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Re-examination of the reef corals of Cocos (Keeling) Atoll

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Abstract

Ninety nine species of reef corals are recorded from Cocos (Keeling) Atoll in the eastern Indian Ocean. Of these, all but twelve are known from Western Australia. Nine species have not previously recorded from the eastern Indian Ocean and three (one being taxonomically doubtful) have not previously been recorded anywhere. Principal factors affecting the diversity of species are summarised: the effects of *Acanthaster* outbreaks, short and long-term changes to water circulation in the atoll lagoon, cyclones, and effectiveness of self-seeding. Surface circulation patterns controlling the origins of coral propagules from major reef areas are summarised as far as present knowledge allows. It is concluded that a minimum of 23 days would be necessary for propagule transport from Indonesia in winter and twice that time in March, when the majority of reef corals spawn in Western Australia.

Historical Background

Reef corals of Cocos (Keeling) Atoll have received more that their fair share of attention, partly because the atoll was the only one ever visited by Darwin (in 1836), and partly because of the intrinsic interest in the atoll's geographic isolation.

The first important coral collection from Cocos was made by Forbes in 1879 and deposited in the British Museum. Ridley (1884) described the new genus, *Anacropora*, from this collection, with *Anacropora forbesi* as type species, and in 1885, Ridley and Quelch gave a taxonomic account of the whole collection. In 1905-1907, Wood-Jones collected corals around the atoll and also made the field studies which led to his prophetic paper "On the growth form and supposed species of corals" (1907). This has remained the only field study of Cocos (Keeling) corals.

Wood-Jones sent his collection to the USNM where it was studied by Vaughan and incorporated into his 1918 monograph. In retrospect this was unfortunate. Vaughan published an integrated account of corals from three very distant localities: (Cocos (Keeling) Atoll in the eastern Indian Ocean, Murray I. on the Great Barrier Reef and Fanning I. in the central Pacific Ocean), a task of impossible complexity for the time. Vaughan did, however, record 51 species in Wood-Jones' collection.

Wells (1950) gave the first detailed account of Cocos (Keeling) corals, again based on a previous collection: that made by Gibson-Hill in 1941 and deposited in the Raffles Museum. Gibson-Hill's original collection has since been destroyed (Chou, pers. comm.), but a duplicate, studied by Wells at the USNM (along with Wood-Jones' collection) remains. Gibson-Hill's collection, and therefore Wells' account, was limited to shallow-water environments, but for reef-flats it is very complete. Wells also records many of Gibson-Hills' field notes which make interesting comparisons with the present

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author's observations some 48 years later. Wells lists a total of 74 species, a number only increased to 99 during the present study, using SCUBA.

The primary interest in Cocos (Keeling) corals is now, as originally, in the atolls' isolation. It is 880 and 1830km from the reefs of Java and Western Australia (respectively), with Christmas I. being the only 'stepping-stone' for westerly movement of propagules. The biogeographic affinities of the coral species, therefore, are considered in this paper. Likewise, this paper gives a brief synopsis of the very recent history of the corals which has led to widespread denudation in the lagoon and the outer slope, as well as surface circulation patterns which provide potential pathways for colonisation from major coral reef regions.

Methods and Study Sites

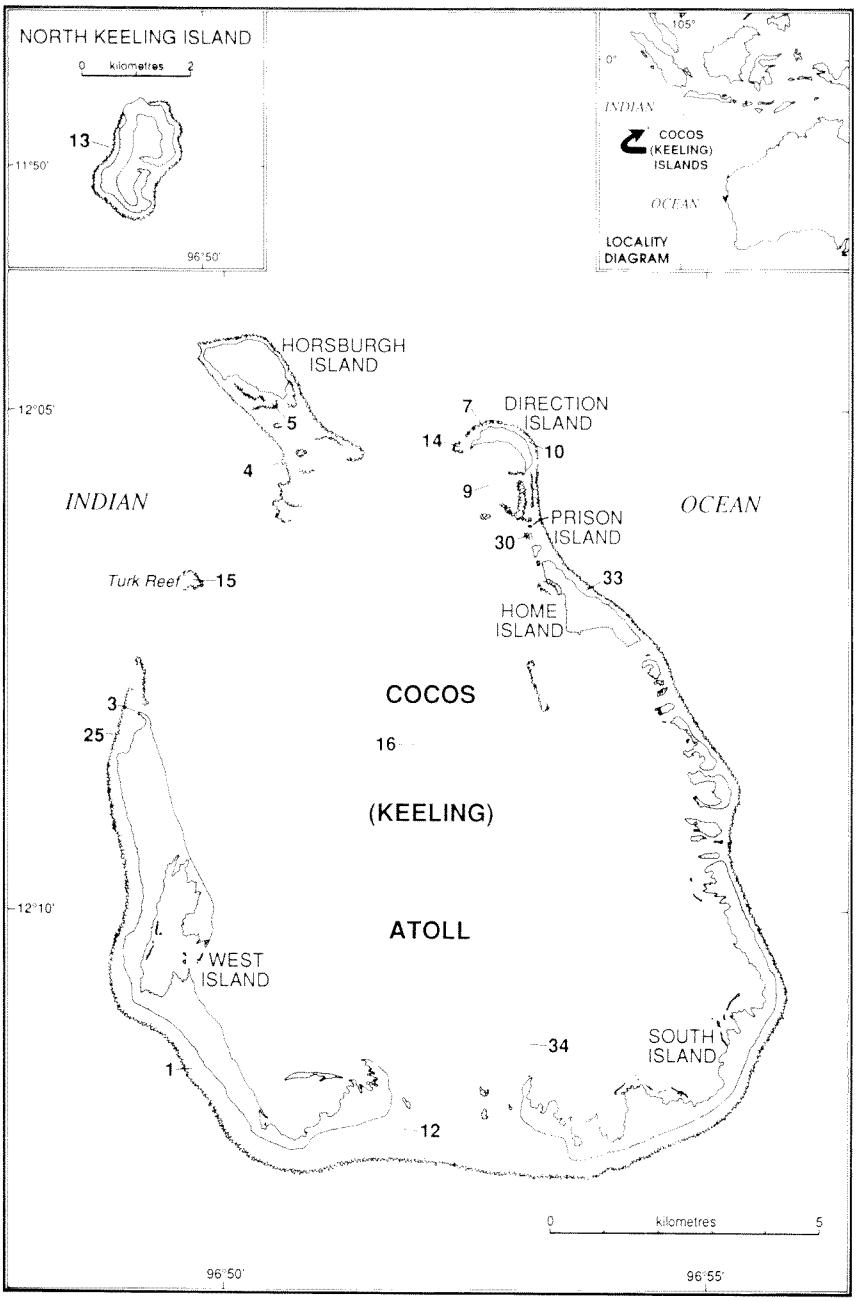
(Figure 1)

Corals were studied at 16 stations around the atoll and at North Keeling I. Numbers given to these stations (below) are expedition collecting stations; only those stations used for the present study are listed. Stations are listed in the order in which they were studied. An accumulative species inventory was compiled, with the aim of reaching a complete list for the atoll as a whole. The total species complement of individual stations is not recorded. Stations were selected to incorporate the widest possible range of environments. SCUBA was used on all reef slopes.

Specimens collected are currently held at the Australian Institute of Marine Science where they were studied and compared with specimens from other geographic regions and with Cocos (Keeling) specimens from the USNM (described by Wells, 1950). No new species are described here but *Stylocoeniella* sp., *Montipora* sp., *Acropora* spp. 1 and 2, *Porites* sp. and *Pavona* sp. remain undetermined and may represent undescribed species. In due course the collection will be lodged in the Western Australian Museum.

In the following account, 'distinguishing characters' are noted only where there are consistent differences between Cocos (Keeling) corals and the same species from geographical (mainland) western or eastern Australia. Nomenclature follows Veron (1986).

1. West I., W side, reef flat. Very low diversity.
3. West I., NW corner, reef flat. *Acropora pulchra, A. aspera* and *A. formosa* occur as compact, extensive stands.
4. Horsburgh I., SW corner, reef slope, 10-20m. Very extensive stands of *Pachyseris speciosa* S of Boat Passage and *Turbinaria reniformis* to the north.
5. Horsburgh I., S side, sand flat, 0-3m. Very extensive intertidal stands of *Montipora digitata.*
7. Direction I., N. side, reef slope, 10-17m. Low diversity, *Pocillopora eydouxi* dominant.
8. Director I., S.E. side, reef channel (the 'rip').
9. Direction I., S side, lagoon, 10-18m. Very extensive stands of *Leptoseris papyracea.*


NORTH KEELING ISLAND
0 kilometres 2
13
11°50'
96°50'
105°
0°
INDIAN
COCOS (KEELING) ISLANDS
OCEAN
LOCALITY DIAGRAM
HORSBURGH ISLAND
12°05'
5
4
INDIAN
7
DIRECTION ISLAND
14
10
9
PRISON ISLAND
OCEAN
30
33
Turk Reef
15
HOME ISLAND
COCOS
3
25
16
(KEELING)
ATOLL
12°10'
WEST ISLAND
34
SOUTH ISLAND
1
12
0 kilometres 5
96°50'
96°55'

10. Direction I., N side, reef flat. *Porites* dominant.
12. West I., SE end, reef flat. *Porites* dominant.
13. North Keeling I., W side, reef slope, 10-25m. Moderate diversity.
14. Direction I., W side, reef flat. *Porites* dominant.
15. Turk Reef, W side, reef slope, 10-30m. Low diversity.
16. Central atoll lagoon, 5-18m. Formerly with extensive stands of *Acropora pulchra* and other *Acropora,* now almost entirely dead.
25. West I., W side of N end, reef slope, 12-30m. Low diversity.
30. Between Prison and Home Is., reef flat.
33. Home I., E side, reef slope, 12-35m. Low diversity.
34. South I., N of W end, reef flat. *Porites* dominant.

Systematic Account of Species

FAMILY ASTROCOENIIDAE Koby, 1890

GENUS STYLOCOENIELLA Yabe & Sugiyama, 1935

Stylocoeniella guentheri (Bassett-Smith, 1890)

Previous Records: Wells (1950)

Present Records: Three specimens, station 13 (WAM 350-89). Found on most reef slopes. Inconspicuous.

Distinguishing Characters: Usually dark green, encrusting to sub-massive. Septa strongly alternate. Primary septa do not reach the boss-like columella.

Stylocoeniella armata (Ehrenberg, 1834)

Previous Records: None

Present Records: Two specimens, stations 4 and 9 (WAM 351-89, 352-89). Rare, inconspicuous.

Distinguishing Characters: Septa clearly alternate. Primary septa reach the columella which is thin, style-like.

Stylocoeniella sp.

Previous Records: None.

Present Records: One specimen, station 9 (WAM 353-89). Not separated from *S. guentheri in situ.*

Distinguishing Characters: Corallites are irregularly exsert. Septa are in two sub-equal cycles, fine. Columellae are very small. Coenosteum spinules very fine. Each corallite has a prominent style. It is likely that this is a new species, to be described if further studied.

FAMILY POCILLOPORIDAE Gray, 1842

Pocillopora is abundant in almost all coral communities, Seriatopora is usually uncommon. The other genera, notably Stylophora, have not been recorded.

GENUS POCILLOPORA Lamarck, 1816

Pocillopora damicornis (Linnaeus, 1758)

Previous Records: Ridley & Quelch (1885) (as *P. brevicornis*), Vaughan (1918); Wells (1950)

Present Records: One specimen, station 3 (WAM 354-89). Uncommon but found in a wide range of environments.

Distinguishing Characters: Usually pink in colour. Indistinguishable from Australian colonies.

Pocillopora verrucosa (Ellis & Solander, 1786)

Previous Records: Vaughan (1918); Wells (1950)

Present Records: Three specimens, stations 7 and 13 (WAM 355-89, 356-89). Common on most upper reef slopes.

Distinguishing Characters: Yellow or pinkish in colour. Indistinguishable from Australian colonies.

Pocillopora meandrina Dana, 1846

Previous Records: Vaughan (1918); Wells (1950), (both as *P. elegans* Dana)

Present Records: One specimen, station 7 (WAM 357-89). Common on most upper reef slopes.

Distinguishing Characters: Distinguished from *P. verrucosa* by having smaller verrucae and as described by Veron & Pichon (1982).

Pocillopora woodjonesi Vaughan, 1918

Previous Records: Vaughan (1918) with the Cocos (Keeling) Is. as type locality; Wells (1950)

Present Records: Two specimens, stations 13 and 25 (WAM 358-89, 359-89). Uncommon.

Distinguishing Characters: Difficult to distinguish from *P. eydouxi*. Colonies identified as *P. woodjonesi in situ* did not have the species specific skeletal characters described by Vaughan (1918) and Wells (1950) and used by the present author. The taxonomic status of this species requires further study.

Pocillopora eydouxi Edwards & Haime, 1860

Previous Records: Vaughan (1918)

Present Records: Seven specimens, stations 3, 7, 13 and 25 (WAM 360-89, 361-89, 362-89, 363-89). Common in most coral communities.

Distinguishing Characters: Indistinguishable from Australian colonies.

GENUS SERIATOPORA Lamarck, 1816

Seriatopora hystrix Dana, 1846

Previous Records: Vaughan (1918) (Wells (1950; both as *S. angulata* Klunzinger)

Present Records: One specimen, station 4 (WAM 364-89). Gibson-Hill notes the species occurs in "large beds in shallow, sandy, slightly weedy water inside the lagoon ..." (Wells, 1950). The few colonies observed during the present study were small and isolated.

Distinguishing Characters: Indistinguishable from Australian colonies.

FAMILY ACROPORIDAE Verrill, 1902

GENUS MONTIPORA de Blainville, 1830

Montipora monasteriata (Forskål, 1775)

Previous Records: None

Present Records: Two specimens, stations 9 and 13 (WAM 365-89, 366-89). Common in a wide range of environments.

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora tuberculosa (Lamarck, 1816)

Previous Records: None

Present Records: Three specimens, stations 3 and 4 (WAM 367-89, 368-89). Common.

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora lobulata Bernard, 1897

Previous Records: Wells (1950)

Present Records: Two specimens, stations 7 and 33 (WAM 369-89, 370-89).

Distinguishing Characters: The holotype from the British Museum (Natural History) from Diego Garcia (figured, Bernard (1897), Pl. XIV) is very similar to one corallum of the present study (from station 7) but less so to the second specimen (from station 33) and Wells' specimen collected by Gibson-Hill (USNM 44327). Further study of intra-specific variation is required before this group of coralla can be conclusively referred to the same species. It has not been recorded from Australia. Bernard's (1897) second specimen, from Mauritius, is likely to be another species, but was not re-examined during the present study.

Montipora mollis Bernard, 1897

Previous Records: None

Present Records: One specimen, station 9 (WAM 371-89). Probably uncommon

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora peltiformis Bernard, 1897

Previous Records: None.

Present Records: Eight specimens, stations 13 and 25 (WAM 372-89, 373-89). Common on some reef slopes.

Distinguishing Characters: Corallites of four specimens from station 13 are larger than usual for coralla from Western Australia. There are no other differences.

Montipora capricornis Veron, 1985

Previous Records: Not recorded

Present Records: Two specimens, station 16 (WAM 374-89). Uncommon except in the atoll lagoon where this species is an early coloniser of denuded areas.

Distinguishing Characters: Intra-specific variation was not studied.

Montipora spumosa (Lamarck, 1816)

Previous Records: Vaughan (1918) and Wells (1950) (two specimen only)

Present Records: Not recorded during the present study.

Distinguishing Characters: Specimen 44326 from the USNM falls within the range of variation of Australian coralla.

Montipora danae (Edwards & Haime, 1851)

Previous Records: None

Present Records: Three specimens, stations 5, 9 and 13 (WAM 375-89, 376-89, 377-89). Uncommon.

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora angulata (Lamarck, 1816)

Previous Records: Vaughan (1918) (as *M. cocosensis* Vaughan, with Cocos (Keeling) Is. as type locality).

Present Records: Five specimens, stations 5, 12, 13 and 30 (WAM 378-89, 379-89, 380-89, 381-89). Uncommon. Found only on reef flat or sub-tidal sand flats with *M. digitata*.

Distinguishing Characters: Thick branches becoming columnar, with conspicuous open corallites.

Montipora digitata (Dana, 1846)

Previous Records: Ridley & Quelch (1886) (as *M. laevis* Quelch); Wells (1950) (as *M. laevis* Quelch *M. ramosa* Bernard and *M. rubra* Quoy & Gaimard)

Present Records: Eleven specimens, stations 3, 5, 9 and 35 (WAM 382-89, 383-89, 384-89, 385-89). Forms extensive monospecific stands on intertidal sand flats, especially station 5.

Distinguishing Characters: Intermixed with *Montipora* sp. Indistinguishable from Australian colonies.

Montipora sp.

Previous Records: None

Present Records: Two specimens, stations 3 and 14 (WAM 386-89, 387-89).

Distinguishing Characters: A sub-arborescent species similar to *M. digitata,* primarily distinguished by high reticulum ridges between corallites and flattened branch tips with few corallites. The present specimens do not belong to any previously recorded or described species known to the author.

Montipora efflorescens Bernard, 1897

Previous Records: None

Present Records: Four specimen, stations 4, 13 and 25 (WAM 388-89, 389-89, 390-89).

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora grisea Bernard, 1897

Previous Records: None

Present Records: Two specimens, stations 4 and 7 (WAM 391-89, 392-89).

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora informis Bernard, 1897

Previous Records: Vaughan (1918)

Present Records: One specimen, station 13 (WAM 393-89). Rare.

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora foliosa (Pallas, 1766)

Previous Records: Vaughan (1918); Wells (1950)

Present Records: Five specimens, stations 4, 9 and 13 (WAM 394-89, 395-89, 396-89). Uncommon.

Distinguishing Characters: Indistinguishable from Australian colonies.

Montipora aequituberculata Bernard, 1897

Previous Records: None

Present Records: Four specimens, stations 4 and 13 (WAM 397-89, 398-89). Common on some outer slopes.

Distinguishing Characters: Usually dark grey or brown. Indistinguishable from Australian colonies.

GENUS ANACROPORA Ridley, 1884

Anacropora forbesi Ridley, 1884

Previous Records: Ridley, 1884, with Cocos (Keeling) Atoll as type locality.

Present Records: Not found during the present study.

Distinguishing Characters: Syntype 1884.2.16.40-47 of this species from the British Museum (Natural History) was re-examined during this study. It is indistinguishable from Australian coralla.

GENUS ACROPORA Oken, 1815

One of the most distinctive characters of Cocos (Keeling) I. corals is the low diversity and, usually, the low abundance of *Acropora*. The only extensive stands of living *Acropora* are on reef flats, notably at station 3. Very extensive stands of dead arborescent species, mainly *pulchra* and *formosa*, occur in the lagoon and extensive dead tabular colonies, no longer identifiable, occur at North Keeling I. (station 13).

Acropora palifera (Lamarck, 1816)

Previous Records: Vaughan (1918)

Present Records: One specimen, station 3 (WAM 399-89). Seldom common.

Distinguishing Characters: Both reef slope and lagoon colonies are similar in growth form and corallite structures and represent only a small part of the variation described by Veron & Wallace (1984) and studied using electrophoresis, Ayre *et al. (in prep.)*

Acropora ocellata (Klunzinger, 1879)

Previous Records: Vaughan (1918), Wells (1950)

Present Records: Four specimens, stations 7 and 25 (WAM 400-89, 401-89). Uncommon.

Distinguishing Characters: This species belongs with the *A. humilis* group, with a growth form similar to *A. humilis* (Dana). Axial corallites are similar in size and shape to those of *A. monticulosa* (Brüggemann). Radial corallites are large, round, irregular, some immersed, others large and elongated, becoming incipient axials.

A specimen described by Wells (USNM 44318) has been re-examined during the present study. All specimens, including those figured by Vaughan (1918), are clearly the same species which shows no difference from the holotype of Klunzinger (Museum fur Natuurkunde der Humboldt Universitat, Berlin 2114).

Living colonies are pale brown with white branch tips.

Acropora robusta (Dana, 1846)

Previous Records: Wells (1950) (as *A. pinguis*, described as a new species from Cocos (Keeling) Atoll).

Present Records: One specimen, station 3 (WAM 402-89). Very rare, found at station 3 only. Gibson-Hill comments, "This coral occurs in two large masses, each about three feet across, on the outer edge of the barrier behind Pulo Tikus. I was unable to find any other examples elsewhere on the island." (Wells, 1950).

Distinguishing Characters: Veron & Wallace (1984) note that "Wells' holotype of *A. pinguis* from the Cocos-Keeling Islands differs from east Australia *A. robusta* by having

relatively small, uniform corallites, but in all other respects it is similar". This specimen (USNM 44317) has been re-examined with the corallum from the present study. These form a clear series. The field observation that Cocos (Keeling) colonies have the very characteristic growth form of *A. robusta* in exposed environments supports the synonymy.

Acropora danai (Edwards & Haime, 1860)

Previous Records: Wells (1950) (as *A. irregularis*, described as a new species from Cocos (Keeling) Atoll).

Present Records: One specimen, station 25 (WAM 403-89). Rare.

Distinguishing Characters: Growth form is the same as Australian colonies. Corallites near branch tips may become relatively elongate.

Acropora sp. 1

Previous Records: Vaughan (1918), Wells (1950) (as *A. pharaonis* Edwards & Haime).

Present Records: Three specimens, stations 3, 12 and 35 (WAM 404-89, 405-89, 406-89). Sometimes common in shallow water.

Distinguishing Characters: Vaughan (1918) gives a very extensive account of this species which incorporates descriptions of earlier authors. The present species corresponds closely with Vaughan's descriptions and photographs and also Wells' specimen (USNM 44314).

Colonies are arborescent, forming thickets in shallow water where some branches may be fused. Branches are mostly straight and tapered. Radial corallites are of two sizes, the larger arranged in rows. They are similar in structure to those of *A. valenciennesi.*

The type specimen of *A. pharaonis* from the Red Sea (Museum National d'Histoire Naturelle, Paris (300d), and a specimen in the Museum of Comparative Zoology, Harvard) are, as noted by Veron & Wallace (1982), close to *A. horrida* (Dana).

Acropora formosa (Dana, 1846)

Previous Records: Wells (1950)

Present Records: Two specimens, stations 3 and 14 (WAM 407-89, 408-89). Uncommon except on some reef flats. Gibson-Hill records it as being "plentiful" (Wells, 1950).

Distinguishing Characters: Reef flat colonies have short branches with proliferous sub-branches. No colonies with long undivided branches were seen. Mostly yellowish in colour.

Acropora microphthalma (Verrill, 1859)

Previous Records: None

Present Records: Two specimen, stations 3 and 4 (WAM 409-89, 410-89). Common on reef flats and some reef slopes.

Distinguishing Characters: Indistinguishable from Australian colonies.

Acropora exquisita Nemenzo, 1967

Previous Records: Possibly Wells (1950) (as *A. irregularis* (Brook)).

Present Records: Two specimens, stations 4 and 9 (WAM 411-89, 412-89). Uncommon.

Distinguishing Characters: Indistinguishable from more robust colonies from Australian North-west shelf reefs. Pale colours.

Acropora aspera (Dana, 1846)

Previous Records: Vaughan (1918) (possibly as *A. spicifera*); Wells (1950) (as *A. hebes*)

Present Records: Two specimens, station 3 (WAM 413-89). Uncommon except at station 3 and only found on reef flats.

Distinguishing Characters: Reddish-brown in colour. Indistinguishable from Australian colonies.

Acropora pulchra (Brook, 1891)

Previous Records: Vaughan (1918)

Present Records: Two specimens, stations 3 and 9 (WAM 414-89, 415-89). Formerly very abundant throughout much of the southern lagoon, forming very extensive stands often over 20m across. Now common on some reef flats, notably station 3 and also found on some reef slopes.

Distinguishing Characters: Indistinguishable from Australian colonies.

Acropora cytherea (Dana, 1846)

Previous Records: None

Present Records: Three specimens, stations 3, 7 and 15 (WAM 416-89, 417-89, 418-89). Uncommon. The largest colonies observed were <1m diameter.

Distinguishing Characters: Indistinguishable from Australian colonies.

Acropora paniculata Verrill, 1902

Previous Records: None

Present Records: Five specimens, stations 1, 4 and 13 (WAM 419-89, 420-89, 421-89). Rare.

Distinguishing Characters: Of the five coralla of the present series, one has an open branching pattern (as illustrated, Figure 756 of Veron & Wallace 1982). The remainder have increasing degrees of branch fusion, two being almost solid. All lack the great profusion of elongate radial corallites common in most eastern Australian coralla. It appears that this series is a distinct geographic sub-species of *A. paniculata*, but as the latter is know in the Indian Ocean from only a single specimen (from Ashmore Reef, Veron & Marsh, 1988), no definite conclusion is possible.

Acropora hyacinthus (Dana, 1846)

Previous Records: None

Present Records: One specimen, station 3 (WAM 422-89). Rare.

Distinguishing Characters: Only stunted reef flat colonies were found.

Acropora latistella (Brook, 1891)

Previous Records: None

Present Records: One specimen, station 3 (WAM 423-89). Rare, found only on reef flats.

Distinguishing Characters: This species was not found as large tabular colonies. Branchlets are thinner than usual for shallow-water Australian colonies.

Acropora nana (Studer, 1878)

Previous Records: Wells (1950)

Present Records: One specimen, station 3 (WAM 424-89). Found only on outer reef flats and upper slopes.

Distinguishing Characters: Colonies are relatively small, otherwise indistinguishable from Australian colonies.

Acropora subulata (Dana, 1846)

Previous Records: None

Present Records: Two specimens, station 3 (WAM 425-89). Rare.

Distinguishing Characters: Recorded only from station 3 where colonies from irregular small

plates. Nothing is known of environment-related growth from variation.

Acropora valida (Dana, 1846)

Previous Records: Vaughan (1918) and Wells (1950) (as *A. variabilis* (Klunzinger)).

Present Records: One specimen, station 3 (WAM 426-89). Rare, Gibson-Hill records this species from several reef flat localities (Wells, 1950).

Distinguishing Characters: Corallites are smaller and have thinner walls than usual for the species, but nothing is known of environment-related variation. Coralla from Cocos (Keeling) illustrated by Vaughan (1918) (pl. 80) have the characters of the species more clearly developed. Gibson-Hill (and this author) records the colour as "dirty-white, with faint lavender-blue tips" (Wells, 1950).

Acropora sp. 2

Previous Records: None

Present Records: Two specimens, stations 4 and 7 (WAM 427-89, 428-89). Rare.

Distinguishing Characters: Colonies are irregularly arborescent. Corallites are very irregular, some being *valida*-like and strongly oppressed. The species was not sufficiently

abundant for detailed study and nothing is known of environment-related skeletal variation.

Acropora schmitti Wells, 1950

Previous Records: Wells (1950), described as a new species from Cocos (Keeling) Atoll.

Present Records: Not found during the present study. Gibson-Hill notes, "This coral, which is rather similar to [*A. valida*] in both colour and form, occurs in shallow pools on the middle section of the barrier, and on part of its seaward edge. It is not very plentiful, but it seems to be most numerous at the back of Pulo Tikus, where [five] specimens were taken" (Wells, 1950).

Distinguishing Characters: Wells (1950) notes that "the distinctive character of this species is the extraordinary thickness of the outer lip of the radial corallites, which gives them the appearance of hemispherical bowls attached to the branch by one side or by a very short thick handle." The holotype (USNM) has been re-examined during the present study. It may be a species recorded from Thailand and the Philippines (called Acropora sp. by Veron & Hodgson, 1989).

GENUS ASTREOPORA de Blainville, 1830

Astreopora myriophthalma (Lamarck, 1816)

Previous Records: Vaughan (1918), Wells (1950)

Present Records: One specimen, station 3 (WAM 429-89). Common in a wide range of environments.

Distinguishing Characters: Indistinguishable from Australian colonies. Colours vary from dark purple to cream and pale pink.

Astreopora gracilis (Bernard, 1896)

Previous Records: None

Present Records: Three specimens, station 7 and 13 (WAM 430-89, 431-89). Usually uncommon.

Distinguishing Characters: Indistinguishable from Australian colonies. Colours are cream and pale pinkish-purple.

FAMILY PORITIDAE Gray, 1842

Goniopora and *Alveopora* have not been recorded from Cocos (Keeling) Atoll.

GENUS PORITES Link, 1807

Porites solida (Forskål, 1775)

Previous Records: Vaughan (1918) and Wells (1950)

Present Records: Two specimens, stations 12 and 30 (WAM 432-89, 433-89). Uncommon.

Distinguishing Characters: Two specimens studied were indistinguishable from Australian coralla.

Porites lobata Dana, 1846

Previous Records: None

Present Records: Three specimens, stations 12 and 13 (WAM 434-89, 435-89).

Distinguishing Characters: Indistinguishable from Australian colonies.

Porites australiensis Vaughan, 1918

Previous Records: None

Present Records: Six specimens, from stations 1, 7 and 13 (WAM 436-89, 437-89, 438-89).

Distinguishing Characters: Corallites have a very distinct wall formed by lateral fusion of denticles.

Porites somaliensis Gravier, 1911

Previous Records: ?Guppy (1889) (as *P. clavaria*), Vaughan (1918)

Present Records: Nine specimens, stations 1, 3, 12, 14 and 34 (WAM 439-89, 440-89, 441-89, 442-89, 443-89). The most abundant massive *Porites* on some reef flats and the dominant species of stations 14 and 34.

Distinguishing Characters: Colonies from shallow water usually have a knobbly growth form. Corallites are closest to *P. stephensoni* but the present species appears to be distinct from any Australian species. The triplet is sometimes fused and columellae are laterally compressed in the line of the directive septa forming a conspicuous line.

Porites cf. ***evermanni*** Vaughan, 1907

Previous Records: None

Present Records: Two specimens, station 9 (WAM 444-89). Rare, but very distinctive.

Distinguishing Characters: Indistinguishable from specimens of this species recorded from Australia, the Philippines (Veron & Hodgson, 1989) and elsewhere.

Porites cylindrica Dana, 1846

Previous Records: Guppy (1889) (as *P. palmata*), Ridley & Quelch (1885) (as *P. levis* Dana), Vaughan (1918) (as *P. nigrescens*), Wells (1950) (as *P. nigrescens* and *P. gibsonhilli*). Cocos (Keeling) atoll is the type locality of *P. gibsonhilli* Wells. The holotype falls within the range of variation of *P. cylindrica,* variation which includes deeply excavated corallites believed by the author to be a product of parasites. Wells' holotype (USNM 44337) and specimens of '*P. nigrescens*' collected by Wood-Jones (USNM) were re-examined during the present study.

Porites cocosensis Wells, described from two specimens from Cocos (Keeling) Atoll, may also be a synonym of *P. cylindrica.* The holotype (USNM 44339), re-examined during the present study, is a corallith and is therefore unlikely to be clearly representative of any species. Corallites are well defined and relatively deeply excavated, more so than in any specimen of the present series. Field notes from Gibson-Hill (Wells, 1950) closely correspond with present-day *P. cylindrica.* The present study, however, cannot resolve this problem.

Present Records: Seven specimens stations 4, 9 and 12 (WAM 445-89, 446-89, 447-89). The most common species of intertidal reef flats and forms extensive stands on some upper reef slopes.

Distinguishing Characters: Indistinguishable from Australian coralla.

Porites lichen Dana, 1846

Previous Records: Vaughan (1918)

Present Records: Not found during the present study.

Distinguishing Characters: Indistinguishable from Australian coralla.

Porites rus (Forskål, 1775)

Previous Records: None

Present Records: Three specimens, stations 4 and 13 (WAM 448-89, 449-89). Common.

Distinguishing Characters: Forms extensive flat plates with short, irregular, columns and branches. Usually fawn or brown.

Porites sp.

Previous Records: None

Present Records: Two specimens, stations 4 and 9 (WAM 450-89, 451-89).

Distinguishing Characters: Forms plates and irregular branches and columns. Corallites are essentially similar to those of *P. rus* and *P. latistella* Quelch, but are smaller than both. The species appears to be undescribed. Usually brightly coloured: green, blue or yellow.

Colonies of this species are readily distinguished from *P. rus in situ*. Skeletal differences between the two require further study.

FAMILY SIDERASTREIDAE Vaughan & Wells, 1943

Pseudosiderastrea and *Coscinaraea* have not been recorded from Cocos (Keeling).

GENUS PSAMMOCORA Dana, 1846

Psammocora sp. of Vaughan (1918) is unlikely to be *Psammocora vaughani* Yabe & Sugiyama, 1936 although this species was named by these authors on the basis that their specimens from Japan were the same species.

Psammocora digitata Edwards & Haime, 1851

Previous Records: Wells (1950) (as *P. togianensis* Umbgrove).

Present Records: This species was not found during the present study.

Psammocora superficialis Gardiner, 1989

Previous Records: Vaughan (1918) (as *Psammocora* sp.). Uncommon.

Present Records: Two specimens, station 4 (WAM 452-89).

Distinguishing Characters: Indistinguishable from Australian colonies. Colonies are encrusting and may be over 1m diameter. These large colonies have relatively coarse skeletal characters. Colour is very uniform within colonies, mostly battleship grey, rarely bright green.

Psammocora profundacella Gardiner, 1898

Previous Records: Vaughan (1918) and Wells (1950) (as *P. haimeana*)

Present Records: Four specimens, stations 1 and 7 (WAM 453-89, 454-89). Very common in a wide range of environments. Gibson Hill notes it "occurs in the pools over the inner and middle portion of the barrier" and that, "it is not plentiful" (Wells, 1950).

Distinguishing Characters: Indistinguishable from Australian colonies. It may form coralliths. Usually pale pink or green, but may be dark green. Sometimes with blue centres. Gibson-Hill, referring to reef-flat colonies, notes that "it is a pearl-grey colour" (Wells, 1950).

FAMILY AGRICIIDAE Gray, 1847

GENUS PAVONA Lamarck, 1801

Pavona cactus (Forskål, 1775)

Previous Records: Wells (1950)

Present Records: Two specimens, station 9 (WAM 455-89). Found only at station 9 where it is common only in small isolated patches. Gibson-Hill records "It is most plentiful in the shallow water immediately internal to the channel [south of Home Island]" (Wells, 1950).

Distinguishing Characters: Indistinguishable from Australian colonies.

Pavona frondifera Lamarck, 1801

Previous Records: None

Present Records: Two specimens, station 9 (WAM 456-89). Found only at station 9 where it is common only in small isolated patches intermixed with *P. cactus*.

Distinguishing Characters: Colonies are partly encrusting and have small, irregular, upright fronds. Dark greenish-brown with pale fronds.

Pavona decussata (Dana, 1846)

Previous Records: Vaughan (as *P. danai* (Edwards & Haime), Wells (1950).

Present Records: Two specimens, station 12 (WAM 457-89). Known from two reef flat colonies only.

Distinguishing Characters: Coralla are composed of highly anastomosed plates, a growth form common on reef flats. Skeletal detail is indistinguishable from Australian coralla.

Pavona explanulata (Lamarck, 1816)

Previous Records: None

Present Records: Nine specimens, station 4, 7 and 13 (WAM 458-89, 459-89, 460-89). Usually uncommon but conspciuous.

Distinguishing Characters: Colonies are massive or columnar. Pale or dark brown in colour. Plate-like colonies, common in Australia, were seldom seen.

Pavona minuta Wells, 1956

Previous Records: None

Present Records: Eight specimens, sites 4, 7 and 13 (WAM 461-89, 462-89, 463-89). Common on some exposed reef sites.

Distinguishing Characters: Colonies are massive or columnar, rarely encrusting. All colonies observed were <0.5m. Grey in colour.

Pavona varians Verrill, 1846

Previous Records: Vaughan (1918)

Present Records: Nine specimens, collecting stations 4, 7, 13, 25 and 30 (WAM 464-89, 465-89, 466-89, 467-89, 468-89). Very common in a wide range of reef slope environments.

Distinguishing Characters: Forms large encrusting plates under overhangs. Very dark colours except in niches exposed to strong sunlight.

Pavona venosa (Ehrenberg, 1834)

Previous Records: None

Present Records: One specimen, station 5 (WAM 469-89). No other records.

Distinguishing Characters: Septa are very coarse making the single specimen found very distinctive.

Pavona maldivensis (Gardiner, 1905)

Previous Records: Vaughan (1918)

Present Records: Three specimens, station 13 (WAM 470-89). Rare.

Distinguishing Characters: Indistinguishable from Australian colonies.

Pavona sp.

Previous Records: None

Present Records: Three specimens, stations 13 and 25 (WAM 471-89, 472-89). Rare.

Distinguishing Characters: Colonies are flat unifacial plates. Corallites are very small, similar to those of *P. bipartita* Nemenzo, but with smaller calice centres and tendency to become sub-plocoid.

GENUS LEPTOSERIS Edwards & Haime, 1894

Leptoseris papyracea (Dana, 1846)

Previous Records: None

Present Records: One specimen, station 9 (WAM 473-89). Forms an extensive carpet of some hundreds of square metres at station 9.

Distinguishing Characters: Indistinguishable from fine, highly compact Australian colonies. Pale pinkish-brown in colour.

Leptoseris explanata Yabe & Sugiyama, 1941

Previous Records: None

Present Records: One specimen, station 9 (WAM 474-89). Rare.

Distinguishing Characters: The single specimens studied is indistinguishable from Australian colonies.

Leptoseris mycetoseroides Wells, 1954

Previous Records: None

Present Records: Two specimens, stations 4 and 25 (WAM 475-89, 476-89). Rare.

Distinguishing Characters: Indistinguishable from Australian colonies.

GENUS GARDINEROSERIS Scheer & Pillai, 1974

Gardineroseris planulata (Dana, 1846)

Previous Records: None

Present Records: Two specimens, stations 4 and 13 (WAM 477-89, 478-89). Uncommon although found in a wide variety of habitats.

Distinguishing Characters: Colonies are flat or dome-shaped, up to 1m high, pale brown in colour. Indistinguishable from Australian colonies.

GENUS PACHYSERIS Edwards & Haime, 1849

Pachyseris speciosa (Dana, 1846)

Previous Records: None

Present Records: One specimen, station 4 (WAM 479-89). Forms very extensive monospecific stands at station 4 south of 'Boat Passage'.

Distinguishing Characters:

Indistinguishable from Australian colonies. The full range of variation of the species, as described by Veron & Pichon (1980), can be seen at station 4.

FAMILY FUNGIIDAE Dana, 1846

GENUS FUNGIA Lamarck, 1801

Fungia fungites (Linnaeus, 1858)

Previous Records: Wells (1950)

Present Records: One specimen, station 13 (WAM 480-89). Uncommon.

Distinguishing Characters: Indistinguishable from Australian coralla.

Fungia concinna Verrill, 1864

Previous Records: None

Present Records: One specimen, station 16 (WAM 481-89). This is the only record of the species.

Distinguishing Characters: The single specimen collected is indistinguishable from Australian coralla.

Fungia granulosa Klunzinger, 1879

Previous Records: None

Present Records: One specimen, station 15 (WAM 482-89). This is the only record of the species.

Distinguishing Characters: Indistinguishable from Australian coralla.

Fungia scutaria Verrill, 1801

Previous Records: Vaughan (1918), Wells (1950)

Present Records: Three specimens, from stations 4, 13 and 15 (WAM 483-89, 484.89, 485-89). Common on reef slopes.

Distinguishing Characters: Indistinguishable from Australian coralla except for colour. Usually cream with blue or white tentacular lobes, occassionally pink.

GENUS HERPOLITHA Eschscholtz, 1825

Herpolitha limax Houttuyn, 1772

Previous Records: Vaughan (1918) (as *H. crassa* Dana), Wells (1950)

Present Records: One visual record, station 9.

Distinguishing Characters: Specimens have not been examined.

GENUS SANDALOLITHA Quelch, 1884

Sandalolitha robusta (Quelch, 1886)

Previous Records: None

Present Records: Four specimens, stations 3 and 4 (WAM 486-89, 487-89). Usually rare.

Distinguishing Characters: Colonies are up to 0.5m diameter, flattened. Small colonies are oval, larger ones are contorted according to irregularities in the substrate. The flattened, irregular appearance combined with wide corallum margins free of centres, suggests a different species from that found in Australia. There are, however, no skeletal details which reliably distinguish Cocos (Keeling) coralla from those from Australia. *Sandalolitha dentata* Quelch may be a distinct species with the growth form of the present species, but this has yet to be established.

FAMILY PECTINIIDAE Vaughan & Wells, 1943

This family is represented only by *Oxypora lacera.*

GENUS OXYPORA Saville-Kent, 1871

Oxypora lacera (Verrill, 1864)

Previous Records: None

Present Records: One specimen, station 4 (WAM 488-89). Rare.

Distinguishing Characters: Indistinguishable from Australian colonies.

FAMILY MUSSIDAE Ortmann, 1890

This family is represented only by *Lobophyllia hemprichii.*

GENUS LOBOPHYLLIA de Blainville, 1830

Lobophyllia hemprichii (Ehrenberg, 1834)

Previous Records: None

Present Records: One specimen, station 4 (WAM 489-89). Usually uncommon but very conspicuous.

Distinguishing Characters: Indistinguishable from Australian colonies and shows the full range of the species except that very large colonies were not found. Often brick red in colour.

FAMILY MERULINIDAE Verrill, 1886

This family is represented only by *Hydnophora microconos.*

GENUS HYNDOPHORA Fischer de Waldheim, 1807

Wells (1950) lists *H. exesa* (Pallas) as recorded from Cocos (Keeling) by Vaughan (1918). This appears to be a mistake.

Hydnophora microconos (Lamarck, 1816)

Previous Records: Vaughan (1918)

Present Records: One specimen, station 3 (WAM 490-89). Uncommon but occurs in a wide range of habitats.

Distinguishing Characters: Indistinguishable from Australian colonies.

FAMILY FAVIIDAE Gregory, 1900

GENUS FAVIA Oken, 1815

Favia stelligera (Dana, 1846)

Previous Records: Vaughan (1918), Wells (1950)

Present Records: Eight specimens, stations 3, 4, 7, 13 and 33 (WAM 491-89, 492-89, 493-89, 494-89, 495-89). Common in most communities with moderate diversity.

Distinguishing Characters: Indistinguishable from Australian colonies.

Favia pallida (Dana, 1846)

Previous Records: Vaughan (1918) (as *F. speciosa*).

Present Records: Five specimens, stations 7, 8, 13 and 25 (WAM 496-89, 497-89, 498-89, 499-89).

Distinguishing Characters: Colonies are small, submassive to encrusting. They are mostly mottled dark colours.

Favia matthaii Vaughan, 1918

Previous Records: None

Present Records: Four specimens, stations 4 and 7 (WAM 500-89, 501-89). Uncommon.

Distinguishing Characters: Corallites are smaller than those of eastern Australian colonies but similar in size to those from equatorial localities. Skeletal detail is similar throughout this range.

GENUS BARABATTOIA Yabe & Sugiyama, 1941

Barabattoia amicorum (Edwards & Haime, 1850)

Previous Records: None

Present Records: One specimen, station 9 (WAM 502-89). Rare.

Distinguishing Characters: Indistinguishable from Australian colonies. All specimens observed were dark brown in colour.

GENUS FAVITES Link, 1807

Favites abdita (Ellis & Solander, 1786)

Previous Records: Vaughan (1918)

Present Records: Eight specimens, stations 4, 13 and 16 (WAM 503-89, 504-89, 505-89). Usually uncommon.

Distinguishing Characters: Colonies are small, usually encrusting. Corallites of colonies in high energy environments may have greatly thickened walls.

Favites pentagona (Esper, 1794)

Previous Records: Vaughan (1918) (as *F. melicerum* Ehrenberg)

Present Records: Twelve colonies, stations 4, 7, 13 and 33 (WAM 506-89, 507-89, 508-89, 509-89). Common.

Distinguishing Characters: Coralla have most of the range of corallite characters described by Veron *et al.* (1977) except that all have exsert irregular septa and no ecomorphs associated with very strong wave action were found. The size of corallites overlaps with those of eastern Australian colonies, but most are slightly smaller.

GENUS LEPTORIA Edwards & Haime, 1848

Leptoria phrygia (Ellis & Solander, 1786)

Previous Records: Vaughan (1918), Wells (1950)

Present Records: One specimen, station 3 (WAM 510-89). Usually uncommon.

Distinguishing Characters: Always a uniform dark grey. Indistinguishable from Australian colonies.

GENUS MONTASTREA de Blainville, 1830

Montastrea curta (Dana, 1846)

Previous Records: None

Present Records: Three specimens, station 7, 13 and 25 (WAM 511-89, 512-89, 513-89). Usually uncommon.

Distinguishing Characters: Colonies are small, encrusting, pale coloured. Corallites are small (most <6mm diameter with calices <3mm) and are uniform in size.

This identification is tentative only because the species is very variable and lacks conservative character and also because no colonies were found on reef flats where it would be expected to be most abundant.

GENUS PLESIASTREA Edwards & Haime, 1848

Plesiastrea versipora (Lamarck, 1816)

Previous Records: Vaughan (1918)

Present Records: One specimen, station 13 (WAM 514-89). Rare.

Distinguishing Characters: Colonies are pale cream, submassive to encrusting. Skeletal structure is indistinguishable from Australian colonies.

GENUS LEPTASTREA Edwards & Haime, 1848

Leptastrea transversa Klunzinger, 1879

Previous Records: None

Present Records: Four specimens, stations 3, 13 and 25 (WAM 515-89, 516-89, 517-89). Uncommon.

Distinguishing Characters: The characters of the species are better defined than in most Australian coralla. Corallites are of relatively uniform size, with well-defined walls.

The species requires revision over a wide geographic range.

Leptastrea pruinosa Crossland, 1952

Previous Records: None

Present Records: Four specimens, stations 4, 7, 9 and 16 (WAM 518-89, 519-89, 520-89, 521-89). Uncommon.

Distinguishing Characters: Indistinguishable from Australian colonies. Usually brightly coloured.

Leptastrea bottae (Edwards & Haime, 1849)

Previous Records: Vaughan (1918), Wells (1950)

Present Records: Eighteen specimens, collecting stations 1, 4, 7, 9, 13, 14, 16, 25 and 30 (WAM 522-89, 523-89, 524-89, 525-89, 526-89, 527-89, 528-89, 529-89, 530-89). Common over a wide range of environments.

Distinguishing Characters: Colonies are submassive or encrusting. Corallites are relatively uniform in size, circular, with well defined walls. Septa are thin, with little ornamentation. Colonies from exposed environments are mostly creamy coloured with very dark calices.

GENUS CYPHASTREA Edwards & Haime, 1848

Cyphastrea serailia (Forskål, 1775)

Previous Records: Wells (1950) record of *C. chalcidicum* (Forskal) appears to be this species.

Present Records: Three specimens, stations 4, 15 and 33 (WAM 531-89, 532-89, 533-89). Common in a wide range of environments.

Distinguishing Characters: Indistinguishable from Australian colonies.

Cyphastrea microphthalma (Lamarck, 1816)

Previous Records: Vaughan (1918)

Present Records: Six specimens, stations 4, 7, 13 and 16 (WAM 534-89, 535-89, 536-89, 537-89). Common.

Distinguishing Characters: Indistinguishable from Australian colonies.

Cyphastrea agassizi (Vaughan, 1907)

Previous Records: None

Present Records: Nine specimens, stations 7 and 13 (WAM 538-89, 539-89). Uncommon.

Distinguishing Characters: Colonies are encrusting with widely spaced, exsert, corallites. Colonies are nearly uniform white in colour. May form coralliths.

GENUS ECHINOPORA Lamarck, 1816

Echinopora lamellosa (Esper, 1795)

Previous Records: Ridley & Quelch (1885), Vaughan (1918), Wells (1950)

Present Records: One specimen, station 9 (WAM 540-89). Only three small colonies were observed *in situ*. Gibson-Hill notes, "this coral, which may reach a width of over two feet across the flat sheets, is plentiful in still, sheltered water inside the lagoon, at a depth of one to three fathoms in the vicinity of the rock masses internal to the reefs in the neighbourhood of [Horsburgh I.]" (Wells, 1950). It is clearly much less common at the time of the present study and was not recorded at all at Gibson-Hill's site.

Distinguishing Characters: Indistinguishable from Australian colonies.

FAMILY DENDROPHYLLIIDAE Gray, 1847

GENUS TURBINARIA Oken, 1815

Turbinaria reniformis Bernard, 1896

Previous Records: None

Present Records: One specimen, station 15 (WAM 541-89). Usually rare but forms very extensive monospecific stands a 2-20m depth at station 4, north of "boat passage".

Distinguishing Characters: Indistinguishable from Australian colonies and has the same yellow polyps as Great Barrier Reef colonies. Polyps were extended during the day.

BIOGEOGRAPHIC AFFINITIES

Many common and widespread Indo-Pacific taxa have not been recorded from Cocos (Keeling) and are almost certainly absent. There are no Oculinidae or Caryophylliidae. The Pectiniidae, Mussidae and hermatypic Dendrophylliidae are represented by only one species each. There are no recorded *Stylophora, Goniopora, Alveopora, Coscinaraea, Cycloseris, Polyphyllia, Lithophyllon, Podabacia, Goniastrea, Platygyra* and many minor east Indian Ocean genera.

Of the genera that are present, only *Sandalolitha* does not have a distribution range crossing the Indian Ocean (Veron, 1986).

Table 1. Species diversity of hermatypic Cocos (Keeling) and Christmas Is. corals.

	Cocos (Keeling) Is.	Christmas I.
Stylocoeniella	?3	2
Pocillopora	5	3
Seriatopora	1	0
Montipora	16	2
Anacropora	1	0
Acropora	19	11
Astreopora	2	2
Porites	9	4
Goniopora	0	4
Alveopora	0	1
Psammocora	3	3
Pavona	9	7
Leptoseris	3	4
Gardineroseris	1	1
Pachyseris	1	1
Cycloseris	0	1
Fungia	4	2
Sandalolitha	1	1
Herpolitha	1	0
Oxypora	1	1
Galaxea	0	2
Acanthastrea	0	1
Lobophyllia	1	3
Symphyllia	0	2
Hydnophora	1	2
Merulina	0	1
Scapophyllia	0	1
Favia	3	2
Barabattoia	1	0
Favites	2	4
Goniastrea	0	1
Platygyra	0	4
Leptoria	1	1
Montastrea	1	1
Plesiastrea	1	0
Diploastrea	0	1
Leptastrea	3	3
Cyphastrea	3	2
Echinopora	1	2
Turbinaria	1	1
Plerogyra	0	1
TOTAL SPECIES	99	85
TOTAL GENERA	29	36

VERON:Cocos-P

At species level, the isolation of the atoll from Australia is reflected in:

(a) the number of species which are known from western Australia but are absent from the atoll: (223 species or 70% of the western Australian total of 318 species),

(b) the number of species which are present but have not been recorded from anywhere in Australia (12 species: *Stylocoeniella* sp., *Montipora lobulata, Montipora* sp., *Acropora ocellata, Acropora* sp. 1, *Acropora* sp 2, *Acropora schmitti, Porites somaliensis, Porites* sp., *Pavona frondifera, Pavona* sp., *Cyphastrea agassizi*), and

(c) the substantial proportion of species (perhaps 30%) which are present but show points of difference from their western Australian counterparts (eg. differences in colour, habitat preferences as well as skeletal and growth form differences).

It may be noted that of the 12 species not recorded from Australia ('b' above), 3 have been recorded from the Philippines (Veron & Hodgson, 1989). The remaining 9 have not been previously recorded from any eastern Indian Ocean locality, but only *Stylocoeniella* sp., *Porites* sp. and *Pavona* sp. have not been previously recorded anywhere. Although it is possible that the latter are endemic, the corals of Indonesia are poorly known and they, along with most or all Cocos (Keeling) species, may well occur in Indonesia.

Table 1 compares number of species recorded for genera found at Cocos (Keeling) Atoll and Christmas I (Done, *in prep.*). The principal difference is in the much greater number of species of *Montipora* at Cocos (Keeling) and the greater generic richness of Christmas I.. The latter, however, is a high island with a very restricted range of habitats, especially sheltered ones. The presence or absence of corals is therefore like to be as much a function of habitat diversity as geographic isolation or relative dispersal ability. The only general observation of this data made here is that there is no clear evidence that Christmas I. has acted as a 'stepping stone' for the dispersal of corals to Cocos (Keeling).

FACTORS AFFECTING CORAL DIVERSITY

Not all abundance and presence/absence records are necessarily the result of geographic isolation. In recent times there have been several catastrophic events which have greatly reduced the abundance of corals. During the 1960s there were one or more outbreaks of *Acanthaster planci* (Marsh, in prep.) and clearly, most outer reef slopes have been very extensively denuded. This may well have affected the total species complement as well as abundance. Many outer slope species are now known only from one or a few colonies and others, notably *Pachyseris speciosa* and *Turbinaria reniformis,* occur in great abundance at one locality but were found nowhere else. This may be the result of denudation by *Acanthaster,* or it may be the result of recent colonisation.

In March, 1983, a sustained reversal in the normal direction of the SE trade winds resulting from a major ENSO event caused very extensive, probably total extermination of lagoon corals except at the northern end (Blake, W. unpubl. manuscript). Colin (1977) records the slopes of one of the 'blue holes' of the southern lagoon as being 'densely covered', whereas this area today contains few live corals (only sporadic *Montipora*

capricornis, Porites spp. and *Fungia concinna*), but very extensive remains of dead skeletons principally *Acropora* spp. Clearly, the abundance of several species has been greatly affected: Gibson-Hill (Wells, 1950) records *Seriatopora hystrix, Acropora formosa, Acropora valida, Pavona cactus* and *Echinopora lamellosa* as being abundant in the lagoon whereas they are now very restricted, both in distribution and abundance. Lagoonal *Acropora pulchra* was also very much more abundant prior to 1983.

Cyclones are not common at Cocos (Keeling), but a severe cyclone in January, 1989 severely damaged the forests of North Keeling I. and appeared to have damaged some reef flat and upper reef slope coral communities. There is, however, no evidence of this on the western side of the island.

Whatever the cause of coral denudation, whether recent or distant past, it is likely that recovery would be slow and the effect long-term. At present, much of the lagoon floor is covered by macro-algae and not readily available for coral recolonisation. More importantly, because of geographic isolation, most reef fauna must be predominantly self-seeding. There is very little coral other than *Porites* spp. and *Montipora digitata* at the southern end of the lagoon where most lagoon water intake occurs. The areas of highest diversity are to the north where it is likely that most larvae produced would be lost to the atoll, but little is known of local water movements and nothing of spawning times.

In the longer term (tens to hundreds of years) there appears to have been a progressive closing of the lagoon by sand accretion on the island arc. Habitat diversity has thus been gradually decreasing and it is likely that the coral death of 1983 was the most recent (and perhaps final) of a series of catastrophic events resulting from closure of the lagoon. It was not, however, the first such event (Hatcher, 1988).

ORIGINS OF COCOS (KEELING) CORALS

Nothing is known of the age of Cocos (Keeling) atoll although Woodfoffe *et al. (in prep.)* have shown that Pleistocene (last interglacial) reef limestones are encountered at depths of 9-15m and are overlain by shallow water reefal deposits that accumulated as sea level rose in the mid Holocene. The atoll, therefore, has been available for colonisation by reef corals during periods of low Pleistocene sea levels, a time when surface circulation patterns would have been substantially different than they are today. The present coral fauna may have its origins at, or before, this time or, alternatively, may be a relatively recent product of modern surface circulation patterns.

Information about modern surface circulation patterns comes from substantially outdated surface circulation atlases together with more recent and ongoing oceanographic studies, the latter primarily concerned with the Leeuwin Current and (at present) with the 'Indonesian throughflow'. No surface circulation atlas has been adequately revised since the existence of the Leeuwin Current, down the west coast of Australia, has become well understood.

The driving force of the Leeuwin Current is believed to be the flow of warm, low salinity water from the western central Pacific Ocean through deep passages in the

Indonesian Archipelago into the Timor Sea and the eastern Indian Ocean (Pearce and Creswell, 1985 and others). The current varies seasonally, being weakest in December to March and strongest in May to August when the along-shore sea level gradient almost doubles and the wind stress is weaker and more variable. It clearly explains the large-scale coral distribution pattern along the coast of Western Australia (Veron and Marsh, 1988).

The most recent studies of throughflow between Indonesia and the Indian Ocean (Wyrtki, 1987; Godfrey *in prep.*) reveal a strong, upper level (200m) pressure gradient which accords well with predictions of a wind-driven numerical model. Thus, Pacific winds and the Indonesian throughflow are primarily responsible for both the winter-flowing Leeuwin Current of Western Australia and the north-east origin of the westward-flowing South Equatorial Current.

According to the most recent surface circulation maps (Tchernia, 1980), Cocos (Keeling) Atoll lies in the South Equatorial Current. It is south of the tropical convergence zone in summer when the South Equatorial Current is at its weakest, and almost central to this current in winter when surface velocities reach 'more than one knot' (Tchernia, 1980). Summer (February-March) velocities are recorded as being less than half this, and as occurring with a greatly reduced regularity.

In summary, surface circulation data indicate no direct route for propagules to Cocos (Keeling) from the western Indian Ocean at any time of the year. The origin of all such currents is in Indonesia and offshore north-west Australia, with substantial inter-annual variation.

Simpson (1985) first recorded mass coral spawning on the western Australian coast (Dampier Archipelago) occurring in March and more recently *(in prep.)* has found that 88% of species studied (46% of all western Australian species) spawn at that time. Given a distance of 1830km and direct current transport of 0.5m/sec., a transport duration of 94days between western Australia and Cocos (Keeling) can be estimated. Approximately half that time (46 days) would be required for direct transport from Indonesia and half that time again (23 days) for direct transport from Indonesia for winter spawning species.

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