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Masquerade, mimicry and crypsis of the polymorphic sea anemone *Phyllodiscus semoni* and its aggregations in South Sulawesi

Bert W. Hoeksema[1, 3], Andrea L. Crowther[1, 2]
[1] *Department of Marine Zoology, Netherlands Centre for Biodiversity Naturalis, PO Box 9517, 2300 RA Leiden, The Netherlands*
[2] *Department of Ecology and Evolutionary Biology, and the Biodiversity Institute, The University of Kansas, 1200 Sunnyside Ave., Lawrence, KS 66045, USA*
[3] *E-mail: bert.hoeksema@ncbnaturalis.nl*

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Abstract

Phyllodiscus semoni is a morphologically variable sea anemone species from the Indo-Pacific with morphotypes ranging from upright and branched to low-lying and rounded. The apparent camouflage strategies of this sea anemone allow it to resemble other species or objects in its environment, such as stony corals, soft corals, seaweeds, or rocky boulders covered by algae, which may help it to avoid recognition by potential predators. Occasionally, it occurs in aggregations that may result from asexual reproduction. A high level of intraspecific morphological variation, including co-occurring aggregations of three different morphotypes, was observed in the Spermonde Archipelago off Makassar, South Sulawesi, Indonesia. The co-occurrence of aggregations with different morphotypes suggests that *Phyllodiscus* is a highly polymorphic monospecific genus. Sea anemones of this genus are not frequently encountered at other localities and the number of morphotypes seems large. Therefore, it is unlikely that we are dealing with more than one species that are all concentrated in a single area. *Phyllodiscus* sea anemones are considered dangerous to humans because their nematocysts contain highly toxic venoms that may inflict harmful stings. Therefore they are the subject of recent toxicological studies. The present paper aims to assist in the recognition of these highly variable hazardous animals and to discuss the appearance of their aggregations.

Contents

Introduction

Phyllodiscus semoni Kwietniewski, 1897 (Actiniaria: Aliciidae) is a species of sea anemone found on coral reefs in the Indo-Pacific, which can inflict harmful stings to humans (Den Hartog, 1997; Fosså and Nilsen, 1998). *Phyllodiscus semoni* can occur as individuals or in aggregations (Strack, 1993) that attach to rock or dead coral and are able to move over the substrate. In this way, they differ from some other stinging sea anemones, such as sand-dwelling actiniarians of the genus *Actinodendron* de Blainville, 1830, which live partly buried and can completely retract into the sediment. Much morphological variation exists within *P. semoni*, but this has not been widely or thoroughly reported, which is why this species is difficult to recognise and has been confused with other sea anemone species, such as *Actinodendron plumosum* Haddon, 1898 (Den Hartog, 1997; Fosså and Nilsen, 1998), other cnidarians, algae, or inanimate objects found in the environment. *Phyllodiscus semoni* is not known from many localities and the range of morphotypes seems so large (with new varieties still being discovered in the field), that it is unlikely that we are dealing with more than one species. The collected material is under investigation for possible genetic differences and morphological variation to indicate different species, but no evidence has been found so far (Crowther and Hoeksema, in prep).

The original descriptions of *Phyllodiscus* Kwietniewski, 1897, and *P. semoni* were based on a sole museum specimen collected from Ambon, Indonesia (Kwietniewski, 1897, 1898). The description lacks information relating to the natural history and habitat of this species, as the author presumably never saw the sea anemone alive nor visited the site where it was

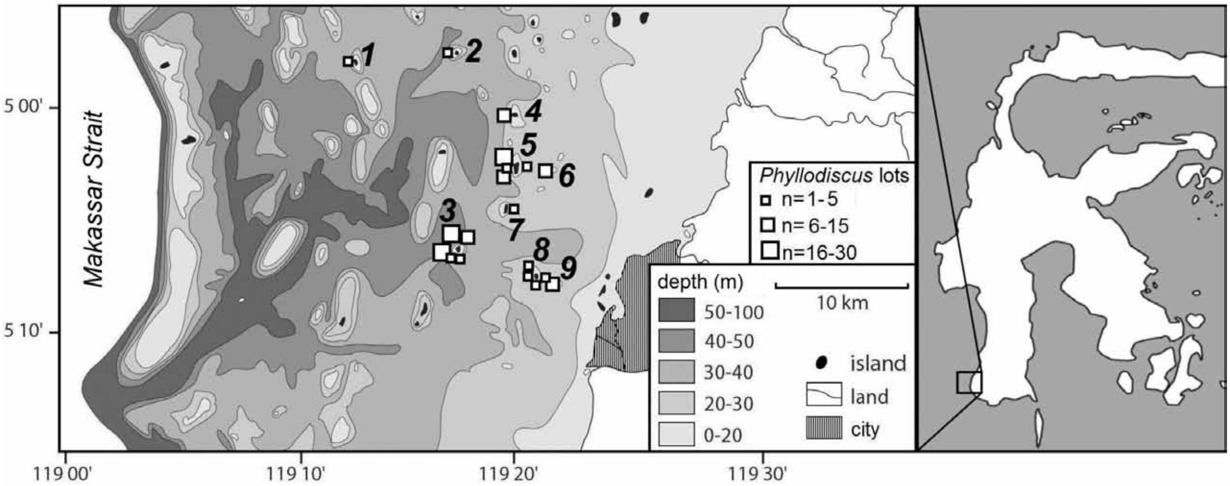

Fig. 1. Map of the Spermonde Archipelago, off Makassar city (hatched pattern), South Sulawesi, where *Phyllodiscus semoni* was observed. Boxes indicate total numbers of observations per site varying from 1 to 30 in the years 1994-1998 (categories n = 1-5, 6-15, 16-30). One observation may concern one or more individuals of a particular morphotype. Reefs: *1* = Lumu Lumu, *2* = Pulau Badi, *3* = Kudingareng Keke, *4* = Bone Batang, *5* = Barrang Lompo, *6* = Bone Lola, *7* = Barrang Caddi, *8* = Samalona, *9* = Bone Baku.

collected. Despite the fact that more recently this species has been recorded in field guides of the Indo-Pacific (*e.g.* Gosliner *et al.*, 1996; Williamson *et al.*, 1996; Coleman, 2000; Halstead, 2000; Erhardt and Knop, 2005; Bergbauer *et al.*, 2007) and is the subject of toxicological studies (*e.g.* Mizuno *et al.*, 2000, 2007; Nagai *et al.*, 2002a, b; Nagata *et al.*, 2006; Satoh *et al.*, 2007), there is still very little published information about the natural history of this species.

Phyllodiscus has been reported to occur as solitary individuals or in aggregations; we use the term aggregation to refer to a dense group of multiple individuals of identical morphotype and colouration at the same locality. Because of the high density of individuals of the same morphotype, we assume that *Phyllodiscus* uses asexual reproduction, and that therefore an aggregation of a certain morphotype consists of cloned individuals.

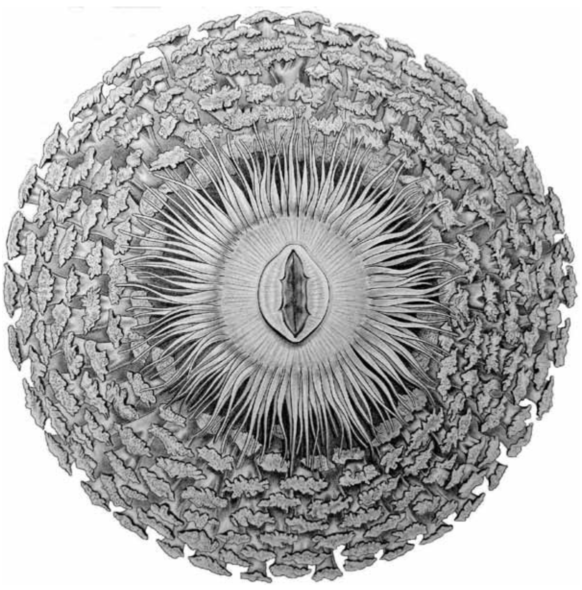

Fig. 2. Holotype of *Phyllodiscus semoni*. Schematic drawing showing column and extended tentacles (after Kwietniewski, 1898). The depicted animal most probably represented a morphotype resembling a relatively smooth disc.

Den Hartog (1997) mentioned the variability of morphology among *Phyllodiscus* specimens, but did not show images of the different morphotypes. Until now, field guides have provided the best information about the range of appearances. The difference among the morphotypes is due solely to the pseudotentacle morphology of each individual. Pseudotentacles are outpocketings of the column wall that can grow and extend in various directions, and can be smooth or uneven, straight and/or branched. During the day, the oral disc, mouth, and tentacles are retracted into the coelenteron, but the pseudotentacles remain extended and visible to other organisms. Because of this posture, *Phyllodiscus* individuals are not easily recognised as sea anemones, and they appear to be camouflaged and to fit in with their environment. This is achieved via crypsis (avoiding detection by blending in with background), masquerade (resemblance of inanimate or inedible objects), and/or mimicry (detected, but misidentified as its model organism) (Skelhorn *et al.*, 2010a, b).

In the present paper we report for the first time on the co-occurrence of various *Phyllodiscus* morphotypes in the Spermonde Archipelago off Makassar (South Sulawesi, Indonesia), each of which appear to exhibit crypsis, mimicry, and/or masquerade by resembling branching and encrusting corals (mostly scleractinians and alcyonaceans) or dead rock covered by algae. *Phyllodiscus* individuals formed aggregations consisting of three different morphotypes: all three morphotypes co-occurring in a single assemblage on a reef slope, with all individuals within 25 m distance of one another. The simultaneous occurrence of multiple *Phyllodiscus* morphotypes in dense aggregations suggests that this is a highly polymorphic single species that uses asexual reproduction to reach high abundances. We provide field photographs to show the extraordinary amount of morphological variation found among individuals of *Phyllodiscus*, and the extent of their apparent camouflage. We also provide information to help distinguish the sea anemones from their model organisms, which will aid in the correct identification of these sea anemones by divers, field guides, and most importantly, scientists performing toxicology studies.

Material and methods

During mushroom coral surveys (in 1994-1998) in the shelf-based Spermonde Archipelago, off Makassar, South Sulawesi, Indonesia (Fig. 1), specimens (>150 lots consisting of one or more individuals) of the highly polymorphic *Phyllodiscus semoni* (Anthozoa: Actiniaria: Aliciidae) were observed by use of the roving diver technique (see Hoeksema and Koh, 2009). The identifications were performed in the field and were based on the original species description and illustration by Kwietniewski (1897, 1898), which were brought to our attention by the late J.C. den Hartog, who also showed an interest in this particular species (Strack, 1993; Den Hartog, 1997). Specimens were photographed with a Sea & Sea SX-1000 TTL Underwater camera with a strobe for extra illumination. Because the sea anemones resembled corals, examples of such look-alikes were also photographed. Unless stated otherwise, the first author is responsible for all fotographs and observations in the field.

The sea anemones were collected, fixed in a 10% formalin solution, and deposited in the coelenterate collection of the Netherlands Centre for Biodiversity, NCB Naturalis (= RMNH, formerly Rijksmuseum van Natuurlijke Historie) in Leiden. Morphology and cnidae of preserved material were further examined at NCB Naturalis in Leiden (the Netherlands) and The University of Kansas in Lawrence (USA). Specimens were dissected and examined under a dissecting microscope to determine fertility, number, and arrangement of mesenteries. Cnidae preparations were made from the vesicles, pseudotentacles, tentacles, mesenterial filaments, and column by smashing tissue with water under a coverslip; slides were viewed using a compound microscope and types of cnidae were noted.

Results

The possession of six pairs of complete mesenteries and nematocyst-laden vesicles of the column indicated that the specimens belonged to the family Aliciidae Duerden, 1895 (Carlgren, 1949). The outgrowths of the column, the pseudotentacles, occurred in a broad zone (rather than a single ring), which indicated that the specimens were in the genus *Phyllodiscus*. *Phyllodiscus* is a monotypic genus, and the specimens belong to the only species, *P. semoni* (Fig. 2). We are currently investigating whether this morphological variability relates to more than one species (Crowther and Hoeksema, in prep.).

Phyllodiscus semoni individuals were observed at nine reefs in the Spermonde Archipelago: Lumu Lumu, Pulau Badi, Kudingareng Keke, Bone Batang, Barrang Lompo, Bone Lola, Barrang Caddi, Samalona, and Bone Baku (Fig. 1). Most encounters with the sea anemone (either as individuals or as aggregations) occurred on mid-shelf reefs (approximately 20-40 m maximum depth), whilst on reefs close to the coastline, no specimens were found, and on the more offshore reefs, the species was rare. The sea anemones were attached to dead coral but could easily be detached, indicating that they were not sessile but sedentary. A few specimens were found detached, more or less drifting on or above the sandy bottom.

Solitary individuals of various morphotypes (including colour morphs) were observed, and most of them resembled dead coral rock covered by algae. Others looked like species of fleshy seaweeds with branched thalli, stony corals (Hexacorallia: Scleractinia) or soft corals (Octocorallia: Alcyonacea and Stolonifera), and therefore showing a large array of apparent mimicry (Figs 3-6). In these figures the sea anemones appear on

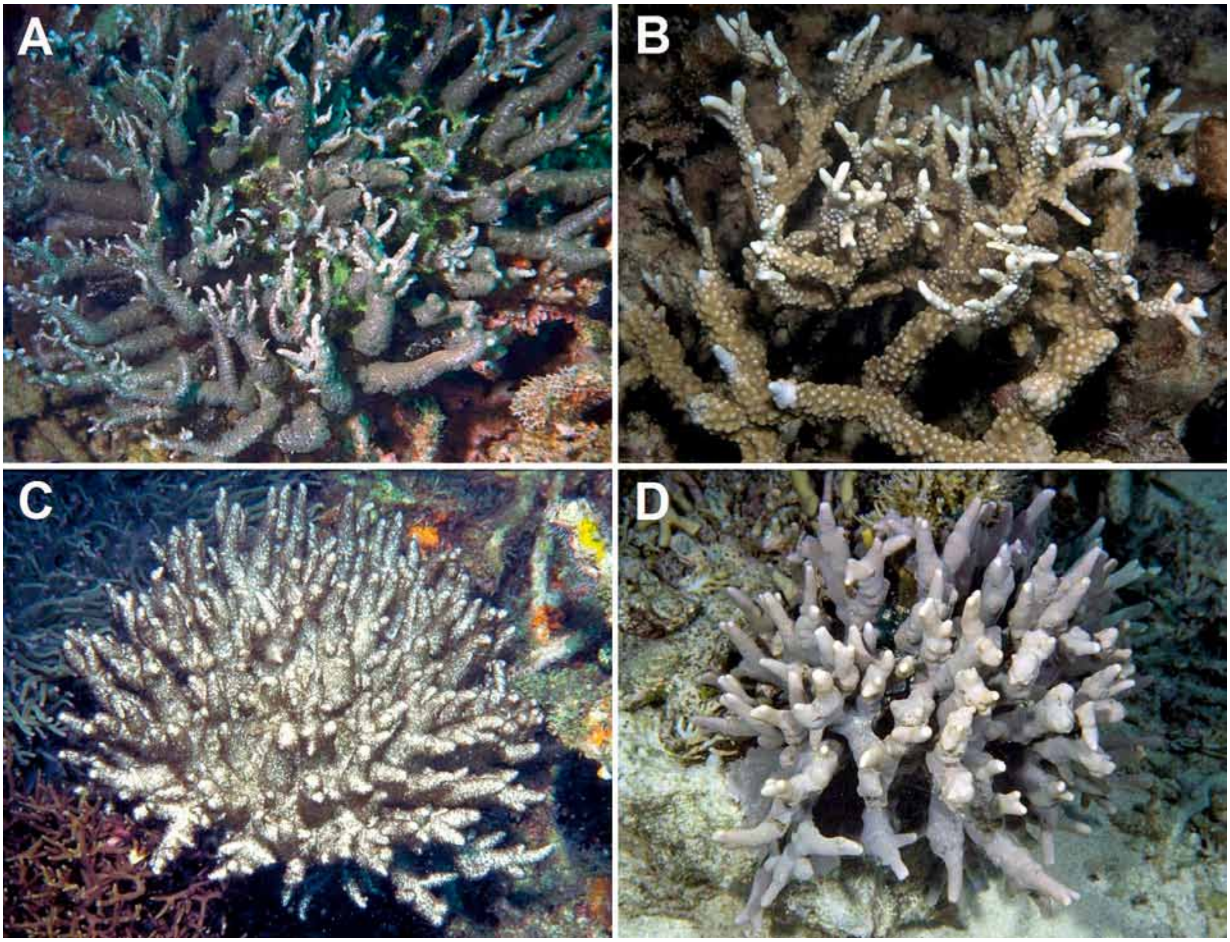

Fig. 3. Phyllodiscus semoni sea anemones (A, C) at South Sulawesi and examples of possible look-alike models (Scleractinia: B, D). A. Branching morph (Pulau Badi, 1997). B. Model for A: *Anacropora* sp. (eastern Sulawesi, 1999). C. Branching morph (Kudingareng Keke, 1997). D. Model for C: *Porites cylindrica* Dana, 1846 (Kudingareng Keke, 1994).

the left panel, and the presumed corresponding model organism on the right panel. Most Scleractinia look-alikes (compare Veron, 2000) mimicked branching corals belonging to the Acroporidae and Pocilloporidae (Figs 3-4). Among the Alcyonacea look-alikes (compare Fabricius and Alderslade, 2001; Van Ofwegen, 2008), *Phyllodiscus* morphotypes resembled encrusting and branching species of, for instance, the soft coral genera *Asterospicularia* Utinomi, 1951 (Asterospiculariidae), *Klyxum* Alderslade, 2000 and *Sinularia* May, 1898 (Alcyoniidae), and *Efflatounaria* Gohar, 1939, or other xeniids (Xeniidae) (compare Fabricius and Alderslade, 2001) (Figs 5-6). Furthermore, one observed specimen appeared to use stoloniferan octocorals as a model, such as *Tubipora* Linnaeus, 1758, but it also appeared to resemble the gorgonian *Briareum violaceum* (Quoy and Gaimard, 1833) (compare Fabricius and Alderslade, 2001) (Fig. 6E-G).

Aggregations of *Phyllodiscus* individuals were observed on and between dead *Acropora* branches (6-12 m depth) on the NW slope of the cay-crowned Kudingkareng Keke reef (5°5.063′S, 119°10.168′E; June 1997). The largest aggregation consisted of three non-intermingling, adjacent groups of morphotypes (Fig. 7AB) within 25 m length of reef slope, each showing crypsis, mimicry, and/or masquerade (following terminology from Skelhorn *et al.*, 2010a, b), either by resembling branching corals (branched shape, Fig. 7C) or dead coral rock covered by algae (shaggy disc, Fig. 7D; smooth disc, Fig. 7E). Each aggregation consisted of 10-25 individuals of various sizes. If these sea anemones had not occurred in aggregations they may have been less

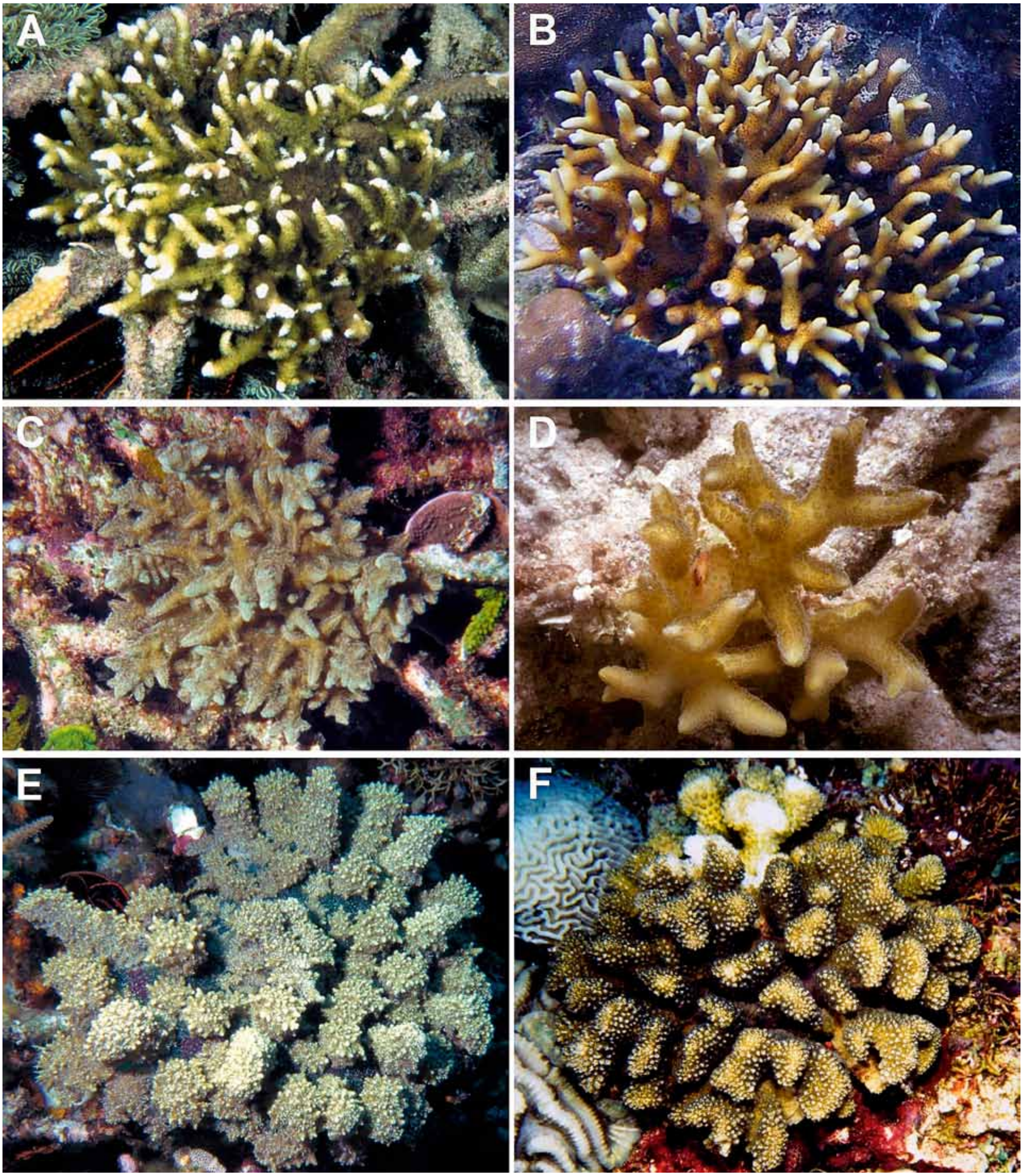

Fig. 4. *Phyllodiscus semoni* sea anemones (A, C, E) at South Sulawesi and examples of possible look-alike models (Scleractinia: B, D, F). A. Branching morph (Kudingareng Keke, 1997). B. Model for A: *Seriatopora hystrix* Dana, 1846 (East Kalimantan, 2003). C. Branching morph (Barang Lompo, 1996). D. Model for C: *Seriatopora caliendrum* Ehrenberg, 1834 (Lankai, 1997). E. Branching morph (Pulau Badi, 1996). F. Model for E: *Pocillopora meandrina* Dana, 1846 (Bali, 1998).

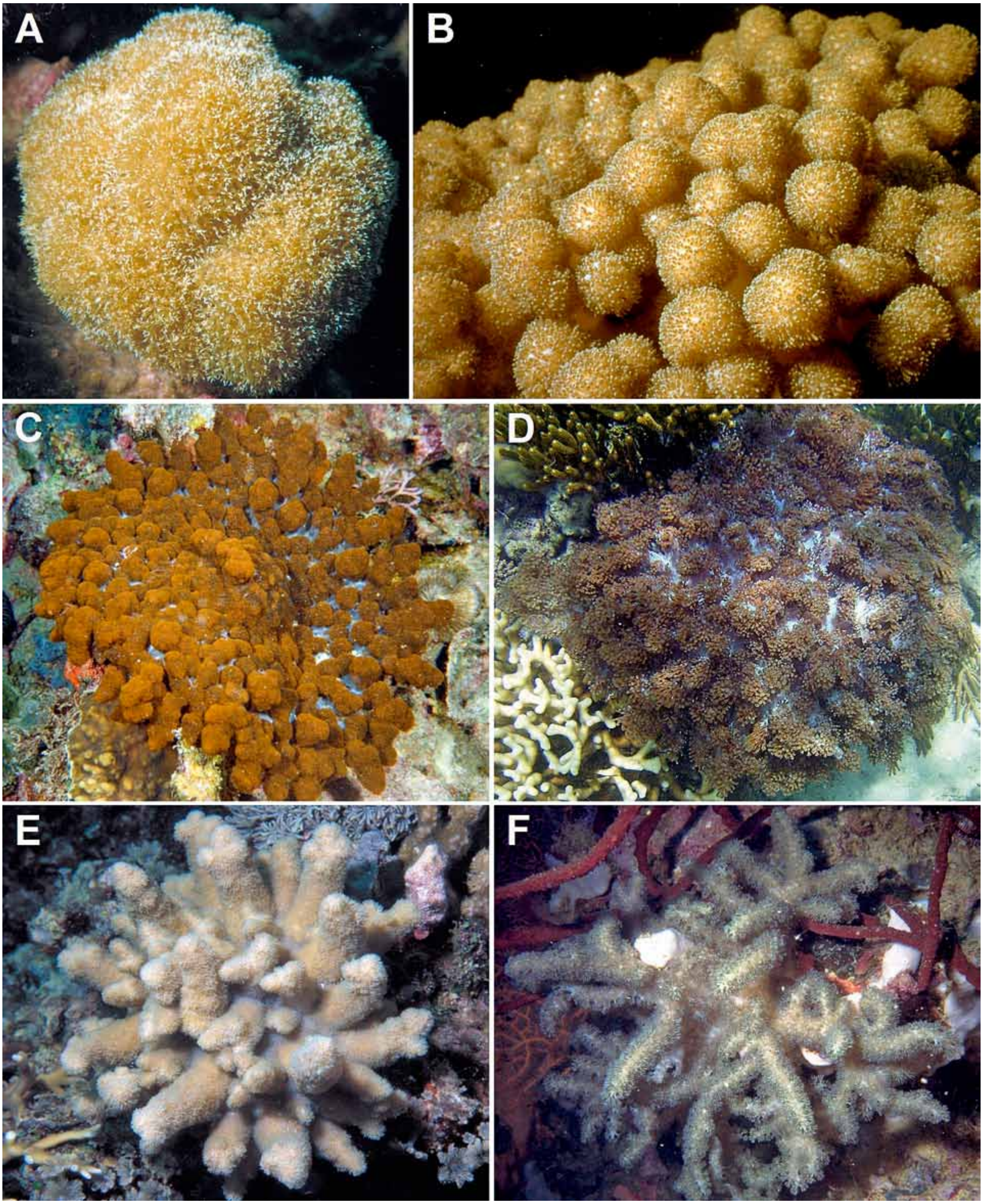

Fig. 5. Phyllodiscus semoni sea anemones (A, C, E) at South Sulawesi and examples of possible look-alike models (Alcyonacea: B, D, F). A. Globular morph (Kudingareng Keke, 1997); see also Fig. 10. B. Model for A: *Asterospicularia* sp. (Bali, 2001, photo L.P. van Ofwegen). C. Discoid morph (Pulau Badi, 1994). D. Model for C: *Efflatounaria* sp. (East Kalimantan, 2003). E. Branching morph (Kudingareng Keke, 1998). F. Model for E: *Klyxum* sp. (Pulau Badi, 1996).

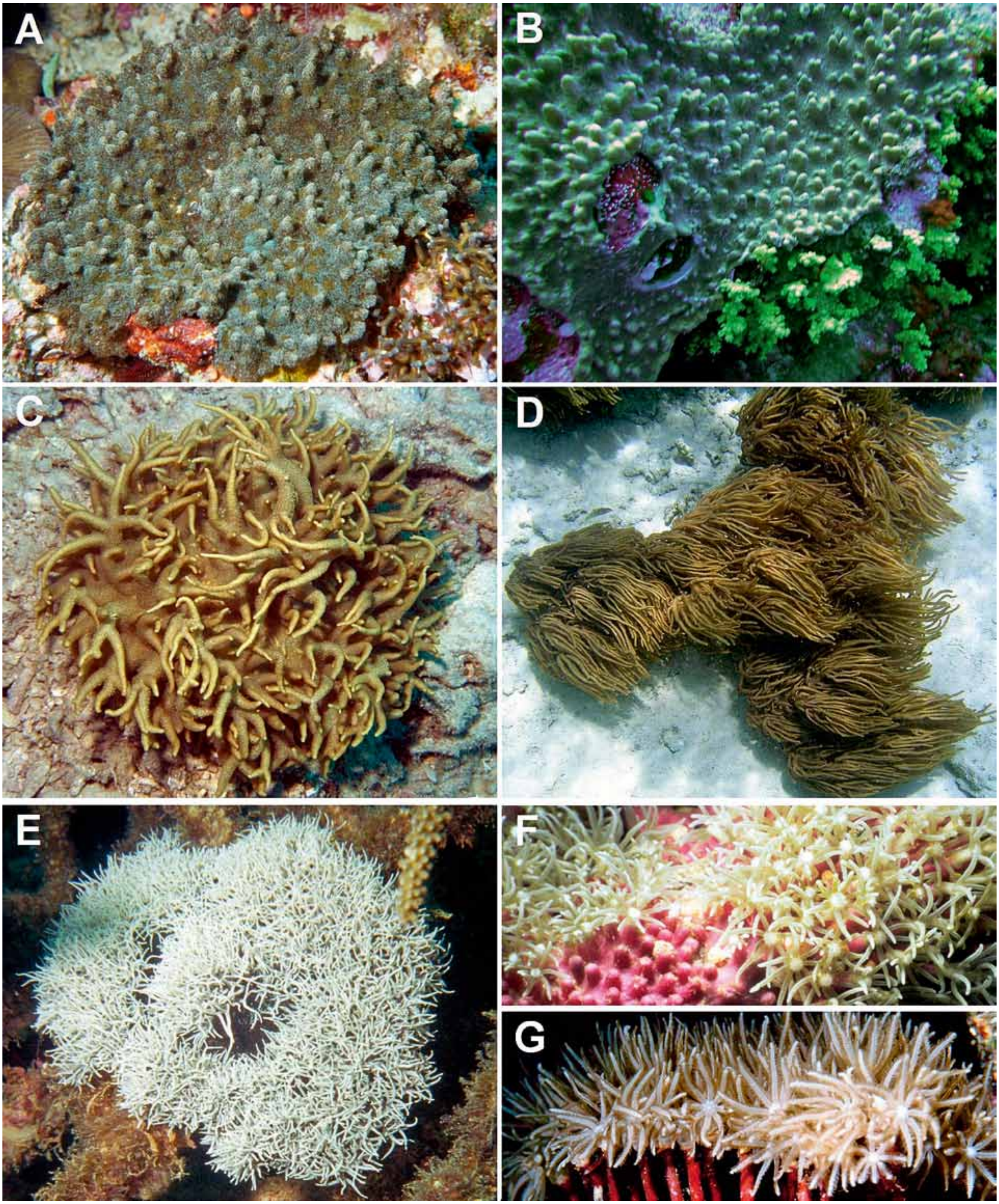

Fig. 6. Phyllodiscus semoni sea anemones (A, C, E) at South Sulawesi and examples of possible look-alike models (Alcyonacea and Stolonifera). A. Discoid morph (Kudingareng Keke, 1997). B. Model for A: *Sinularia gravis* Tixier-Durivault, 1970 (Palau, 2005, photo L.P. van Ofwegen). C. Branching morph (Bone Lola, 1997). D. Model for C: *Sinularia flexibilis* (Quoy and Gaimard, 1833) (East Kalimantan, 2003). E. Discoid morph (Barang Lompo, 1996). F. Model for E: *Briareum* sp. (Philippines, 1999, photo L.P. van Ofwegen). G. Model for E: *Tubipora musica* Linnaeus, 1758 (Bali, 2001).

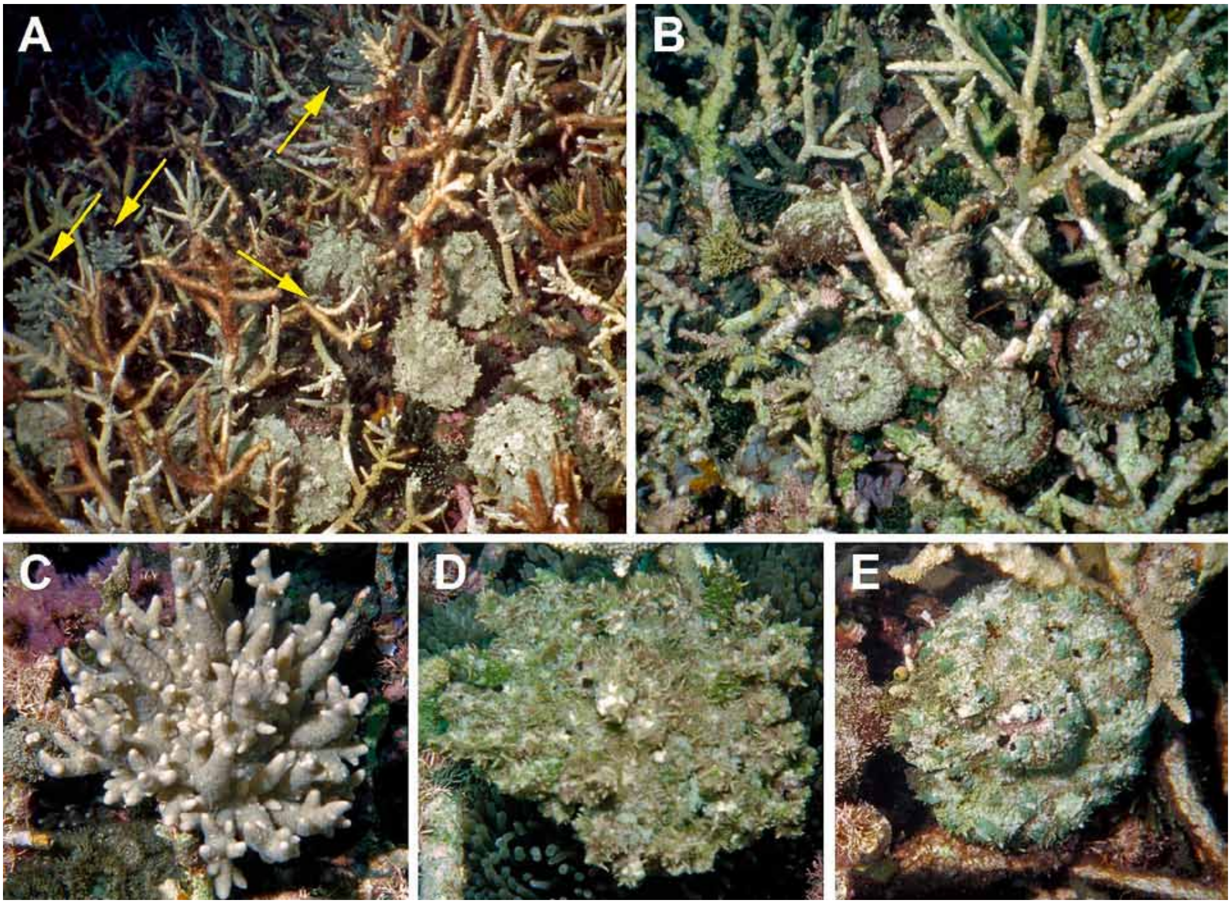

Fig. 7. Phyllodiscus semoni at South Sulawesi (Northwest side Kundingkareng Keke reef, Spermonde Archipelago, June 1997). Aggregations and individuals of three morphotypes: branched (A: arrows, C), shaggy disc (A, D), smooth disc (B, E). The latter resembles the schematic drawing of the holotype (Fig. 2).

obvious because of their camouflage. This is the first published account of a combined clustering of three distinct *Phyllodiscus* morphotypes. At a nearby location, a small aggregation of three well-camouflaged individuals of another morphotype was photographed (Fig. 8).

Discussion

Cross-shelf distribution

The habitat diversity of the Spermonde archipelago offers suitable conditions for *Phyllodiscus* to thrive, especially in the mid-shelf zone. The highest concentrations of individuals and the most morphotypes (including in aggregations) were encountered on mid-shelf reefs, and particularly on the wave-exposed northwest and west slopes of Kudingareng Keke reef, which is located outside the reach of the Jeneberang river plume (Hoeksema, 1990). This side of the reef is the most exposed to storm-generated waves (Hoeksema, 1988, 1990). Besides dense patches of living *Acropora* corals, areas of dead coral branches and unconsolidated rubble can be found here, which together form an ideal habitat for sea anemones that live attached to hard substrata, such as *Phyllodiscus*. As a whole, the Spermonde archipelago with its high concentration of patch reefs of wide-ranging distances offshore, and with slopes of varied exposures to wind energy and depth ranges, is rich in diverse species of reef-dwelling organisms such as reef corals, sea urchins, sea anemones, sponges, boring bivalves, gastropods, and large foraminifera (De Beer, 1990; Hoeksema, 1990; Renema *et al*., 2001; Kleemann and Hoeksema, 2002; Cleary *et al*., 2005; Becking *et al*., 2006; De Voogd *et al*., 2006; Cleary and De Voogd, 2007; Kokshoorn *et al*., 2007).

Polymorphism

Intraspecific morphological variation is not uncommon in anthozoans such as corals and zoanthids (Hoeksema and Moka, 1989; Hoeksema, 1993, in press; Reimer *et al*., 2004, 2008; Gittenberger and Hoeksema, 2006; Todd, 2008; Stefani *et al*., 2011), but in actiniarians no other cases involving such a large range of morphotypes are known to us. Within sea anemone species, most of the documented intraspecific variation is due to colour; for example the temperate East Atlantic species *Actinia equina* (Linneaus, 1758) (Haylor *et al*., 1984; Solé-Cava and Thorpe, 1992; Watts *et al*., 2000) and the (sub)tropical West Atlantic *Condylactis gigantea* (Weinland, 1860) (Stoletzki and Schierwater, 2005), and the tropical species *Cryptodendrum adhaesivum* Klunzinger, 1877 and *Heteractis magnifica* (Quoy and Gaimard, 1833), both of which are known to host clownfishes (Dunn, 1981; Fautin and Allen, 1992). Even at the genus level, there is no other actiniarian (or even anthozoan) taxon that possesses this much morphological variation.

The extensive morphological variation seen in *Phyllodiscus* is due to the outgrowths of the column, the pseudotentacles. *Phyllodiscus* sea anemones, like many other shallow-water actiniarians, possess zooxanthellae. In some members of Aliciidae, including *Phyllodiscus*, the zooxanthellae are concentrated in special outgrowths of the column called pseudotentacles. The pseudotentacles provide increased surface area to house and display zooxanthellae to the sun, therefore providing maximum exposure to light for photosynthesis. During the day, the pseudotentacles are expanded, while at night the tentacles on the oral disc are expanded (Gladfelter, 1975; Fig. 9). Multiple pseudotentacles occur per *Phyllodiscus*, extending out from two-thirds of the column (the very top and bottom of the column are free from pseudotentacles). These outgrowths can be branched in various directions and to various degrees, thereby creating variation in pseudotentacle morphology, and therefore the different morphotypes.

For this publication, we assume that the differences in pseudotentacle morphology indicate intraspecific variation, although it has been hypothesised that they can also represent interspecific variation (Den Hartog, 1997). This question is difficult to answer, as there is apparently a continuum of morphotypes, from branched to flat or disc shapes. We are currently investigating whether this morphological diversity is intra- or interspecific, using pseudotentacle morphology and molecular sequence data, and in particular whether the pseudotentacle morphology can be used to delimit species boundaries in *Phyllodiscus* (Crowther and Hoeksema, in prep).

Den Hartog (1997) described three morphotypes of *Phyllodiscus* that he observed in Indonesia, and all descriptions relate to how the morphology of the sea anemone is similar to another organism at the locality; he describes ‘variegated patches of algae-covered substratum’, ‘a bunch of algae’, and ‘a branched coral’ (Den Hartog, 1997: 360). We suspect that the morphotypes of *P. semoni* are a result of the sea anemones employing the tactics of crypsis, mimicry, and/or masquerade via camouflage (Skelhorn *et al*., 2010a, b). Using camouflage to fit in with the surroundings, cryptic organisms avoid detection by predator or prey through blending in with their background. The three *Phyllodiscus* individuals in Fig. 8 are cryptic, as they are fitting in with the mottled algal-covered background to which they are attached. Organisms employing masquerade are also camouflaged, but resemble an inanimate or inedible object; it is assumed that the predator or prey detect the masquerading organism, but misidentify it as its model organism. The *Phyllodiscus* morphotypes that resemble algal-covered boulders or clumps of algae may be using masquerade to deter predation. Organisms that employ mimicry resemble a defended organism; it is assumed that the predator or prey detect the mimic but misidentify it as the defended model organism. The branched morphotypes of *Phyllodiscus* sea anemones resemble corals, which also possess nematocysts.

Without experimental trials, it is impossible to identify whether the morphotypes are employing any type of camouflage, including crypsis, mimicry, masquerade, or a combination of these. Experiments would need to demonstrate that appropriate organisms (*i.e.* potential predators or prey) perceive the sea anemones as cryptic or may mistake them for the items/organisms that they appear to resemble. So far, assumptions are based on the field observations by the authors.

Aggregations

Aggregations of large reef-dwelling sea anemones are not uncommon (Richardson *et al*., 1997; Brolund *et al*., 2004; Scott *et al*., 2011). Strack (1993: 49), in an account of the Rumphius Biohistorical Expedition to Ambon, mentioned that Den Hartog ‘found an aggregation of ca. 80 individuals of the large and extremely painful stinging *Phyllodiscus semoni*’. He (Strack, 1993: Fig. 50) showed individuals of *P. semoni* clustered closely

Fig. 8. Three *Phyllodiscus* individuals (arrows) camouflaged against their background (West side Kundingkareng Keke reef, Spermonde Archipelago, South Sulawesi, November 1997).

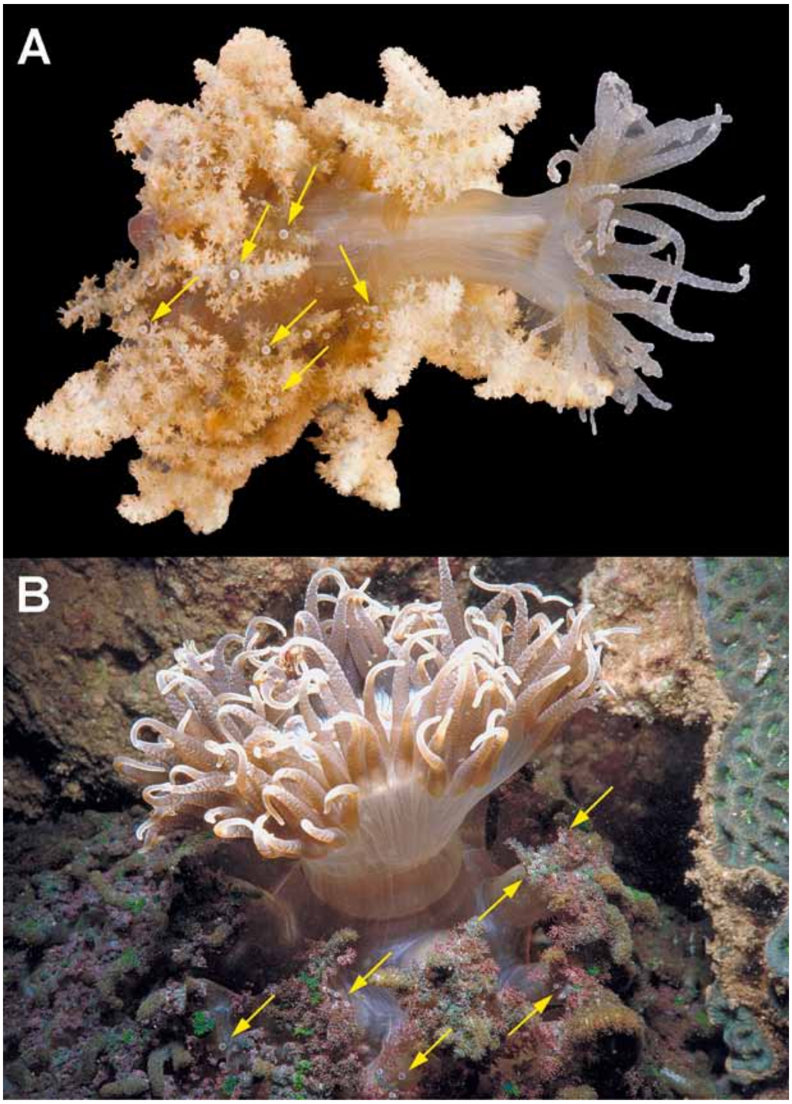

Fig. 9. *Phyllodiscus semoni* at South Sulawesi. Extended tentacles and pseudotentacles with vesicles (arrows) in a branched morphotype (A) and a smooth disc (B), West side Bone Baku reef, Spermonde Archipelago, May 1997.

together in high abundance at a reef at the Islet of Pompo, east of Ambon. All individuals are of the same morphotype: the shape of the individual when tentacles are retracted is reminiscent of a head of cauliflower (also resembling specimens of the soft coral genus *Asterospicularia*) (Fig. 5AB). *Phyllodiscus semoni* is not mentioned again in Strack's (1993) report, so it is unknown whether other morphotypes were found in Ambon on that expedition.

We observed several individuals of this morphotype and others at Ambon (in 1996), including small specimens clustered next to a larger individual (Fig. 10). From this observation, we infer that *Phyllodiscus* relies on asexual reproduction (perhaps pedal laceration, but the mode of asexual reproduction is unknown) to reach high densities of individuals in a given area. Similarly, free-living mushroom corals (Scleractinia: Fungiidae) can form dense monospecific populations as a result of asexual reproduction by either budding or fragmentation (Hoeksema, 2004; Hoeksema and Gittenberger, 2010; Hoeksema and Waheed, 2011). Such monospecific aggregations are very striking because dense mushroom coral assemblages usually consist of mixed species (*e.g.* Hoeksema, 1991; Goffredo and Chadwick-Furman, 2000; Elahi, 2008; Hoeksema and Koh, 2009; Hoeksema and Matthews, 2011). In populations of other anthozoan species that rely on asexual reproduction, the relative frequencies of different morphotypes appear to depend heavily on the replication rate of clonal genotypes (Ayre and Willis, 1988; McFadden, 1997; Whitaker, 2006). That *Phyllodiscus* aggregations generally consisted of individuals ranging in size but not in morphology suggests that these sea anemones were clones. If the aggregations were a result of sexual reproduction, we would not expect each aggregation to consist of identical morphotypes but to be a mixed assemblage of morphotypes or of closely related species. Moreover, if the *Phyllodiscus* individuals would be of different genotypes, they might attack each other, causing adjacent individuals to move away from one another as in the sedentary temperate sea anemone *Actinia equina*, leading to well-spaced distributions instead of aggregations (Briffa and Greenaway, 2011).

Asexual reproduction or cloning may play an important role in the life history of anthozoans and other cnidarians as a mechanism to occupy substrate surface, while some also use mobility to spread outward and to remain literally on top of competitors (Francis, 1988; Karlson, 1988; Fautin, 1991; Hoeksema, 2004; Geller *et al.*, 2005; Hoeksema and Gittenberger, 2010). Some competitive anthozoans show aggressive behavior and are known to reach high concentrations and dense substrate cover at the expense of other benthic animals by use of their venom or by simply overgrowing them (Chadwick, 1987; England, 1987; Chadwick and Adams, 1991; Chadwick-Furman and Spiegel, 2000; Chen *et al.*, 2008). Due to the high toxicity of their venoms, some anthozoans, especially sea anemones, are also know to be potentially harmful to man by inflicting long-lasting wounds (Hansen and Halstead, 1971; Halstead, 1988; Williamson *et al.*, 1996; Mizuno *et al.*, 2000; Nagata *et al.*, 2006; Bergbauer *et al.*, 2007).

Co-occurrence of morphotypes in aggregations

We provide the first observations (Fig. 7) of three different morphotypes co-occurring within aggregations on the same reef. As discussed in the previous section, we suspect that the individuals of identical morphotypes within one aggregation are clonal. Once the pseudotentacles have been developed, it is unlikely they are plastic and can change their growth and therefore appearance and morphotype. For example, we consider it highly unlikely that individuals with branching pseudotentacle morphology (Fig. 7C) could change their morphology to become more disc-shaped like the other morphotypes at this locality (Fig. 7D, E). Regarding *Phyllodiscus* morphotypes, which all occur in more or less the same environment, there appears to be no indication of ecophenotypic plasticity as shown by many scleractinian corals (*e.g.* Todd, 2008; Stefani *et al.*, 2011). Accordingly, we presume that each morphotype aggregation in Fig. 7 is a separate clonal group. The co-occurrence of three morphotypes at the same locality, and therefore under the same environmental influences, indicates that the morphology is not due to ecophenotypic variation, but that it is under genetic control.

Misidentification of venomous sea anemones

Correct identification is important for specimens of *P. semoni*, because they are used in many toxicological studies. The toxin of *P. semoni* is known to be very dangerous to humans; it may cause skin lesions, ulcers, and necrosis (Williamson *et al.*, 1996: Plates 8.16-8.18), and at least one fatal sting is known from the central Philippines (Erhardt and Knop, 2005).

Particularly in Japan, where specimens were found at Okinawa, *P. semoni* has been subjected to various toxicological analyses (Mizuno *et al.*, 2000, 2007; Nagai *et al.*, 2002a, b; Nagata *et al.*, 2006; Satoh *et al.*,

Fig. 10. Two small (yellow arrows) and one large (black arrow) *Phyllodiscus* individuals of the same morphotype at Ambon (northern coastline of Ambon Bay, near Tawari, November 1996).

2007). Its toxin not only causes damage to skin that has been in contact with the sea anemone (of which the first author knows too well), but also affects the human kidney (Nagai *et al.*, 2002a, b; Mizuno *et al.*, 2007; Satoh *et al.*, 2007). Illustrations of the Okinawan specimens (Oshiro *et al.*, 2001; Uchida, 2001) resemble the smooth disc morphotype (Fig. 7E) and have been locally called 'Unbachi-isoginchaku' (Nagai *et al.*, 2002a, b; Mizuno *et al.*, 2007), which means Wasp Sea Anemone in Japanese. There are also reports of another venomous sea anemone from Okinawa, which is referred to as 'Fusa-unbachi-isoginchaku' (Uechi *et al.*, 2005a, b), meaning Tassel-shaped Wasp Sea Anemone, owing to its branched appearance resembling a scleractinian coral (Oshiro *et al.*, 2004; Uechi *et al.*, 2005a, b). Based on figures in Oshiro *et al.* (2001) and Uchida (2001), these individuals are a branched morphotype of *Phyllodiscus*, resembling a soft coral (Fig. 6E, 7C), but have been erroneously identified as *Actineria villosa* Quoy and Gaimard in De Blainville, 1830 (for nomenclature, see Fautin *et al.*, 2007). The identification of specimens reported as *A. villosa* and used in other toxicological studies (Oshiro *et al.*, 2001, 2004; Uechi *et al.*, 2005a, b), should be treated with caution, because of the confusion between *A. villosa* and *P. semoni*.

Hansen and Halstead (1971) reported on a sea anemone found at Cam-Ranh Bay, southern Vietnam, that stung US military personnel who swam in the bay. They identified it as the actinodendrid *Actinodendron plumosum* Haddon, 1898, another species known for its painful sting. However, we agree with Den Hartog's (1997) statement that the sea anemones of Hansen and Halstead (1971) were erroneously identified, and were actually individuals of *P. semoni*. We base this on multiple lines of evidence. Figure 4b of Hansen and Halstead (1971: 128) shows a nematocyst type that is found in vesicles of Aliciidae sea anemones, the family to which *P. semoni* belongs, and this nematocyst type is never found in Actinodendridae, the family to which *A. plumosum* belongs. Photographs in Hansen and Halstead (1971) show two morphotypes that they called the 'flowery- type' and 'top hat', which correlate strongly with the morphotypes of *P. semoni* shown in

Fig. 7B, E. Additionally, Hansen and Halstead (1971) mentioned that the sea anemones lived attached to rock (like *P. semoni*) rather than buried in sand (like *A. plumosum*). Based on these re-evaluations, we are certain Hansen and Halstead (1971) were not dealing with *Actinodendron plumosum*, but with *P. semoni*.

It is important to understand and appreciate that *Phyllodiscus* sea anemones have a wide range of morphotypes, some of which have been confused with other actiniarian species. The co-occurrence of multiple morphotypes at high densities is an important observation towards a better understanding and recognition of these hazardous sea anemones, especially because their high densities increase the risk of injuries to man.

Distinguishing mimics from models

Phyllodiscus sea anemones can be distinguished from their look-alike counterparts in various ways. Sea anemones are strictly soft-bodied and never produce a hard skeleton like a scleractinian coral. Also, sea anemones are always solitary individuals and never form colonies (with a possible exception, see Häussermann and Försterra, 2003); however, the single oral disc and mouth are retracted and are not usually noticed during the day. Superficially, the sea anemones differ from corals and other models by showing more radial symmetry in their body plan (Figs 3-8) and having a body surface that is fluffier. By being softer, their body moves more in turbulent water. After aggravation, specimens extend the column and oral disc with mouth and tentacles, while globular vesicles remain visible on the pseudotentacles of the main body around the column (Fig. 9). These vesicles are small bubble-like bumps of which the ectoderm is dense with nematocysts. Compared to sea anemones of Actinodendridae (which they have been confused with), *Phyllodiscus* individuals are sedentary by having a distinct pedal disc that attaches to a hard substrate, while actinodendrids burrow into soft sediment. Finally, *Phyllodiscus* sea anemones are common hosts to commensal shrimp species of the pontoniid genera *Ancylomenes* Okuno and Bruce, 2010 and *Periclimenes* Costa, 1844, like *A. sarasvati* (Okuno, 2002), *A. venustus* (Bruce, 1989), and *P. brevicarpalis* (Schenkel, 1902) (Fig. 11A; Fransen, 1997; Humann and DeLoach, 2010: 121), which dwell in pairs or in swarms over their upper surfaces. Unlike their model counterparts, the sea anemones are also occasionally parasitised by host-specific wentletrap snails of the genus *Epitonium* Röding, 1798 (Fig. 11BC; Kokshoorn *et al*., 2007).

The kind of mimicry involved is most likely Müllerian mimicry because the mimics and their models both may have to defend themselves against potential predators, while in the case of Batesian mimicry, the mimic (*Phyllodiscus*) would be considered harmless and the imitated model dangerous (Ruxton *et al*., 2004). The possibility that corals and other model animals would mimic the sea anemones rather than the other way is very unlikely. This would imply that this kind of evolution would have re-occurred many times in various groups of anthozoans, such as scleractinians and octocorals (Figs 3-6). Moreover, not only the resembling counterpart species would have evolved to resemble a sea anemone model but also many of their relatives that look like the model, which in that case should also resemble the sea anemone. Hence, closely related model species, such as some pocilloporids, are exceptional (Fig. 4). Furthermore, the coral models are generally more common and widespread than *Phyllodiscus* and would not have an advantage by mimicking rare counterparts. It would also not be clear why some particular coral species would need to employ mimicry and many others not.

Application of multiple defense strategies

Phyllodiscus employs various camouflage strategies to hide itself, by the application of crypsis, mimicry, or masquerade. Despite being zooxanthellate, the animals need to eat, thus being inconspicuous may increase chances of prey coming into contact with the sea anemone. However, it is more likely that *Phyllodiscus* uses adaptive colouration to avoid predation. Sea turtles, for instance, are known to feed on sea anemones and other stinging cnidarians despite their venomous nematocysts (Den Hartog, 1979; Den Hartog and Van Nierop, 1984; Van Nierop and Den Hartog, 1984; Ates, 1991; Plotkin *et al*., 1993; Tomas *et al*., 2001; Arai, 2005). Some fishes, for example reef-dwelling butterfly fishes (Chaetodontidae), also eat sea anemones (Ottaway, 1977; Ates, 1989; Yoshiyama *et al*., 1996; Augustine and Muller-Parker, 1998; Porat and Chadwick-Furman, 2004). While the camouflage/adaptive colouration helps to avoid detection by predators, the extreme morphological variation may assist even further by preventing the development of search images by predators that otherwise are able to recognise prey despite the camouflage. In other words, it is more difficult for predators to know what

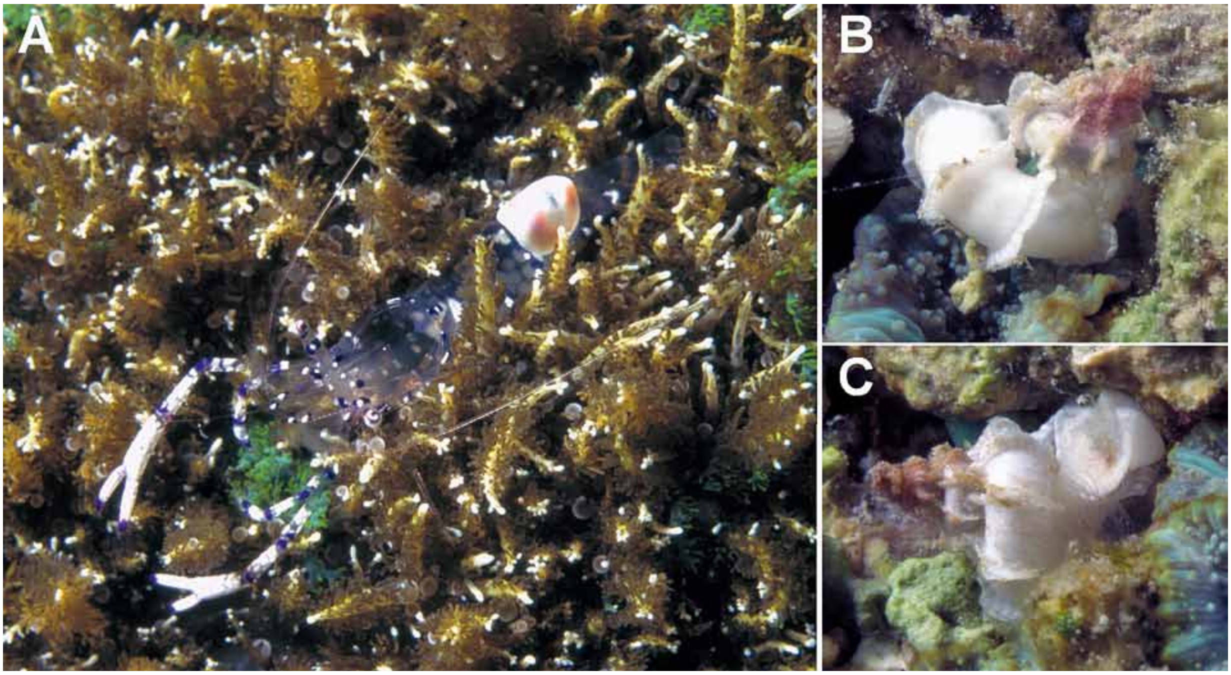

Fig. 11. Associated invertebrates with *Phyllodiscus semoni* at South Sulawesi (Spermonde Archipelago, Kudingareng Keke, 1997). A. A shrimp *Ancylomenes venustus* (Pontoniinae), on the upper surface of a sea anemone. B, C. A gastropod, *Epitonium* sp. (Epitoniidae), from the base of a sea anemone.

Phyllodiscus individuals may look like when they are trying to detect and locate it as a possible prey (Lawrence and Allen, 1983; Reid and Shettleworth, 1992). The pseudotentacles of *Phyllodiscus* may provide camouflage and therefore protection during the day by evading recognition as an actiniarian.

Occurrence in aggregations may not be a benefit because masquerading species are most successful in avoiding predation when they are rare in comparison to their models (Skelhorn *et al*., 2011): the repetition shown by the same shape facilitates recognition (see *e.g.* Figs 7-8). Therefore it remains a question why such aggregations occur. Either, after reproduction most aggregated *Phyllodiscus* individuals did not have a chance to disperse (for instance by a lack of currents) or sea anemones that did not disperse far from parent individuals had a higher rate of survival than those that distributed further away to a less suitable habitat. This could be because the morphotype, for camouflage purposes, is most effective in the current background. The occurrence of polymorphism (or polyphenism) as shown by *Phyllodiscus* in the present study, and the polymorphic American peppered moth caterpillar that mimics different tree twigs (Skelhorn and Ruxton, 2010), may compensate for the large number of individuals present. Hence, polymorphism together with camouflage may function as synergetic antipredatory traits.

In this study, we present new information on *Phyllodiscus* to aid in recognition of this highly polymorphic and presumably camouflaged sea anemone. Further studies are underway to evaluate whether the large amount of morphological variation is intra- or interspecific.

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