Adult animals are free-living and usually monostomatous. They may occasionally form some supernumerary stomata by circum- or intrastomadaeal budding (figs. 6G, 10-11). The oral surface is even, not humped. The corallum outline is more or less regularly oval with rounded ends. The coralla vary in thickness and are either flat or slightly arched. The length of the central fossa, measured at its bottom, varies from  $\frac{1}{7}$  to  $\frac{1}{2}$  of the coral length. The columella is formed by a mingled mass of densely packed trabeculae and paliform lobes with tips usually pointing upward. The length of the specimens varies from 3.5 to 15.0 cm.

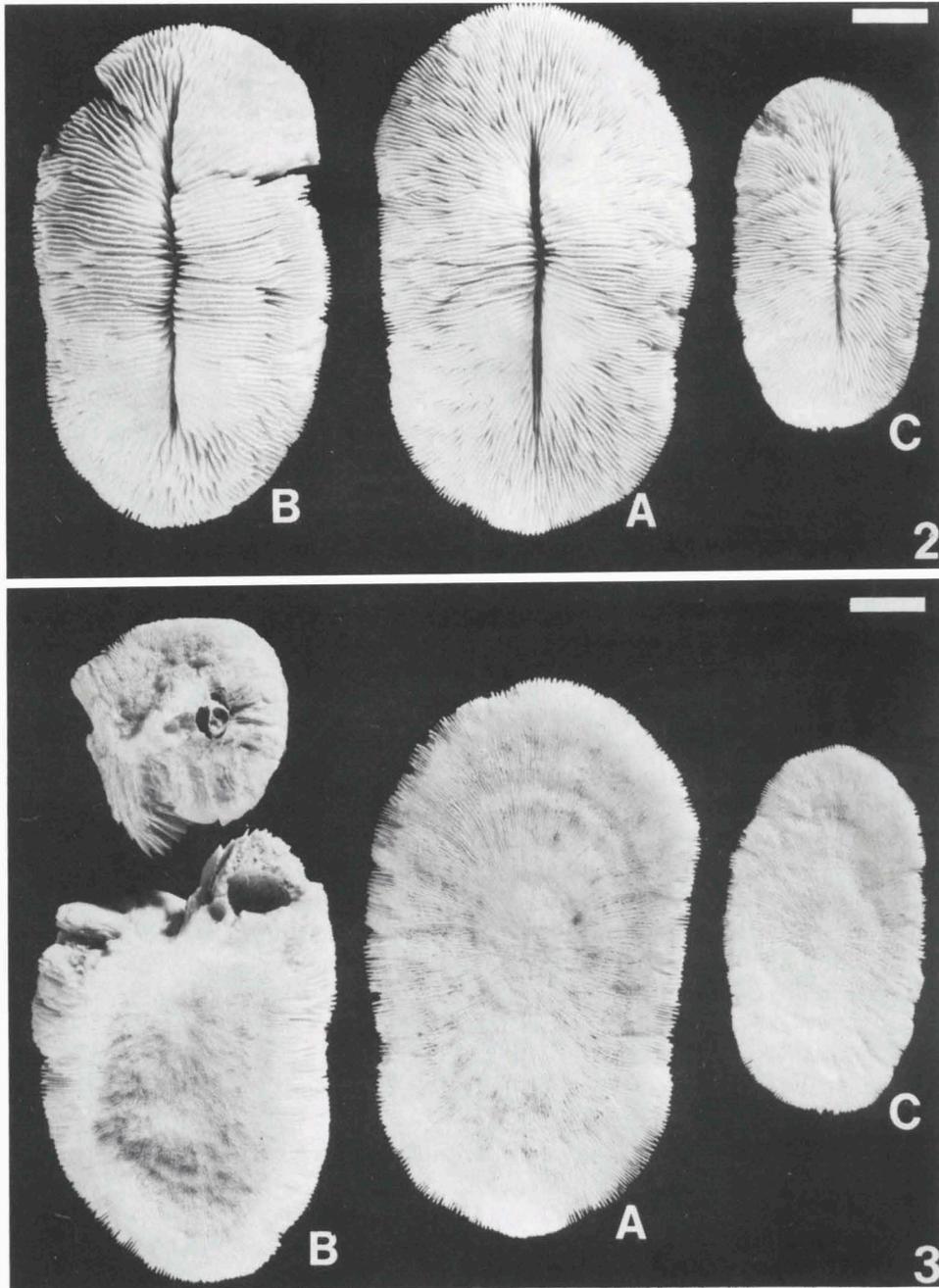
The septa are densely packed and usually sinuous, particularly in adult corals (figs. 2, 4, 6-11, 15). The septa of lower orders are usually thick and solid, and more exsert than those of higher orders, which are thinner and more perforated. In juvenile specimens all septa are perforated. Tentacular lobes are not present or at most inconspicuous. The septal margins are finely ornamented with septal dentations, which vary in shape from granular to slightly angular (figs. 8-11). Their number varies from 25 to 55 per cm septum. The septal sides are densely granulated. The granulations are fine and usually arranged in rows parallel to the septal margin; they may also be arranged in rows perpendicular to the septal margin, or otherwise they are evenly distributed (fig. 10). The compound synapticulae connecting the septa laterally can easily be distinguished despite the tight septal arrangement (figs. 8, 11).

The corallum wall is solid in relatively small coralla, whereas it is perforated in large ones (figs. 12-14). A detachment scar is only present at the aboral side of small detached specimens; in larger specimens it has disappeared (figs. 3, 5, 12-13). The costae are of almost equal size, straight, and distinct over their whole length, i.e., from the centre towards the periphery. They are finely to coarsely ornamented. The costal spines are blunt, granular and flattened at their sides. Their number varies from 15 to 45 per cm costa.

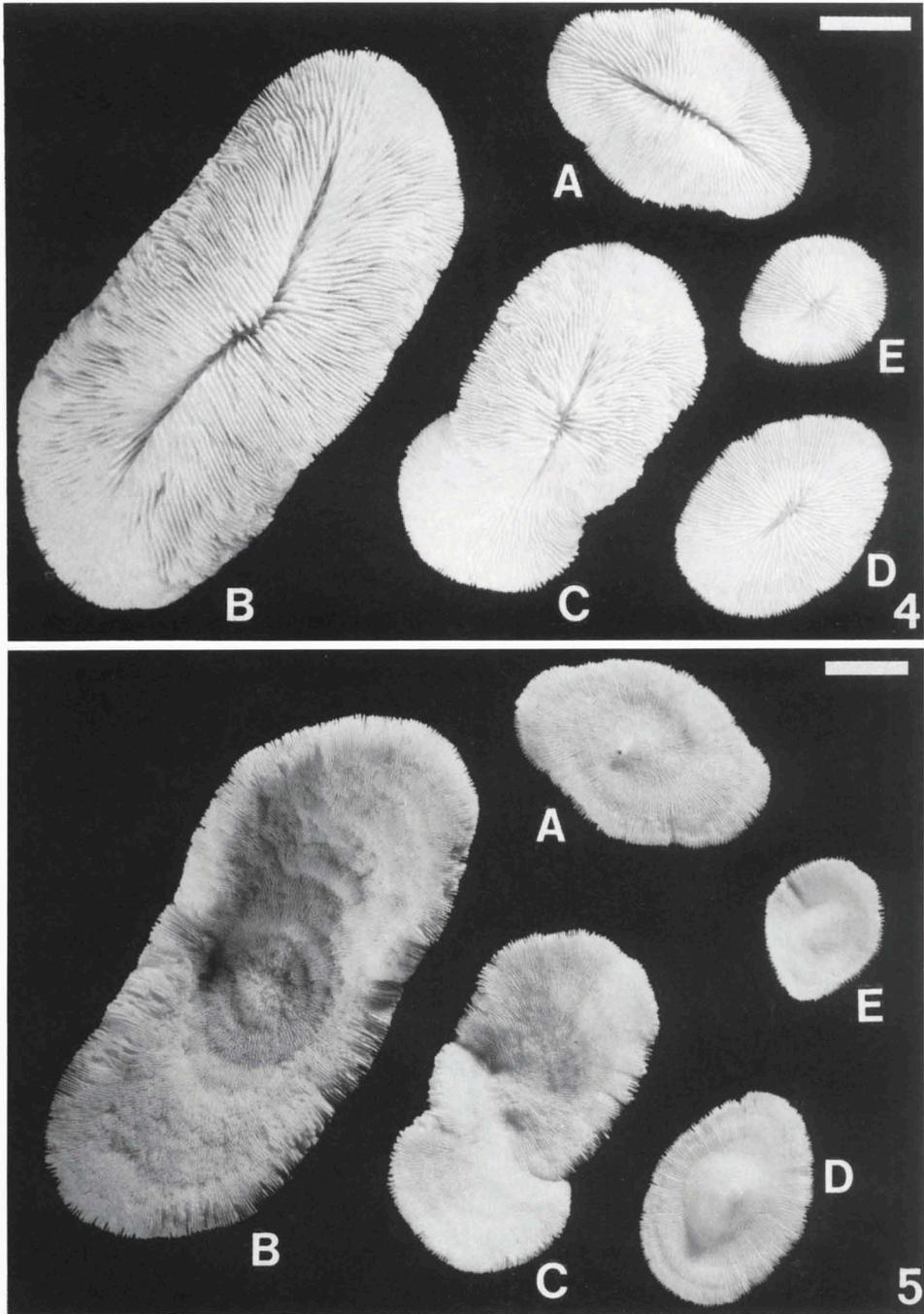
The colour of the live animals is predominantly brown. The small tentacles (fig. 15) are translucent and whitish.

Habitat.— The specimens were usually found in clear water, on shallow, flat substrata (5-10 m depth) or on steep slopes (10-25 m depth).

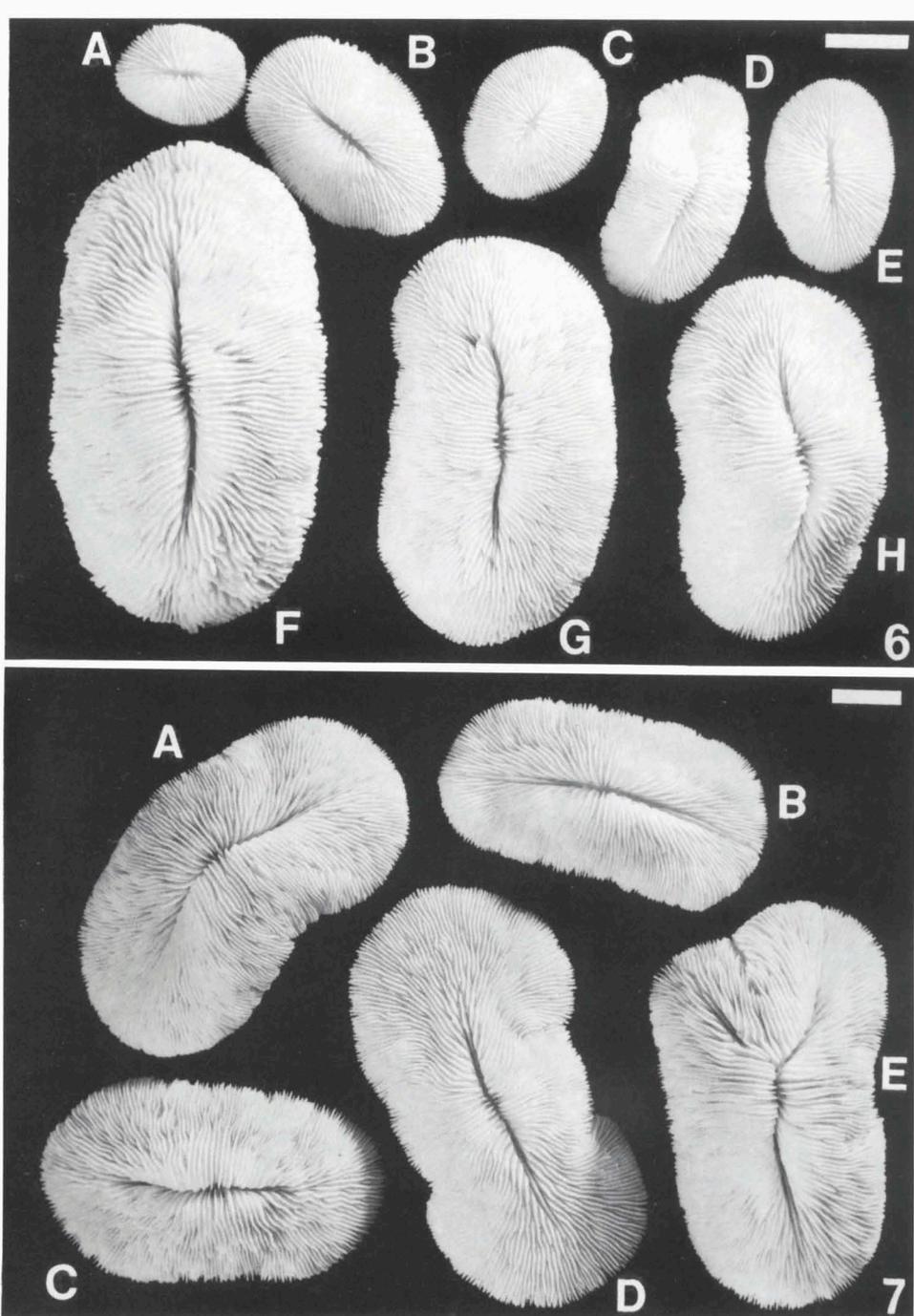
Remarks.— Earlier records of *Fungia* (*Pleuractis*) from the Seychelles concerned material from Aldabra that was identified as *F. paumotensis* (Rosen, 1971a, 1979), but since no Aldabra material of this species was found in museum collections, this identification could not be verified (Hoeksema, 1989). The record of *F. gravis* by Hoeksema (1989: 140) appears to be a misidentification (see above). In other accounts on the reef coral fauna of the Seychelles no *F. (Pleuractis)* species are mentioned (Rosen, 1971b; Pillai et al., 1973; Wijsman-Best et al., 1980; Selin et al., 1992), with the exception of *F. scutaria*, which is now classified with *F. (Lobactis)*.



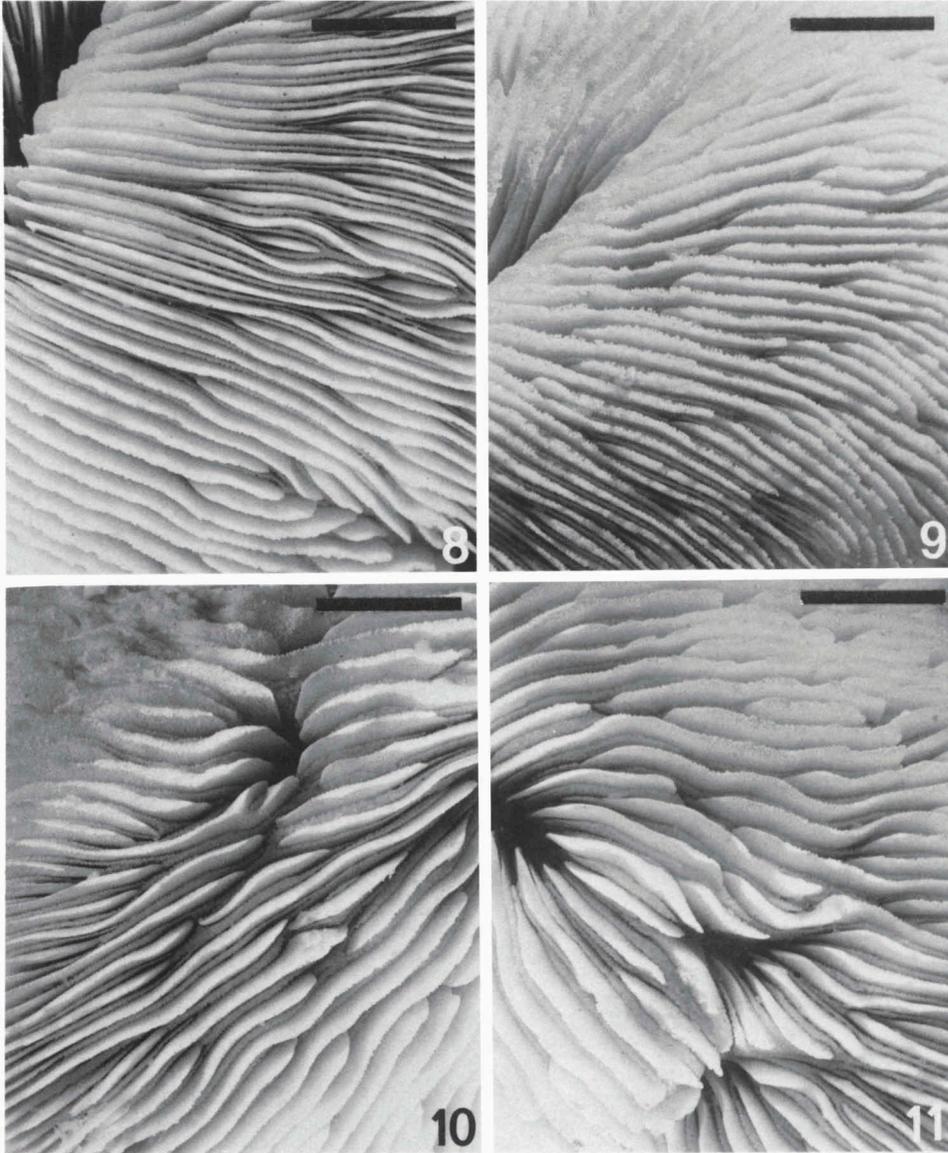
Figs. 2-3. Oral and aboral surfaces of *Fungia* (*Pleuractis*) *seychellensis* coralla. Scale bars: 2 cm. A. Holotype (RMNH Coel. 18303) from NW Mahé. B. Paratype (RMNH Coel. 18305) containing shells of *Leptoconchus* spec. (Gastropoda: Coralliophilidae) from SW La Digue Island. C. Paratype (USNM 78293) from NE Mahé.



Figs. 4-5. Oral and aboral surfaces of *Fungia (Pleuractis) seychellensis* coralla. Scale bars: 2 cm. A. Paratype (RMNH Coel. 18308) from W Desroches Atoll. B-E. Paratypes (RMNH Coel. 18310) from NW St. François Atoll.

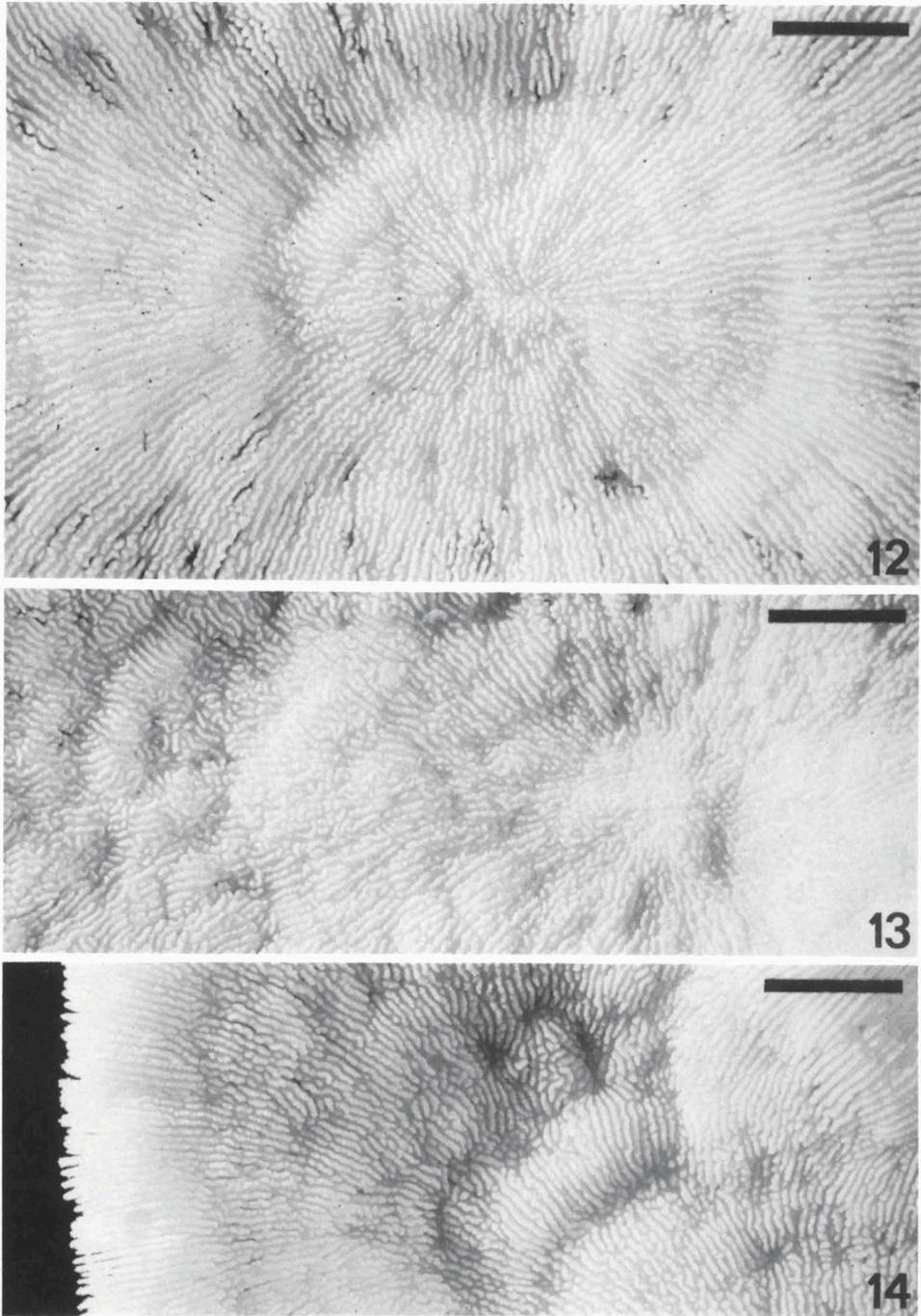


Figs. 6-7. Coralla of *Fungia* (*Pleuractis*) *seychellensis*. Scale bars: 2 cm. Fig. 6. Paratypes (RMNH Coel. 18307) from N of Poivre Island. Fig. 7 Paratypes (RMNH Coel. 18311) from N of Platte Island.



Figs. 8-11. Septa of *Fungia (Pleuractis) seychellensis*. Scale bars: 0.5 cm. Fig. 8. Holotype (RMNH Coel. 18303). Fig. 9. Paratype (RMNH Coel. 18310). Figs. 10-11. Paratype (RMNH 18305) showing supernumerary mouths.

With regard to other *Fungia (Pleuractis)* species, the new one is most easily confused with *F. paumotensis* and *F. gravis*, from which it differs by the wavy appearance of the septa. *F. gravis* occasionally shows sinuous septa, but then usually in combination with the presence of distinct septal lobes, which are absent in *F. seychellensis*. The humped oral surface, which is common in full-grown specimens of *F. gravis*, is absent in the new species. *F. paumotensis*, which also lacks a humped oral surface, has larger septal dentations than found in any of the other *F. (Pleuractis)* species.



Figs. 12-14. Costae of *Fungia (Pleuractis) seychellensis*. Scale bars: 0.5 cm. 12. Holotype (RMNH Coel. 18303). 13. Paratype (RMNH Coel. 18305). 14. Paratype (RMNH Coel. 18310).

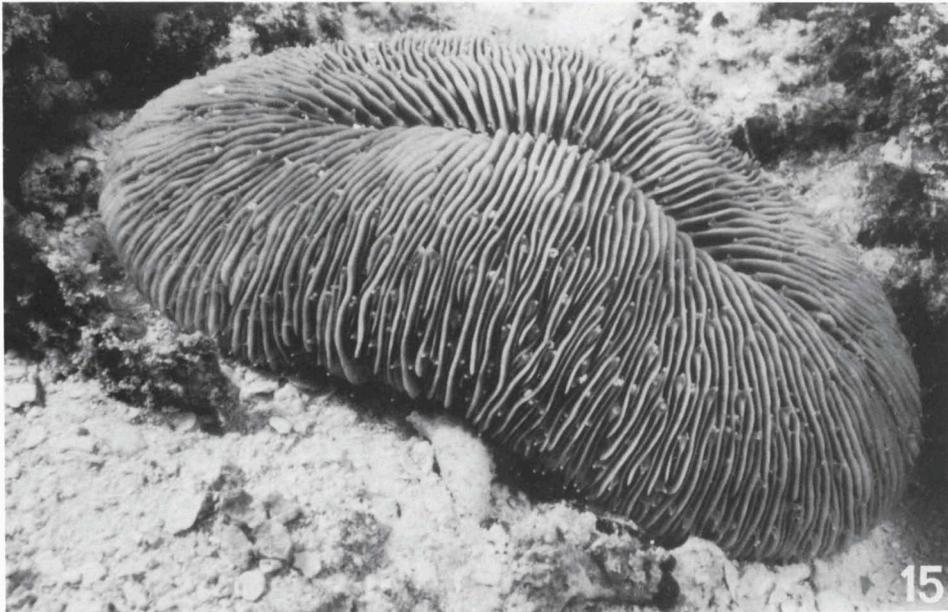


Fig. 15. Live specimen (paratype; length 14.5 cm) of *Fungia (Pleuractis) seychellensis* (RMNH Coel. 18311) from N of Platte Island (photo Mr. W.W.C. Kolvoort).

At first sight, corals of *F. seychellensis* also resemble specimens of *F. (Lobactis) scutaria* Lamarck, 1801, a monostomatous species with a wide distribution range, including the Seychelles. It also has an oval corallum outline and its septa are usually also sinuous, but only where they have to give place to thick tentacular lobes of neighbouring septa. *F. scutaria*, however, is phylogenetically not directly related to any of the *F. (Pleuractis)* species (Hoeksema, 1989); the oval coral outline and the sinuous septa found in both *F. scutaria* and *F. seychellensis* represent apomorphic character states (as compared to an circular coral outline and straight septa) that occur as homoplastic similarities. *F. scutaria* differs from *F. seychellensis* by the presence of small, sharp septal dentations with granulations exclusively in rows perpendicular to the septal margin (a plesiomorphic character state), and by the presence of small costal spines carrying sharp granulations (an apomorphy as compared to the plesiomorphic presence of small simple spines), representing an entirely different evolution lineage than the one leading to the apomorphic blunt, compound spines in *F. (Pleuractis)* (see below, and Hoeksema, 1989).

Geographical distribution.— The species is known exclusively from the reefs around the granitic higher islands on the Seychelles Bank, and from the atolls of the Amirantes Bank and Platte Island (figs. 1, 20).

#### Historical biogeography

Since the most recent review on the taxonomy, phylogeny and biogeography of the Fungiidae (Hoeksema, 1989), two species have been added to *Fungia (Pleuractis)*, namely *F. taiwanensis* and *F. seychellensis*.

Table 1. Character state transformations relevant to the phylogeny of *Fungia* (*Pleuractis*) (partly after Hoeksema, 1989). Characters refer to full-grown specimens.

Apomorph (1, 2, 3)		Plesiomorph (0)	
1a.	(1) Distribution of granulations on septal sides even or irregular	1.	Granulations in rows perpendicular to septal margin
1b.	(2) Granulations on septal sides predominantly in rows parallel to septal margin		
1c.	(3) Granulations more or less fused in ridges parallel to septal margin		
2.	Coral outline oval-elongate	2.	Coral outline round
3.	Coral outline irregular	3.	Coral outline regular
4.	Aboral surface uneven	4.	Aboral surface even
5.	Costae (nearly) equal in size	5.	Costae unequal in size
6.	Costal spines compound, blunt, appearing laterally compressed	6.	Costal spines simple, granular
7.	Oral surface even	7.	Oral surface usually humped
8.	Tentacular lobes absent	8.	Tentacular lobes may be present
9.	Large detachment scar remaining	9.	Detachment scar disappearing
10.	Corals polystomatous by circumoral budding	10.	Corals usually monostomatous
11.	Maximum coral size > 25 cm	11.	Maximum coral size < 22 cm
12.	Septal dentations large (with density usually < 30 per cm)	12.	Septal dentations small (with density usually > 30 per cm)
13.	Septa consistently sinuous	13.	Septa straight or occasionally sinuous
14.	Septa loosely arranged	14.	Septa densely packed
15.	Septal dentations predominantly angular	15.	Septal dentations predominantly granular
16.	Margins of primary septa solid	16.	Margins of primary septa may be perforated

To find out to which other species these two are most closely related, a phylogenetic analysis has been performed using the cladistic computer programme HENNIG86 (Farris, 1988). A total of 16 characters has been used, which are considered relevant to the reconstruction of the phylogeny of *Fungia* (*Pleuractis*) taxa (tables 1-2). This resulted in a single cladogram (fig. 16), which shows a distinction between two monophyletic groups, one consisting of *F. moluccensis* and *F. taiwanensis*, and the other one of *F. gravis*, *F. seychellensis*, and *F. paumotensis*. Apparently, the first two species became isolated from the other three in a relatively early stage in the evolution of *F. (Pleuractis)*. The range of *F. moluccensis* (fig. 18) is nearly similar to the one of *F. paumotensis* (fig. 17). Probably, the range of their most recent common ancestor became disjunct, after which dispersal might have brought them together again. Of these two species, only *F. moluccensis* has been sampled from the Seychelles (see above).

*F. taiwanensis* resembles most closely *F. moluccensis* (Hoeksema & Dai, 1991; Hoeksema, 1991). Full-grown corals of the former species differ by (1) the occurrence of additional mouths, (2) a larger maximum coral size, and (3) the healing of the detachment scar. *F. moluccensis* has a wide distribution (fig. 18), whereas *F. taiwanensis* is known from southern Taiwan (fig. 20). The latter may have evolved sympatrically if its ancestral population at Taiwan became temporarily isolated from other populations by a change in the northward warm Kuroshio current, which at present passes

Table 2. The occurrence of apomorphic (1, 2, 3) and plesiomorphic (0) character states (see table 1) in *Fungia (Pleuractis)* spp. and the outgroup, *F. (Wellsofungia) granulosa*.

Species	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>F. (W.) granulosa</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>F. (P.) moluccensis</i>	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>F. (P.) taiwanensis</i>	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0
<i>F. (P.) gravis</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>F. (P.) seychellensis</i>	2	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0
<i>F. (P.) paumotensis</i>	3	1	0	0	1	1	1	1	0	0	0	1	0	1	1	1

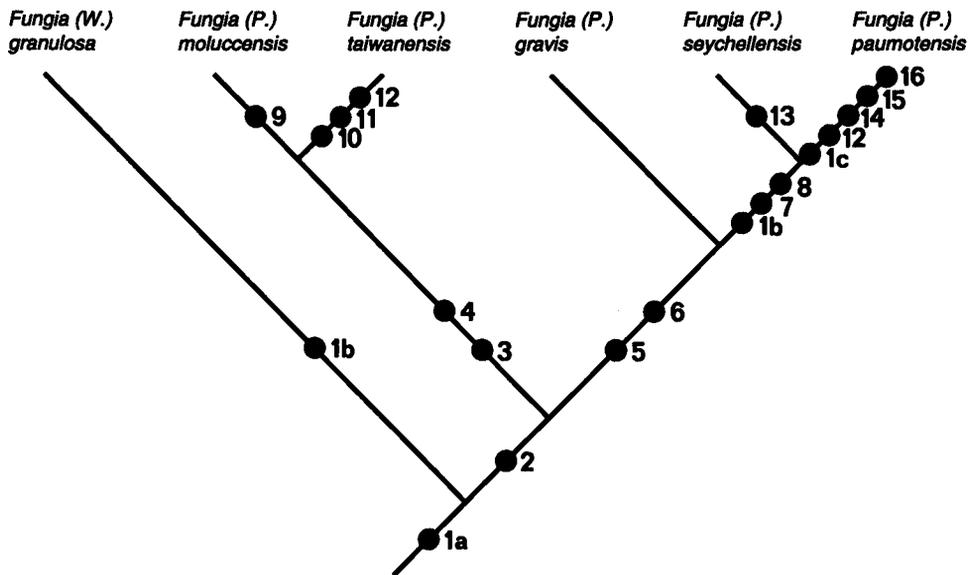


Fig. 16. Phylogenetic reconstruction of *Fungia (Pleuractis)* with *F. (Wellsofungia) granulosa* as outgroup. The tree is composed of 19 steps, it has a consistency index,  $ci = 89$  (indicating that there is little homoplastic similarity), and a retention index,  $ri = 81$  (as measure for apomorphy). Numbers of the character state transformations are explained in table 1.

predominantly east of Taiwan, from the Philippines to Japan, with a westward current branching off south of Taiwan (see Veron, 1992: fig. 3).

The two sister-species co-occur at Taiwan, where they show relatively deep, overlapping depth ranges (Hoeksema & Dai, 1991). *F. taiwanensis* is the most common of the two, particularly on substrata rich in loose sediments. Its convex oral surface enables it to shed sediments, while the extra mouths facilitate the uptake of food, allowing it to overcome size-related constraints (Hoeksema, 1991).

*F. seychellensis* apparently is the sister-species of *F. paumotensis* (fig. 16), which shows the highest number of apomorphic character states among the *F. (Pleuractis)*

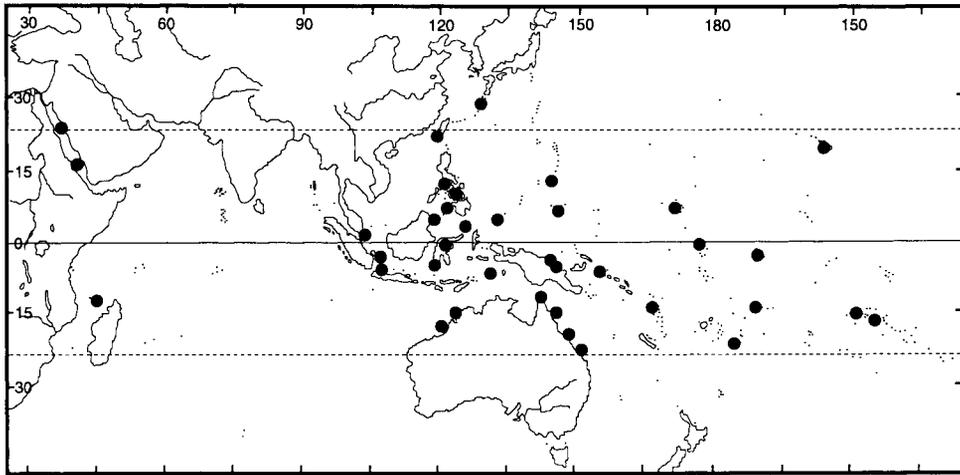


Fig. 17. The known range of *Fungia (Pleuractis) paumotensis* (after Hoeksema, 1989, with new records).

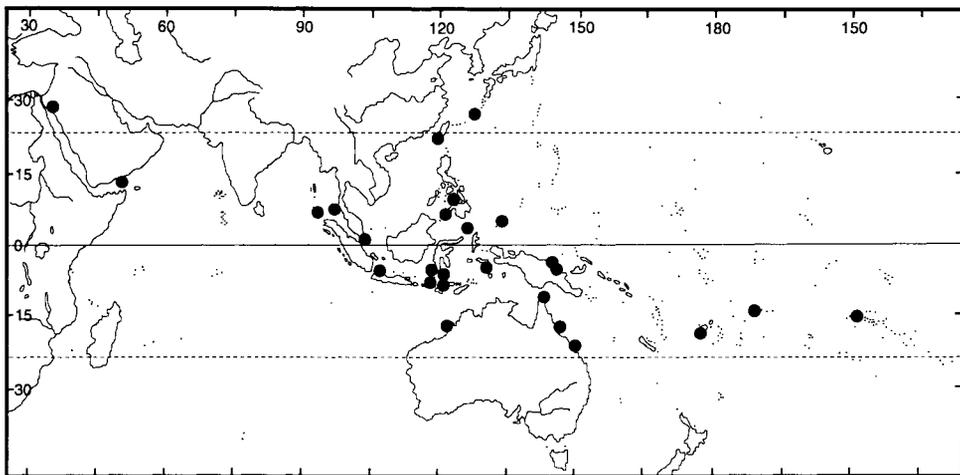


Fig. 18. The known range of *Fungia (Pleuractis) moluccensis* (after Hoeksema, 1989, with a new record).

species. *F. gravis*, which previously was considered the sister-species of *F. paumotensis* (Hoeksema, 1989), resembles *F. seychellensis* more at first sight but appears to be less closely related, since it shares fewer apomorphic character states.

The distributions of *F. seychellensis* (fig. 20) and *F. paumotensis* (fig. 17) are not clearly disjunct, but so far the species have not been found together. Although *F. paumotensis* is not known from the Seychelles, it has been recorded from the Comoro Islands (see above). Perhaps it also occurs on Aldabra (Rosen, 1971a, 1979). Future studies of the fungiid fauna of the western Indian Ocean may confirm whether the ranges of these two sister-species really show no overlap.

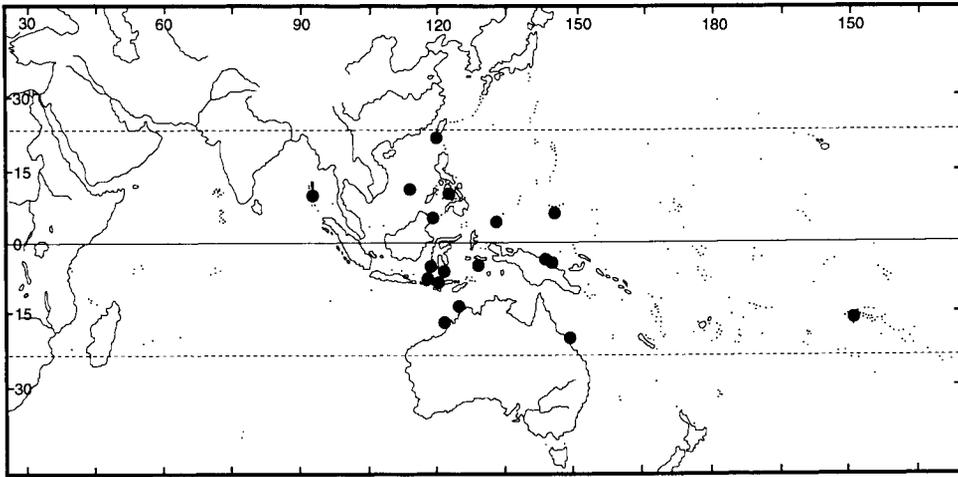


Fig. 19. The known range of *Fungia (Pleuractis) gravis* (after Hoeksema, 1989).

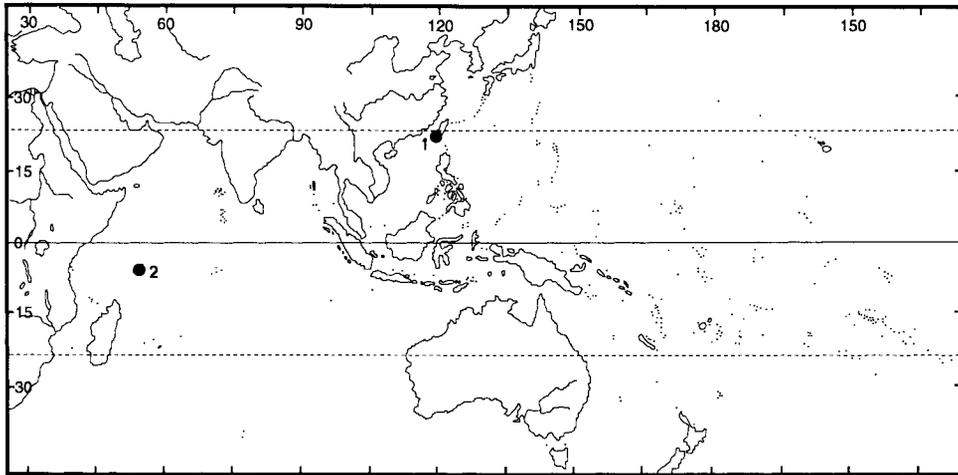


Fig. 20. The localities where *Fungia (Pleuractis) taiwanensis* (1) and *F. (P.) seychellensis* (2) have been found.

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