The hydrocoral genus *Millepora*  
(Hydrozoa: Capitata: Milleporidae) in Indonesia

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Key words: Taxonomic revision; *Millepora*; Indonesia; new records; *M. boschmai*.

This revision of Indonesian *Millepora* species is based on the morphology of museum specimens and photographed specimens in the field. Based on the use of pore characters and overall skeleton growth forms, which are normally used for the classification of *Millepora*, the present study concludes that six of seven Indo-Pacific species appear to occur in Indonesia, viz., *M. dichotoma* Forskal, 1775, *M. exaesa* Hemprich & Ehrenberg, 1834, *M. intricata* Milne-Edwards, 1857 (including *M. intricata* forma *murrayi* Quelch, 1884), *M. tenera* Boschma, 1949, and *M. boschmai* de Weerdt & Glynn, 1991, which so far was considered an East Pacific endemic. Of the 13 species previously reported from the Indo-Pacific, six were synonymized. *M. murrayi* Quelch, 1884, has been synonymized with *M. intricata*, which may show two distinct branching patterns, that may occur in separate corals or in a single one. *M. latifolia* Boschma, 1948, *M. tuberosa* Boschma, 1966, *M. cruzi* Nemenzo, 1975, *M. xishaensis* Zou, 1978, and *M. nodulosa* Nemenzo, 1984, are also considered synonyms. *M. foveolata* Crossland, 1952, is a distinct species but it has not been found in Indonesia.

**Introduction**

The hydrozoan family Milleporidae, popularly known as fire corals, consists of a single genus viz., *Millepora* Linnaeus, 1758. Each coral is actually a modular (colonial) hydrozoan that secretes calcium in order to build a massive calcareous skeleton (coenosteum). *Millepora* differs from Scleractinia, coral-building Anthozoa, by the absence of corallites and by the presence of minute pores that are scattered over the corallum surface.

There are two types of pores, i.e., gastropores and dactylopores. Gastropores harbor short gastrozooids, used for feeding, with tentacles reduced to nematocyst-filled knobs. Dactylopores contain elongated dactylozooids that have scattered capitate tentacles used for food capture. Usually, gastropores and dactylopores are arranged together into cyclosystems, in which a single gastropore is surrounded by approximately five to seven dactylopores. However, such a pattern does not occur in all species (Boschma, 1956).

Milleporids occur on coral reefs in almost all tropical seas (Wood, 1983; Lewis, 1989) from less than 1 m deep to about 40 m (Boschma, 1948a). They are most common in shallow water because their symbiotic zooxanthellae require sunlight for photosynthesis (Boschma, 1956).

Earlier works on *Millepora*, from Linnaeus (1758) to Crossland (1948), have been reviewed extensively by Boschma (1948a), who recognized seven species occurring in the Indo-Pacific waters: *M. exaesa* Forskal, 1775; *M. dichotoma* Forskal, 1775; *M. platyphylla* Hemprich & Ehrenberg, 1834; *M. intricata* Milne-Edwards, 1857; *M. murrayi*
Quelch, 1884; *M. tenella* Ortmann, 1892; *M. latifolia* Boschma, 1948. Later he changed the name *M. tenella* Ortmann, 1892 into *M. tenera* Boschma, 1949, since the former name was preoccupied.

In addition, he described a new species, *M. tuberosa* Boschma, 1966, based on specimens from Mauritius. He remarked that the type specimen of *M. tuberosa* shows some similarity to specimens of *M. exaeosa*. He considered *M. exaeosa* doubtful, since its description was based on specimens of various species, and therefore he separated the two species based on their distribution ranges. He concluded that most of the *M. exaeosa* records from localities other than its type locality, the Red Sea, actually concern *M. tuberosa*.


Nemenzo (1975, 1976) initially reported eight species from the Philippines including one new species viz., *M. cruzi* Nemenzo, 1975, in addition to six species revised by Boschma (1948a) and one described by Crossland (1952) viz., *M. foveolata*. Later, he added *M. nodulosa* Nemenzo, 1984, but in his compilation of Philippine corals (Nemenzo, 1986), he only referred to eight *Millepora* species without *M. nodulosa*.

Two branching species depicted by Nemenzo, *M. cruzi* and *M. nodulosa*, have the same general appearance as other Indo-Pacific branched *Millepora* species. They form a hemispherical corallum and consist of anastomosing branches. Their main distinctive character among other Indo-Pacific branching milleporids is the presence of elevations on the corallum surface. In *M. cruzi* each tiny swelling harbours a gastropore, while *M. nodulosa* shows bigger nodules that never bear gastropores. Boschma (1948a), however, claimed that depressions on the corallum surface never seem to occur in the branching Indo-Pacific *Millepora* species, except in plate-like *M. platyphylla* infested by the parasitic barnacle *Pyrgoma milleporae* Darwin, 1854.

Randall & Cheng (1984) described eight species from Taiwan, including *M. foveolata* and seven species that have been mentioned by Boschma (1948a, 1966), except *M. exaeosa*. They mainly emphasised their work on habitat, community structure and distribution patterns of Taiwanese *Millepora*. They believed that the species problem in *Millepora* is due to environmentally induced intraspecific variation. Therefore, they used the ecomorph concept in *Millepora* classification, which implies a relationship between morphology and a particular environmental setting.

Moshchenko examined the importance of several species characters used in earlier studies i.e., corallum growth form (Moshchenko, 1992), structure of the pore apparatus (Moshchenko, 1994, 1995b, 1996a), structure of the ampullae (Moshchenko, 1997), anatomy and morphology of hard and soft tissue (Moshchenko, 1993) and metabolism (2000a, 2000b). Moshchenko et al. (1993) used enzyme electrophoresis to study the systematic status of *Millepora* species. Moshchenko (1997) concluded from his studies on Vietnamese *Millepora* that only two species of *Millepora* exist. According to him, the plate-like *M. platyphylla* represents one valid species and all branched milleporids should be referred to as *M. dichotoma* in which the variety of branching patterns should be attributed to intraspecific variability.
The aim of the present study is to revise Indonesian *Millepora* based on the morphology of the pore characters and the corallum growth forms in museum specimens and photographed specimens in the field.

**Materials and Methods**

*Millepora* specimens from Indonesia were studied in the National Museum of Natural History, Leiden. Of the 173 specimens examined, only 144 showed characters that were clear enough for further analyses. The specimens were sampled from 1863 until 1996, mostly by Boschma in 1920-1922 (off Jakarta), Umbgrove in 1955 (off Jakarta and Togian Islands), Hoeksema in 1994-1996 (S.W. Sulawesi, N. Sulawesi, Ambon) and during ship-based expeditions in Indonesia, such as Siboga in 1899-1900, Snellius in 1929-1930, Snellius II in 1984-1985 (table 1). The material is deposited in the National Museum of Natural History, Leiden, The Netherlands, and catalogued under numbers of the former Rijksmuseum van Natuurlijke Historie (RMNH).


**Table 1. Localities of Indonesian *Millepora* corals studied in the present research.**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Number of specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sumatra</td>
<td>3</td>
</tr>
<tr>
<td>Java Sea and Jakarta Bay</td>
<td>63</td>
</tr>
<tr>
<td>Komodo, Sumba, and Sumbawa</td>
<td>6</td>
</tr>
<tr>
<td>Timor</td>
<td>17</td>
</tr>
<tr>
<td>Moluccas</td>
<td>26</td>
</tr>
<tr>
<td>Sulawesi</td>
<td>56</td>
</tr>
<tr>
<td>Unknown</td>
<td>2</td>
</tr>
<tr>
<td>TOTAL</td>
<td>173</td>
</tr>
</tbody>
</table>

**Table 2. Morphological characters of *Millepora* specimens.**

<table>
<thead>
<tr>
<th>Characters</th>
<th>Sample size per corallum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Growth form of corallum</td>
<td></td>
</tr>
<tr>
<td>2. Growth form of branches and branchlets</td>
<td></td>
</tr>
<tr>
<td>3. Branch width (BW)</td>
<td></td>
</tr>
<tr>
<td>4. Branch thickness (BT)</td>
<td></td>
</tr>
<tr>
<td>5. Gastropore diameter (GPD)</td>
<td>10 - 15 pores</td>
</tr>
<tr>
<td>6. Dactylopore diameter (DPD)</td>
<td>10 - 15 pores</td>
</tr>
<tr>
<td>7. Pore density per cm² (PD)</td>
<td>10 replicates</td>
</tr>
<tr>
<td>8. Percentage of gastropores ((number of gastropores in 9mm² observation square / total pore density) × 100%) (PG)</td>
<td>10 - 15 replicates</td>
</tr>
<tr>
<td>9. Distances between gastropores (DG)</td>
<td>10 replicates</td>
</tr>
<tr>
<td>10. Presence of cyclosystems</td>
<td></td>
</tr>
<tr>
<td>11. Number of dactylopores per cyclosystem</td>
<td></td>
</tr>
</tbody>
</table>
Pore characters include the diameter of gastropores and dactylopores. Of each corallum, the diameters of both gastro- and dacylopores (10-15 each) were measured using a dissecting microscope with a magnification of 50 times. Pore densities were measured by counting the number of pores inside a 9 mm² square at ten different areas (see de Weerdt, 1984; de Weerdt & Glynn, 1991; Moshchenko, 1995b; Randall & Cheng, 1984).

In addition, observations and measurements were made of the percentage of gastropores among all pores (within 9 mm² samples of coral surface area), distances between gastropores, the presence of cyclosystems, and the number of dactylopores per cyclosystem (table 2).

According to de Weerdt (1984), measurements of pore characters should only be obtained from measurable parts of the corallum surface. Therefore, edges and unexposed areas, where pores are minute or absent, were excluded in the present study.

**Taxonomic account**

- **Phylum Cnidaria Hatschek, 1888**
- **Superclass Hydrozoa Owen, 1843**
- **Class Leptolida Haeckel, 1879**
- **Subclass Anthoathecatae Cornelius, 1992**
- **Order Capitata Kühn, 1913**
- **Superfamily Zancleoidea Russel, 1828**
- **Family Milleporidae Fleming, 1828**
- **Genus *Millepora* Linnaeus, 1758**

Classification.— The present classification of the leptolid Hydrozoa has been introduced by Cornelius (1992). In old classifications of hydrocorals, the family Milleporidae was categorized in the suborder Athecata Broch, 1924, within the order Milleporina Hickson, 1901 (see Boschma, 1956). Although Bouillon (1995) in his classification of the Hydrozoa referred to the family Milleporidae Milne-Edwards & Haime, 1849, we follow Boschma (1956) by giving priority to Milleporidae Fleming, 1828.


Most of the branched milleporids form a hemispherical corallum and consist of crowded masses of anastomosed branches. *M. dichotoma* is the only branching species that forms a vertical and erect reticulate plate instead of a hemispherical clump. There
are several types of branching pattern viz., fan-like, finger-like and dichotomous. We consider these branching modes as a useful character to separate the Indonesian branched milleporids into three species, viz., *M. dichotoma*, *M. intricata* (with *M. intricata f. murrayi*) and *M. tenera*.

Two fragments (RMNH Coel. 9090, 31095) and pictures of a living corallum (fig. 15) show that *M. murrayi* is actually a growth form of *M. intricata*. Similar observations were made in the field by Hoeksema. Therefore we decided to merge *M. murrayi* with *M. intricata* and refer to the morpho-type *M. intricata forma murrayi*. The two different growth forms viz., the subcylindrical dichotomous branches of *M. intricata* and the flattened finger-like branchlets of *M. murrayi*, can be observed in a single corallum without any indication of one overgrowing the other. They are part of the same calcareous formation that shifts its shape within the same corallum (figs 16, 19). However, these growth forms are most commonly found separated from each other.

The plate-like milleporid, *M. platyphylla*, is very distinct from the rest of the genus. The corallum is formed by solid and thick upstanding plates. They are composed either of parallel tiers of plates or of interconnected plates forming a honeycombed structure. Another species present in this description is *M. exaesa*. The corallum forms irregular swellings with numerous short and thick tubercular knobs. The corals can be found attached to the substrate as well as free-living. The latter has irregular shapes as a result of encrusting over coral fragments and assembling them into an irregular mould. Water movement causes free-living milleporids to roll, which prevents them to grow attached as specimens of other *Millepora* species.

A species reported as new for Indonesia and as for the Indo-West Pacific is *Millepora boschmai* de Weerdt & Glynn, 1991, which was previously considered endemic to the eastern Pacific (de Weerdt & Glynn, 1991; Glynn & Feingold, 1992). Five observed specimens (RMNH Coel. 23146, 23153, 31061, 31092, 31093) are unambiguously showing the characteristic cyclosystem arrangement of *M. boschmai*. They have a particular growth shape that is composed of irregular erect columns and as the columns grow upward, they usually increase in width. Occasionally, the column divides dichotomously (fig. 25).

A *Millepora* cyclosystem consists of three to nine dactylopores, which are commonly arranged into a circle surrounding a single gastropore. The occurrence of cyclosystems on the surface varies considerably from one part of the colony to another. They are generally present on broader parts of the surface and are indistinct where nodules or verruccae are present, pore densities are high on the growing edges. No other species resembles *M. boschmai* in its conspicuous evenly distributed cyclosystem arrangement. They are clearly separated from each other and consistently have five to eight dactylopores. In contrast, no cyclosystem was found on the surface of *M. exaesa* coralla. This is strongly related with the abundant occurrence of nodules over the corallum surface. On the broader areas, however, pores may be arranged into a circle in which more than 10 dactylopores encircle a gastropore, but this does not resemble a common cyclosystem arrangement.

Pores are generally distributed over the entire corallum surface and are reduced or may even be absent in shaded or cryptic parts of the corallum. The general shape of the pore is circular. Occasionally, septa-like stellate apertures occur in milleporids but vary highly from one part of the corallum to another. In all observed specimens
the diameter of the gastropores, more or less, doubles that of dactylopores.

The morphological variables of the pore characters were measured in six Indonesian Millepora species (table 3). With respect to mean dactylopore size, M. intricata and M. intricata f. murrayi form a group with minute pores (± 0.10 mm), whereas M. dichotoma, M. tenera, M. boschmai, M. exaesa and M. platyphylla have larger pores (0.13–0.14 mm). Average gastropore sizes in the (sub-) massive milleporids are clearly larger (0.26–0.28 mm) than in the branching milleporids (0.19–0.22 mm).

The distances between adjacent gastropores did not reveal significant differences within the six milleporid species from Indonesia. Pore densities and gastropore percentages are quite variable within the milleporids, values in M. intricata, M. intricata f. murrayi and M. exaesa are higher (264–303 pores/cm² and 11.2–12.7%) than in M. dichotoma, M. tenera, M. boschmai, and M. platyphylla (167–240 pores/cm² and 6.4–9.0%).

Table 3. Mean values, standard deviations and ranges of seven characters obtained from 144 Indonesian specimens belonging to six Millepora species. Data of pore characters (means ± standard deviations) obtained from measurable parts of the corallum, i.e., growing edges and unexposed areas are excluded. Abbreviations of characters are explained in table 2.

<table>
<thead>
<tr>
<th>Characters:</th>
<th>GPD (mm)</th>
<th>DPD (mm)</th>
<th>DG (mm)</th>
<th>PD per cm²</th>
<th>PG</th>
<th>BW (mm)</th>
<th>BT (mm)</th>
<th>Samples (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. dichotoma</td>
<td>0.22 ± 0.03</td>
<td>0.13 ± 0.01</td>
<td>1.5 ± 0.3</td>
<td>168 ± 61</td>
<td>6.3 ± 1.1</td>
<td>8.8 ± 0.9</td>
<td>7.2 ± 1.0</td>
<td>27</td>
</tr>
<tr>
<td>M. intricata</td>
<td>0.20 ± 0.02</td>
<td>0.10 ± 0.01</td>
<td>1.5 ± 0.1</td>
<td>296 ± 72</td>
<td>12.7 ± 3.1</td>
<td>5.6 ± 1.3</td>
<td>4.5 ± 1.5</td>
<td>22</td>
</tr>
<tr>
<td>M. intricata f. murrayi</td>
<td>0.19 ± 0.02</td>
<td>0.10 ± 0.01</td>
<td>1.4 ± 0.1</td>
<td>284 ± 57</td>
<td>11.6 ± 3.6</td>
<td>N/A</td>
<td>4.8 ± 1.1</td>
<td>35</td>
</tr>
<tr>
<td>M. tenera</td>
<td>0.22 ± 0.03</td>
<td>0.13 ± 0.02</td>
<td>1.5 ± 0.2</td>
<td>172 ± 43</td>
<td>6.8 ± 1.1</td>
<td>N/A</td>
<td>5.7 ± 1.4</td>
<td>10</td>
</tr>
<tr>
<td>M. boschmai</td>
<td>0.27 ± 0.03</td>
<td>0.14 ± 0.02</td>
<td>1.7 ± 0.2</td>
<td>199 ± 40</td>
<td>8.6 ± 3.8</td>
<td>21.8</td>
<td>12.0 ± 5.8</td>
<td>18</td>
</tr>
<tr>
<td>M. exaesa</td>
<td>0.26 ± 0.03</td>
<td>0.14 ± 0.01</td>
<td>1.6 ± 0.2</td>
<td>269 ± 36</td>
<td>11.7 ± 2.5</td>
<td>N/A</td>
<td>N/A</td>
<td>5</td>
</tr>
<tr>
<td>M. platyphylla</td>
<td>0.26 ± 0.04</td>
<td>0.14 ± 0.02</td>
<td>1.4 ± 0.1</td>
<td>240 ± 61</td>
<td>7.6 ± 2.6</td>
<td>N/A</td>
<td>9.2 ± 4.1</td>
<td>27</td>
</tr>
<tr>
<td>M. cf. latifolia</td>
<td>0.24 ± 0.03</td>
<td>0.13 ± 0.02</td>
<td>1.4 ± 0.1</td>
<td>194 ± 24</td>
<td>7.0 ± 1.7</td>
<td>N/A</td>
<td>N/A</td>
<td>11</td>
</tr>
</tbody>
</table>

Key to the Indonesian species of Millepora

1. Corallum branching ................................................................. 2
   - Corallum massive and sub-massive ........................................... 3
2. The lower parts never unite into a plate; branches subcylindrical; growing in all directions; continuously dichotomous; the upper edges with tapering tips .................... M. intricata
   - The lower parts unite into a plate; branches flattened; lateral branches radiating from the central point (ogive structure); the upper edges with blunt or rounded tips ................................................................. 4
3. Massive plate, upright and tall, forming a honeycombed or a parallel tier structure; cyclosystem distinct on a flat surface .................................................. M. platyphylla
- Submassive short knobbed branches, growing upward; or free-living, encrusted on coral fragments; no cyclosystem arrangement .............................................. \textit{M. exaesa}
- Submassive columnar or slender upright plates, irregular in outline; cyclosystem very conspicuous everywhere on the surface below the growing margins ........
  
\textit{M. boschmai}

4. Anastomose branches forming a tall and erect reticulate plate, no coalescence between plates .......................................................... \textit{M. dichotoma}
- Branchlets arise on the upper edge ......................................................... \textit{M. intricata \textit{f. murrayi}}
- Branchlets fan-shape ................................................................................ \textit{M. tenera}

\textbf{Systematic descriptions}

\textit{Millepora dichotoma} Forskål, 1775
(figs 1–6)

\textit{Millepora intricata}; Manchenko et. al, 1993: 731 fig. 1c.
\textit{Millepora tenera}; Nishihira, 1988: 232; Veron, 1986: 617 fig. 3, 618 fig. 2.
\textit{Millepora sp.}; Veron, 1986: 619 fig. 4.


\textbf{Description.} – Corallum attached, consisting of upright reticulate plates formed by anastomosing flattened branches; usually consisting of more than one plate; coalesces between plates are absent. Branches in the lower parts frequently unite into solid plates; in the centre of the plate 7.1 - 8.8 ± 0.9 - 10.5 mm wide by 5.3 - 7.2 ± 1.0 - 9.5 mm thick; the upper edges are free and bifurcate, with rounded or blunt tips.

Surface smooth and even, seldom infested with barnacles and worms. Pores clear and numerous; density 126 - 168 ± 61 - 413 pores/cm² with 4.9 - 6.3 ± 1.1 - 8.2% of gastropores. Gastropores 1.2 - 1.5 ± 0.3 - 2.2 mm apart, diameter 0.18 - 0.22 ± 0.03 - 0.29 mm. Dactylopores 0.10 - 0.13 ± 0.01 - 0.17 mm in diameter. Cyclosystem arrangements occur, sometimes in a very obvious circle; 3-8 dactylopores encircle a gastropore.
Fig. 1. *Millepora dichotoma*. Living corallum consisting of several reticulate plates (Cebu, the Phillipines).

Fig. 2. *Millepora dichotoma*. Living corallum infested with barnacles (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 3. *Millepora dichotoma*. RMNH Coel. 31079 (Kera I., West Timur, Indonesia).

Fig. 4. *Millepora dichotoma*. RMNH Coel. 31080 (Damar Besar I., Jakarta Bay, NW Java, Indonesia).

Fig. 5. *Millepora dichotoma*. RMNH Coel. 31081 (Tukang Besi Islands, SE Sulawesi, Indonesia).

Fig. 6. *Millepora dichotoma*. Close-up of corallum surface showing pores, RMNH Coel. 31079 (Kera I., West Timur, Indonesia).
Distribution.—Indonesia (see material). Published records. Australia: east and west coast (Veron, 1986); Xisha Is., China (Zou, 1978); Guam (Randall & Myers, 1983); Japan (Nishihira, 1988); The Philippines: Pangasinan I., Albay I., Batangas I., Mindoro I., Cebu I. (Nemenzo, 1975, 1976, 1986); South China Sea (Moshchenko, 1998a); Taiwan: Nan-Wan Bay, SE and SW coast, Lan-Yu I. (Randall & Cheng, 1984; Dai, 1989); Thailand (Ditlev, 1980); Vietnam (Manchenko et al., 1993; Moshchenko, 1995b, 1997, 1999a).

Millepora intricata Milne-Edwards, 1857
(figs 7–12, 15-16)


Description.—Corallum attached, forming a hemispherical cluster of thinly (figs 7, 10) or densely arranged (figs 8, 9) Anastomose branches. Branches subcylindrical, continuously dichotomous, growing in all directions; branch diameters in thinly branched coralla are greater (5.1-9.4 mm by 3.8-8.4 mm) than in densely clustered branches (4.1-5.9 mm by 2.9-4.5 mm); branches in the lower part never unite into a solid plate; terminal branches always bifurcate with tapering tips.

Surface smooth. Pores minute and not very conspicuous; density 178 - 296 ± 72 - 450 pores/cm² with 8.3 - 12.7 ± 3.1 - 20.3% of gastropores. Gastropore diameter 0.16 - 0.20 ± 0.02 - 0.24 mm; distance between gastropores 1.3 - 1.5 ± 0.1 - 1.8 mm. Dactylopores minute 0.09 - 0.10 ± 0.01 - 0.12 mm in diameter. Cyclosystems rare, only in broader spaces, with 5-9 dactylopores around a gastropore.

Distribution.—Indonesia (see material). Published records. China (Zou, 1978); Japan (Nishihira, 1988); The Philippines (Nemenzo, 1975, 1976, 1986); Taiwan (Randall & Cheng, 1984; Dai, 1987); Thailand (Ditlev, 1980); Vietnam (Manchenko et al., 1993; Moshchenko, 1995b, 1997).

Fig. 7. *Millepora intricata*. Living corallum consisting of sparsely arranged branches (Madang, Bismarck Sea, Papua New Guinea).

Fig. 8. *Millepora intricata*. Living corallum consisting of densely arranged branches (Tulamben, Bali, Indonesia).

Fig. 9. *Millepora intricata*. Corallum consisting of densely arranged branches, RMNH Coel. 10547 (Sumatra, Indonesia).

Fig. 10. *Millepora intricata*. Corallum consisting of thinly arranged branches, RMNH Coel. 31071 (Taka Bone Rate, South Sulawesi, Indonesia).

Fig. 11. *Millepora intricata*. RMNH Coel. 31074 (Selayer I., South Sulawesi, Indonesia).

Fig. 12. *Millepora intricata*. Close-up of corallum surface showing pores, RMNH Coel. 31074 (Selayer I., South Sulawesi, Indonesia).
Millepora intricata forma murrayi Quelch, 1884
(figs 13–20)

Millepora murrayi; Boschma, 1948a (previous synonymy): 20, 40, 105, pl. II figs 1-2 (right), pl. XI figs 1-2, pl. XV figs 1, 3; Ditlev, 1980: 89; Moshchenko, 1992: 9, pl. IV figs 1-6; 1995b: 270; 1997: 241 figs 2e-2f, 242 figs 3a-3d; Nemenzo, 1975: 25, pl. IV fig. 2; 1976: 281-282, pl. II fig. 3; 1986: 249, fig. 299; Randall & Cheng, 1984: 57-62, pl. III figs 1-5.

Millepora dichotoma; Moshchenko 1997: 242 fig. 3e.

Material.—


Description.—Corallum attached, forming a hemispherical, dense cluster of intermingled branches; lateral branches radiating from a central point forming an ogive structure (fig. 23). Branches flattened, 3.2 - 4.8 ± 0.9 - 7.1 mm thick, highly coalescent; in the lower part often united into a small arched plate; in the upper edge, a row of secondary branches arises forming a finger-like branchlet; tips blunt to flat. Branchlets in rows of 3-6 upright tubercular branches arranged like fingers in a hand.

Surface smooth and even. Pores clearly visible, especially abundant on the upper edges; density 190 - 284 ± 57 - 393 pores/cm²; gastropore percentage 6.5 - 11.6 ± 3.6 - 24.9%. Gastropores 1.0 - 1.4 ± 0.1 - 1.8 mm apart; diameter 0.13 - 0.19 ± 0.02 - 0.23 mm. Dactylopores 0.07 - 0.10 ± 0.01 - 0.13 mm in diameter. Cyclosystems are very indistinct except in broader places; 6-10 dactylopores in a circle.

Distribution.—Indonesia (see material). Published records. The Philippines (Nemenzo, 1975, 1976, 1986); Taiwan (Randall & Cheng, 1984); Thailand (Ditlev, 1980); Vietnam (Moshchenko, 1992, 1995b, 1997).

Millepora tenera Boschma, 1949
(figs 21-24)


Millepora intricata; Nishihira, 1988: 234.

Millepora tenella Ortmann, 1892 (preoccupied name); Boschma, 1948a (previous synonymy): 20, 41-42, 86, 98-99, 105-107, pl. XII figs 1-2, pl. XIII figs 1-3, pl. XIV figs 1-2, pl. XV fig. 2, text-figs 3-5, 12, 13; Ditlev, 1980: 88, figs 118, 387.
Fig. 13. *Millepora intricata* f. *murrayi*. Living corallum showing hand-shaped branching pattern at branch tips (Tulamben, Bali, Indonesia).

Fig. 14. *Millepora intricata* f. *murrayi*. Living corallum showing hand-shaped branching pattern at branch tips (Tulamben, Bali, Indonesia).

Fig. 15. *Millepora intricata*. Living corallum showing two growth forms, dichotomous and hand-shaped (*f. murrayi*) branching patterns (Tulamben, Bali, Indonesia).

Fig. 16. *Millepora intricata*. Fragment with two growth forms, a dichotomous and a hand-shaped (*f. murrayi*) branching pattern, RMNH Coel. 9090 (Damar Besar I., Jakarta Bay, NW Java, Indonesia).

Fig. 17. *Millepora intricata* f. *murrayi*. RMNH Coel. 31094 (Damar Besar I., Jakarta Bay, NW Java, Indonesia).

Fig. 18. *Millepora intricata* f. *murrayi*. RMNH Coel. 23147 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 19. *Millepora intricata* f. *murrayi*. RMNH Coel. 31095 (Damar Besar I., Jakarta Bay, NW Java, Indonesia).

Fig. 20. *Millepora intricata* f. *murrayi*. Close-up of corallum surface showing pores, RMNH Coel. 23147 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 21. *Millepora tenera*. Living corallum showing a fan-shaped branching pattern (Togian Islands, Tomini Bay, East Central Sulawesi, Indonesia).

Fig. 22. *Millepora tenera*. (Togian Islands, Tomini Bay, East Central Sulawesi, Indonesia).

Fig. 23. *Millepora tenera*. Ogive structure with fan-shaped branchlets, RMNH Coel. 10528 (Ambon, Mollucas, Indonesia).

Fig. 24. *Millepora tenera*. Close-up of corallum surface showing pores, RMNH Coel. 10529 (Ambon, Mollucas, Indonesia).

Description.— Corallum attached, forming a hemispherical cluster of fan-shaped branches radiating from a central point. Branches flattened, 3.9 - 5.7 ± 1.4 - 7.8 mm thick; adjacent ones highly anastomose; in the lower part fuse into a small arched plate, resemble those of *M. intricata f. murrayi* but bigger in size; in the upper edge forming a fan-shape structure with a flat apices.

Surface very fine and smooth. Pores difficult to notice because of the fine surface structure; density 124 - 172 ± 43 - 258 pores/cm² with 5.8 - 6.8 ± 1.1 - 8.6% of gastro pores. Gastropores 1.3 - 1.5 ± 0.2 - 1.8 mm apart, diameter 0.18 - 0.22 ± 0.03 - 0.24 mm. Dactylopores 0.10 - 0.13 ± 0.02 - 0.16 mm in diameter. Cyclosystems arrangements nearly absent.

Remarks.— Coralla of *M. tenera* resembles very much those of *M. intricata f. murrayi* in the possession of lateral branchlets arising in the upper margin. Besides larger branchlets, they also show broader, rows of secondary branches, giving a fan-shaped appearance. Branch tips of *M. tenera* usually look like those of *M. dichotoma* but they never grow taller forming a reticulate plate and their branch pattern is bushier. *M. tenera* is more or less having an intermediate but distinct form between *M. intricata f. murrayi* and *M. dichotoma*.

Distribution.— *Indonesia* (see material). Published records. China (Zou, 1978); Japan (Nishihira, 1988); The Philippines (Nemenzo, 1975, 1976, 1986); Taiwan (Randall & Cheng, 1984; Dai, 1989); Thailand (Ditlev, 1980); Vietnam (Moshchenko, 1995b, 1997).

*Millepora boschmai* de Weerdt & Glynn, 1991
(figs 25–30)


Fig. 25. *Millepora boschmai*. Fragment of a long column branching off dichotomously, RMNH Coel. 31093 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 26. *Millepora boschmai*. Submassive fragments, RMNH Coel. 31092 (Sumba, Indonesia).

Fig. 27. *Millepora boschmai*. RMNH Coel. 23146 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 28. *Millepora boschmai*. RMNH Coel. 23153 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 29. *Millepora boschmai*. Submassive fragments, RMNH Coel. 31061 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 30. *Millepora boschmai*. Close-up of corallum surface showing distinct cyclosystems, RMNH Coel. 31093 (Spermonde Archipelago, South Sulawesi, Indonesia).
Description.— Corallum attached, consisting of upright slender plates. Plates are dividing dichotomously toward the apices or forming irregular columns; 7.7 - 12 ± 5.8 – 18.6 mm thick.

Surface smooth or filled with growing nodules. Pores very obvious; density 146 - 199 ± 40 - 244 pores/cm² and 6.3 - 8.6 ± 3.8 - 15.4% gastropores. Gastropores 1.5 - 1.7 ± 0.2 - 2.0 mm apart, diameter 0.23 - 0.27 ± 0.03 - 0.31 mm; dactylopores are obviously smaller 0.13 - 0.14 ± 0.02 - 0.17 mm in diameter. Cyclosystems are very conspicuous; uniformly distributed all over the surface from the basal to the top below the growing margin; far separate from each other; each cyclosystem often forms and resides on a particular elevated surface; continuously 5-8 dactylopores around a gastropore.

Remarks.— The specimens of Indonesian M. boschmai have smaller pore sizes in comparison to the specimens from Gulf Chiriquí, Panama, viz. with gastropore diameter 0.28 - 0.37 ± 0.03 - 0.44 and dactylopore size 0.12 - 0.18 ± 0.03 - 0.26 (de Weerdt & Glynn, 1991). The differences in sizes are conspicuous and can be observed clearly by unaided eyes. Nevertheless, the cyclosystem arrangements and the corallum growth forms are particular for this species. The cyclosystems of the Indonesian coralla, however, tend to form elevations on the corallum surface in which they are residing.

Distribution.— Indonesia (see material). Published records. Gulf of Chiriquí, Panama Pacific Province (de Weerdt & Glynn, 1991; Glynn & Feingold, 1992).

Millepora exaesa Forskål, 1775
(figs 31–36)


Description.— Corallum attached or free-living; consisting of submassive irregular protuberances. Attached corallum consisting of short knobbed branches, growing vertically upward; resembles the common encrusting stage of young Millepora species,
Fig. 31. *Millepora exaesa*. Living corallum consisting of short knobbed branches (Lembeh Strait, North Sulawesi, Indonesia).

Fig. 32. *Millepora exaesa*. Living corallum consisting of short knobbed branches (Togian Islands, Tomini Bay, East Central Sulawesi, Indonesia).

Fig. 33. *Millepora exaesa*. Attached corallum, RMNH Coel. 31062 (Togian Islands, Tomini Bay, East Central Sulawesi, Indonesia).

Fig. 34. *Millepora exaesa*. Three free-living coralla, RMNH Coel. 23152 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 35 *Millepora exaesa*. Close-up of corallum surface showing pores, Coel. 23152 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 36 *Millepora exaesa*. Close-up of corallum surface showing pores, Coel. 23152 (Spermonde Archipelago, South Sulawesi, Indonesia).
except in the thickly knobbed forms. Free-living corallum form determined by the coral fragments that act as the substrates. Branches at the surface abundantly covered with nodules, adjacent knobs often coalescing into bigger and broader protuberances, tips rounded and blunt.

Surface filled with nodules. Pores obvious; density 225 - 269 ± 36 - 338 pores/cm² with 7.9 - 11.7 ± 2.5 - 16.7% gastropores. Gastropore distance between adjacent ones 1.3 - 1.6 ± 0.2 - 1.9 mm, diameter 0.23 - 0.26 ± 0.03 - 0.33 mm. Dactylopore 0.12 - 0.14 ± 0.01 - 0.17 mm in diameter. Usually more than 10 dactylopores encircle a gastropore, but do not resemble a single circle of a cyclosystem; there are lower numbers of encircling dactylopores in the surface valleys (6-7 pores).

**Distribution.** — **Indonesia** (see material). **Published records.** Australia (Veron, 1986); China (Zou, 1978); Guam (Randall & Myers, 1983); Japan (Nishihira, 1988); The Philippines (Nemenzo, 1975, 1976, 1986); Taiwan (Randall & Cheng, 1984); Thailand (Ditlev, 1980).

*Millepora platyphylla* Hemprich & Ehrenberg, 1834
(figs 37-42)


**Description.** — Corallum attached, consisting of upright massive plates. Plates stand vertically, 5.4 - 9.2 ± 4.1 - 25.9 mm thick; forming parallel tiers of plates or fusing into a honeycombed structure; upper edges straight or divided into lobes.

Surface abundantly covered with small verrucae and frequently infested by barnacles. Pores abundant and very conspicuous; 149 - 240 ± 61 - 473 pores/cm² and 4.9 - 7.6
Fig. 37. *Millepora platyphylla*. Living corallum showing honey-combed structure of upright plates (Cebu, the Phillipines).

Fig. 38. *Millepora platyphylla*. Living corallum showing structure of parallel tiers (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 39. *Millepora platyphylla*. RMNH Coel. 23145 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 40. *Millepora platyphylla*. RMNH Coel. 31051 (Selayer I., South Sulawesi, Indonesia).

Fig. 41. *Millepora platyphylla*. Close-up of corallum surface showing pores, RMNH Coel. 23145 (Spermonde Archipelago, South Sulawesi, Indonesia).

Fig. 42. *Millepora platyphylla*. Close-up of corallum surface showing pores, RMNH Coel. 23145 (Spermonde Archipelago, South Sulawesi, Indonesia).
± 2.6 - 18.5% of gastropores. Gastropores 1.1 - 1.4 ± 0.1 - 1.7 mm apart, diameter 0.21 - 0.26 ± 0.04 - 0.34 mm, clearly larger than dactylopores 0.09 - 0.14 ± 0.02 - 0.17 mm. Cyclosystems are obvious on the flat surfaces, but are indistinct on nodulous surfaces; 5-7 dactylopores in a cyclosystem. Underwater colour light brown with yellowish tips.

Distribution.— Indonesia (see material). Published records. Australia (Veron, 1986); China (Zou, 1978); Guam (Randall & Myers, 1983); Japan (Nishihira, 1988); Oman (Coles, 1996); The Philippines (Nemenzo, 1975, 1976, 1986); Taiwan (Randall & Cheng, 1984; Dai, 1987; Dai, 1989); Thailand (Ditlev, 1980); Vietnam (Manchenko et al., 1993; Moshchenko, 1995a, 1997, 1998a, 1998b).

Discussion

Twelve species of Millepora have been reported to occur in the Indo-Pacific, viz., M. dichotoma Forskål, 1775; M. intricata Milne-Edwards, 1857; M. murrayi Quelch, 1884; M. tenera Boschma, 1949; M. cruzi Nemenzo, 1975; M. xishaensis Zou, 1978; M. exesa Forskål, 1775; M. platyphylla Hemprich & Ehrenberg, 1834; M. latifolia Boschma, 1948; M. tuberosa Boschma, 1966; M. foveolata Crossland, 1952; and M. nodulosa Nemenzo, 1984. The present study revealed the occurrence of six Millepora species in Indonesian waters, including the new record of M. boschmai de Weerdt & Glynn, 1991. This finding proves that M. boschmai is not endemic to the eastern Pacific as suggested earlier, when this species was still not named (Glynn, 1972; Glynn & de Weerdt, 1991) and after it was described (de Weerdt & Glynn, 1991; Glynn & Feingold, 1992). Hence, M. boschmai, like the other two species reported from the Gulf of Chiriquí, the Panama Pacific Province, viz., M. intricata and M. platyphylla, occurs not only in the East Pacific but also in the Indo-West Pacific. M. boschmai may so far have been overlooked in Indonesia because it is relatively rare or because it is not well known.

We assume that Millepora murrayi is a growth form of M. intricata based on the observation of two museum specimens (figs 16, 19) and a picture of a living corallum (fig. 15). The two different growth forms were found within the same corallum without any indication of one form overgrowing the other. We propose to merge M. murrayi with M. intricata and refer to the first as the morpho-type M. intricata forma murrayi. However, the two growth forms are most commonly found independent from each other.

M. xishaensis is, unambiguously, a synonym of M. intricata Milne-Edwards. It has the conspicuous growth form of M. intricata, consisting of anastomose subcylindrical branches that branch dichotomously, diverge in all directions and never unite into a plate. Zou’s (1978) measurement of branch thickness at the basal part of the corallum, i.e., 10 mm, shows similarity with the present measurement of M. intricata, i.e., 9.4 mm.

From its description, M. cruzi (Nemenzo, 1975, 1976, 1986) seems to resemble M. tenera, particularly in the growth mode. The main branches are expanded and subdivided on the upper margin into branchlets consisting of flattened or cylindrical branches with blunt tips. They only differ in the occurrence of tiny elevations bearing the gastropores and less expanded branchlets in M. cruzi. Since its record by Nemenzo, M. cruzi is hardly reported from the Indo-Pacific, except by Moshchenko (1997, p. 241 figs 2c-2d) which in fact is M. intricata according to us. We regard the elevation on the corallum surface of M. cruzi as fitting within the intra-specific variation of M. ten-
era without specific value and synonymise it under *M. tenera* Boschma, 1949.

The specific status of the other branched milleporid described by Nemenzo (1984), i.e. *M. nodulosa*, is still unclear, since its description was based on a single museum specimen and because it has never been reported by other authors. However, judging from its photograph (Nemenzo, 1984 p. 158 fig. 3) it resembles *M. intricata* although it is described as having “flat stems, branches and branchlets marked with irregular distributed nodules that never bear gastropores” while *M. intricata* has a smooth surface and is characterised by its subcylindrical branches.

*M. exaesa* and *M. tuberosa* are very similar in form, but Boschma (1966) separates them on the basis of their geographical distribution. He concluded that the former is restricted to the Red Sea and that all other *M. exaesa* that have been described from the Indo-Pacific represent *M. tuberosa*. However, several authors have ignored Boschma’s separation of the two species based on their geographical range and referred to *M. exaesa* as an Indo-Pacific species (Nemenzo, 1975, 1976, 1986; Nishihiro, 1988; Veron, 1986; Zou, 1978).

*M. foveolata* Crossland, 1952, with the Great Barrier Reef as type locality, is considered a valid species. No specimens are known from Indonesia. *M. foveolata* is clearly separated from the other milleporids by the possession of low ridges that circumcribe single pores or groups of pores, giving the corallum surface a finely wrinkled appearance. *M. foveolata* could be confused with *M. exaesa*, since both have an encrusting growth form with the presence of nodules on the corallum surface, but in *M. exaesa* the ridges are absent and the nodules are more prominent.

We are not convinced that *M. latifolia* Boschma, 1948, is a valid species. With regard to the corallum growth form it builds plates resembling those of *M. dichotoma*, but detailed observation on the upper plate margin of the type specimen (RMNH Coel. 15878) shows the similarity to the finger-pattern also found in *M. intricata f. morrayi*. Moreover, the measurement results of the pore characters from eleven *Millepora cf. latifolia* (table 3) revealed that *M. latifolia* is more closely related to *M. dichotoma* than to the *M. intricata* group. It has a larger gastropore diameter (0.19 - 0.24 ± 0.03 - 0.30 mm) resembling that of (sub-) massive milleporids, and like *M. dichotoma*, it has lower pore densities (154 – 194 ± 24 – 234 pores/cm²) and a lower gastropore percentage (4.9 – 7.0 ± 1.7 – 10.1%). The occurrence of cyclosystems varies highly within the observed specimens. They can be very distinct or even absent. In the present study, the taxonomical status of *M. latifolia* remains undetermined.

In conclusion, due to intermediate growth forms it is very ambiguous to classify branched milleporids into different species. The present revision of Indonesian *Millepora* is merely based on museum specimens without considering the environmental setting that is believed to have a great influence on the morphological characteristics of corals. The (sub-)massive milleporids, on the other hand, are much easier to classify.

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