

## Sexual and Asexual Reproduction of the Tropical Corallimorpharian *Rhodactis* (= *Discosoma*) *indosinensis* (Cnidaria: Corallimorpharia) in Taiwan

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(Accepted October 6, 1994)

**Chao-Lun A. Chen, Chang-Po Chen and I-Ming Chen (1995)** Sexual and asexual reproduction of the tropical corallimorpharian *Rhodactis* (= *Discosoma*) *indosinensis* (Cnidaria: Corallimorpharia) in Taiwan. *Zoological Studies* 34(1): 29-40. Reproduction of the tropical corallimorpharian *Rhodactis* (= *Discosoma*) *indosinensis* Carlgren 1943, was studied for two years (1988-1990) in shallow waters off Wanglitung, southern Taiwan. *Rhodactis indosinensis* occurred gregariously, and formed three large aggregations in the study site. *R. indosinensis* is gonochoristic. Oogenesis takes about nine months, while spermatogenesis three months. Mature eggs are large (maximum diameter 850  $\mu$ m). Both sperm and eggs matured in May and spawning occurred between May and June. Three modes of asexual reproduction, i.e., longitudinal fission, inverse budding, and two-mouth fission, were recorded; the latter two have not been reported previously for anthozoans. Longitudinal fission is the dominant mode and occurs with high frequency during summer in polyps greater than 50 mm in oral disc diameter. Inverse budding is the second most common mode, occurring in the period between winter and spring in polyps from 30 to 60 mm in oral disc diameter. Two-mouth fission occurs only occasionally. Asexual reproduction occurred earlier in the aggregation located near the shore, and the frequency of asexual reproduction was higher when water temperature increased, suggesting that environmental factors (e.g., temperature) affect the onset of asexual reproduction in *R. indosinensis*.

**Key words:** Reproductive periodicity, Gametogenesis.

Corallimorpharians are a small order of anthozoans, consisting of about 50 species, morphologically intermediate between actinarians (sea anemones) and scleractinians (hard corals) (Carlgren 1949, Schmidt 1974, den Hartog 1980, Fautin and Lowenstein 1992). The reproductive biology of sea anemones (see reviews by Chia 1976, Strathmann 1987, Fautin 1990, Shick 1991) and hard corals (see reviews by Fadlallah 1983, Harrison and Wallace 1990, Richmond and Hunter 1990) has been well documented, but that of corallimorpharians is still not well understood. Until recently, sexual reproduction had only been

studied in a temperate corallimorpharian *Corynactis californica* (Holts and Beauchamp 1993).

Both temperate and tropical corallimorpharians typically form large aggregations by asexual reproduction and may be the major components of some shallow-water benthic fauna (Foster 1958, Fishelson 1970, den Hartog 1980, Chadwick and Adams 1991). However, their modes of asexual reproduction have never been described in as much detail as those of the sea anemones (Stephenson 1935, Robson 1966, Atoda 1976, Sebens 1983), or hard corals (for review, see Cairns 1988), although fission and pedal fragmentation have been

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mentioned for some corallimorpharians (den Hartog 1980, Chadwick and Adams 1991, Holts and Beauchamp 1993). In sea anemones, environmental factors which affect asexual reproduction may vary from species to species. For example, the temperate species *Anthopleura elegantissima* has a high asexual reproductive rate in winter (Sebens 1982), *Metridium senile* in later fall (Bucklin 1987) and the tropical species *Anthopleura dixoniana* in summer (Lin et al. 1992). No equivalent information has been available for corallimorpharians to the present.

*Rhodactis indosinensis* is a tropical corallimorpharian that occurs in eastern Asia (Carlgren 1943). The corallimorpharian harbor zooxanthellae and they form aggregations in shallow-water reef crevices in southern Taiwan. In the present study, we describe the synchronous gametogenesis and asexual reproductive modes, as well as the environmental factors related to temporal variations of asexual reproduction in *R. indosinensis* from Taiwan.

## MATERIALS AND METHODS

Specimens of *R. indosinensis* Carlgren, 1943, were collected at Wanglitung, southern Taiwan (120° 41'E; 22° 01'N). At this site, *R. indosinensis* formed three large, bowl-like aggregations (Fig. 1), as well as many other smaller patches. The smaller patches were scattered not only around the aggregations but also occurred singly isolated in reef crevices. *R. indosinensis* remained immersed even during spring low tides, except for polyps



Fig. 1. *Rhodactis indosinensis*. Aggregation from study site at Wanglitung, south Taiwan. Arrow point is a longitudinal fission polyp. (Scale bar = 1 cm).

near the margins of each aggregation. The three aggregations were labelled A, B, and C, moving seaward from the coastline. All three aggregations were irregular in outline. The longest and shortest dimensions of each aggregation were: A, 4.2 m × 2.5 m; B, 2.5 m × 1.0 m; C, 2.4 m × 1.0 m.

## Relationship between size and oral disc diameter

In order to find a non-destructive method for later sampling, we tested whether oral disc diameter was correlated with wet weight, using the following technique. The diameters of the oral discs of 50 polyps were measured twice at right angles to each other, the mean of the two diameter measurements was recorded for further reference. Specimens were then chiselled off, placed in sea water and brought back to the laboratory. After being anesthetized in 7-10% magnesium chloride, the specimens were fixed in 10% neutral formalin for 24-48 hrs. The wet weight of each specimen was measured to the nearest 0.1 g after excess water was removed by blotting. A significant linear regression was found between measurements of mean oral disc diameter ( $x$ ) and body weight ( $y$ ) of *R. indosinensis* ( $r = 0.87$ ,  $p < 0.05$ ,  $y = -4.17 + 0.23x$ ,  $n = 50$ ) (Fig. 2). Thereafter, the oral disc diameters of *R. indosinensis* polyp were measured in the field and used as a parameter for size measurement.

## Relationship between size and sex

The relationship between size and sex was determined in May 1989, just prior to spawning, for 168 polyps chosen haphazardly from all three

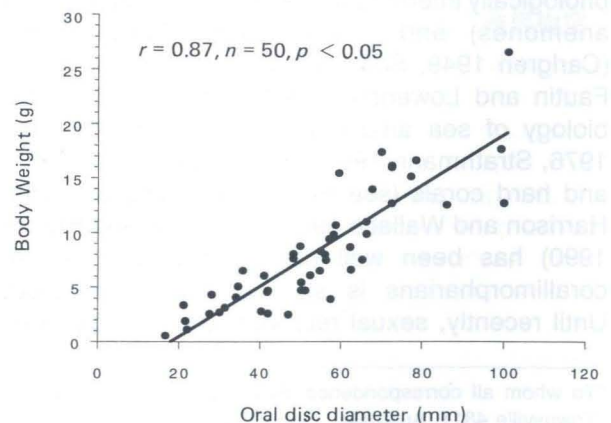


Fig. 2. *Rhodactis indosinensis*. The linear regression of oral disc diameter and wet weight.

aggregations. The oral disc diameters of the 168 polyps were measured and the colors and shapes of the gamete bundles were recorded. A small piece of tissue containing gametogenetic mesenteries was collected from each polyp and fixed in 10% neutral formalin. These samples were embedded in paraffin, sectioned at 5–8  $\mu\text{m}$ , and stained with basic fuchsin and picro-indigo-carmin (Clark 1980). The distributions of males, females, and reproductively inactive polyps among ten size classes were compared using a goodness-of-fit test (Sokal and Rohlf 1981).

### Reproductive periodicity

In order to document gametogenesis, samples, which included ten to twenty polyps of *R. indosinensis*, were collected haphazardly at one time from the three aggregations between April 1988 and May 1990, at approximately monthly intervals. All specimens were examined histologically and the diameters of 50 oocytes that contained nucleoli were measured from each female. The mean of the longest and shortest perpendicular diameters was used to measure the diameter of any irregular shaped oocyte. The development of male gametes was divided into three stages: Stage I – only spermatogonia present; Stage II – spermatocytes the most mature cells present; Stage III – spermatids the most mature cells present.

### Modes of asexual reproduction

A polyp with a fission scar was interpreted as presenting evidence of having recently undergone asexual reproduction. In the field, all polyps in the process of asexual reproduction or with fission scars were photographed and their oral disc diameters were measured. More than 30 polyps were transported to the laboratory in aerated seawater and kept in an aquarium for further observation. Photographs were taken to record the process of asexual reproduction in polyps kept in the aquarium. For histological examination, polyps were allowed to expand their oral discs and were then anesthetized in 10% seawater-magnesium chloride and fixed in 10% neutral seawater formalin for 24 to 48 hrs. Paraffin sections were processed as described above. A Chi-square test (Sokal and Rohlf 1981) was used to compare the sizes of polyps in the process of asexual reproduction with those of polyps with scars. The same test was also used to make comparisons between the sizes of polyps exhibiting different modes of asexual reproduction.

### Temporal variation of asexual reproduction

More than 70 polyps per aggregation were surveyed haphazardly during the lowest tide in each month from May 1989 to April 1990. The proportion of polyps undergoing asexual reproduction in each month was calculated as the number of asexual reproductive polyps divided by the total number of observed polyps during that particular survey. The relative frequencies of different modes of asexual reproduction were tested by using a Chi-square test (Sokal and Rohlf 1981). The frequencies of asexual reproduction in the three monitored aggregations were compared by use of the Kruskal-Wallis test (Sokal and Rohlf 1981). Water temperature was measured in situ monthly during the lowest tides. Air temperatures and tidal heights in Wanglitung were tabulated from the database of the Central Weather Bureau, Republic of China. Linear regressions between total frequency of asexual reproduction and each environmental factor (i.e., water temperature and tidal height) were also calculated and tested (Sokal and Rohlf 1981).

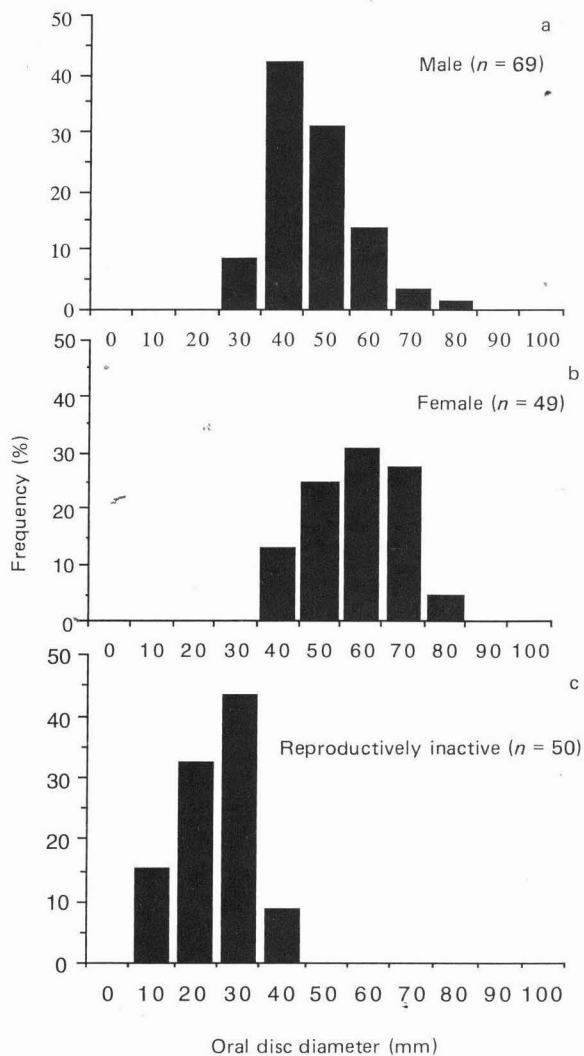
## RESULTS

### Size and sex

Of the 168 polyps examined in May 1989, 69 were male, 49 were female and 50 were indeterminate. No hermaphroditic polyps were found. Females were significantly larger than males (Figs. 3a, b;  $G = 50.82$ ,  $p < 0.01$ ). Polyps with oral disc diameters  $< 30$  mm showed no gamete development (Fig. 3c).

### Reproductive periodicity

The sex of *R. indosinensis* polyps could be determined in the field by the color and shape of gamete bundles. Just prior to the spawning period (April to early May), mature egg bundles were deep blue, dark red, or pale green in color and grape-like in shape, while the mature sperm bundles formed elongated white spirals. During the non-spawning period (July to March of the following year), the immature egg bundles appeared as clusters of small, white spheres. Sperm bundles appeared as long, thin opaque strips of tissue in the mesenteries and were first detected microscopically at the end of March. Those polyps in which no gametes were visible were classified



**Fig. 3.** *Rhodactis indosinensis*. Relative size frequency of males, females, and reproductively inactive polyps collected in May 1989.

as reproductively inactive.

Oogonia were  $34 \pm 7 \mu\text{m}$  in diameter and their nuclei measured  $17 \pm 3 \mu\text{m}$  ( $n = 20$ , in two polyps). The cytoplasm characteristically stained blue with indigo-carmin and the nucleolus stained red with basic fuchsin. During vitellogenesis, the germinal vesicle was located peripherally and the yolk stained green with indigo-carmin. Oocytes lacked zooxanthellae and had a maximum diameter of  $710 \mu\text{m}$  in section. The maximum diameter of a spawned oocyte was  $850 \mu\text{m}$ . Oogonia first appeared in the mesoglea from August to November. Oocytes gradually increased in size until March, followed by a sharp increase during April, reaching their maximum diameter in May. No polyps col-

lected in June possessed oocytes (Fig. 4a).

Spermatogonia were  $4.8 \pm 0.8 \mu\text{m}$  in diameter ( $n = 50$ , observed from five polyps), with cytoplasm staining blue with indigo-carmin. These cells appeared in the mesoglea and formed "sperm packets". The diameter of sperm packets averaged  $29 \pm 8 \mu\text{m}$  ( $n = 40$ , observed from four polyps). Later in their development, spermatocytes stained red with basic fuchsin. Spermatids were concentrated in the center of sperm packets. Sperm packets full of mature sperm were not observed. Spermatogenesis began in March/April, and spermatids appeared in May. None of the polyps collected in June possessed sperm packets (Fig. 4b). Overall, *R. indosinensis* took nine months to develop eggs, and three to four months to develop sperm. Spawning was inferred to have occurred in late May to June because of the disappearance of gametes between these samples (Figs. 4a, b). Spawning was observed in the laboratory in early June 1989 and June 1990, but was not observed in the field.

### Modes of asexual reproduction

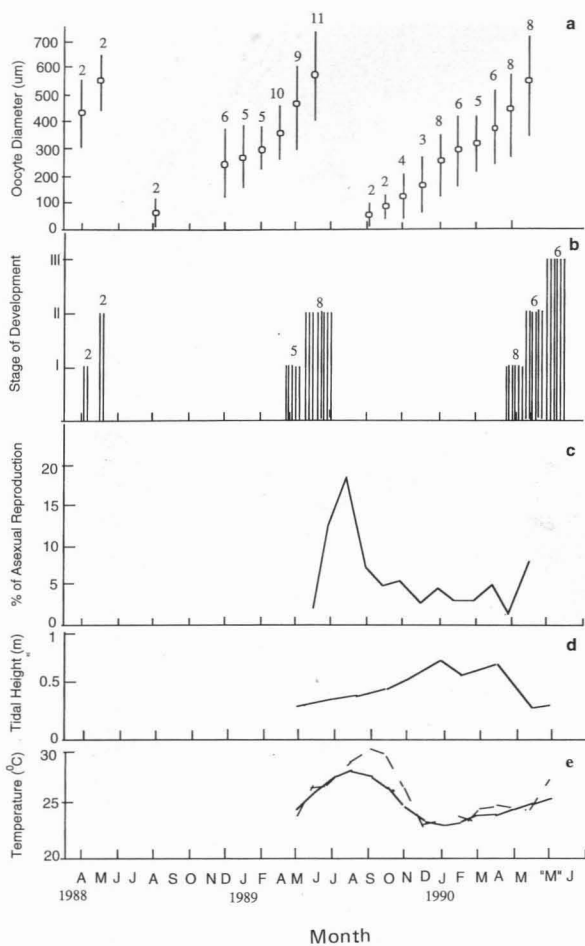
Three modes of asexual reproduction were observed in *R. indosinensis*.

#### 1) Longitudinal fission

Since no siphonoglyphs occur in the actinopharynx of *R. indosinensis*, the direction of longitudinal fission cannot be oriented as in sea anemones (Sebens 1983). The first indication of fission was a split through the mouth (Fig. 5a). Then the oral disc pinched in from the margins in the plane of the split (Fig. 5a). Fission started from one side of the split, and extended to the pedal disc. The animal was completely bisected exposing the actinopharynx, mesenteries, etc. (Fig. 5b). The torn ends of the column rolled inward and fused, forming a new polyp. The process of longitudinal fission took about one week, and the scar lasted about one month.

#### 2) Inverse budding

During inverse budding, a portion of pedal disc was first released from the substratum and raised to the level of the oral disc, forming a nodule with a fold of column (Fig. 5c). The portion of pedal disc freed upward and the ultimate orientation of the nodule was upside down compared to the maternal polyp. The folded edges of the maternal polyp fused together, thus separating the bud. This bud adhered to the maternal polyp with its



**Fig. 4.** *Rhodactis indosinensis*. (a) Size range of oocytes; bars are the size distribution of oocytes, circles are the mean sizes of the oocytes; numbers above the bars indicate numbers of females observed each month. (b) Developmental stages of spermatogenesis; stage I- only spermatogonia present; stage II- spermatocyte present; stage III- spermatids present; each bar represents one polyp; numbers above the bars indicate numbers of males observed each month. (c) Percentage occurrence of asexual reproduction recorded from three aggregations in monthly samples. (d) Lowest-tide height at Wanlitung; data from Central Weather Bureau (CWB), Republic of China. (e) Monthly air temperature (dash line), data from CWB and in situ water temperature at low tide. Symbol "M" on the x-axis represents spermatogenesis samples collected in the middle of May 1990.

tentacles against the oral disc of the maternal polyp (Fig. 5d). As inverse budding proceeded, the bud progressively bent up and down (Fig. 5e) and eventually separated from the maternal polyp (Fig. 5f). After detaching from the maternal polyp, the bud attached itself to the substrate by its pedal disc and formed a new mouth and actinopharynx. It took about one month to produce a bud and one month for the bud to grow and detach from

the maternal polyp.

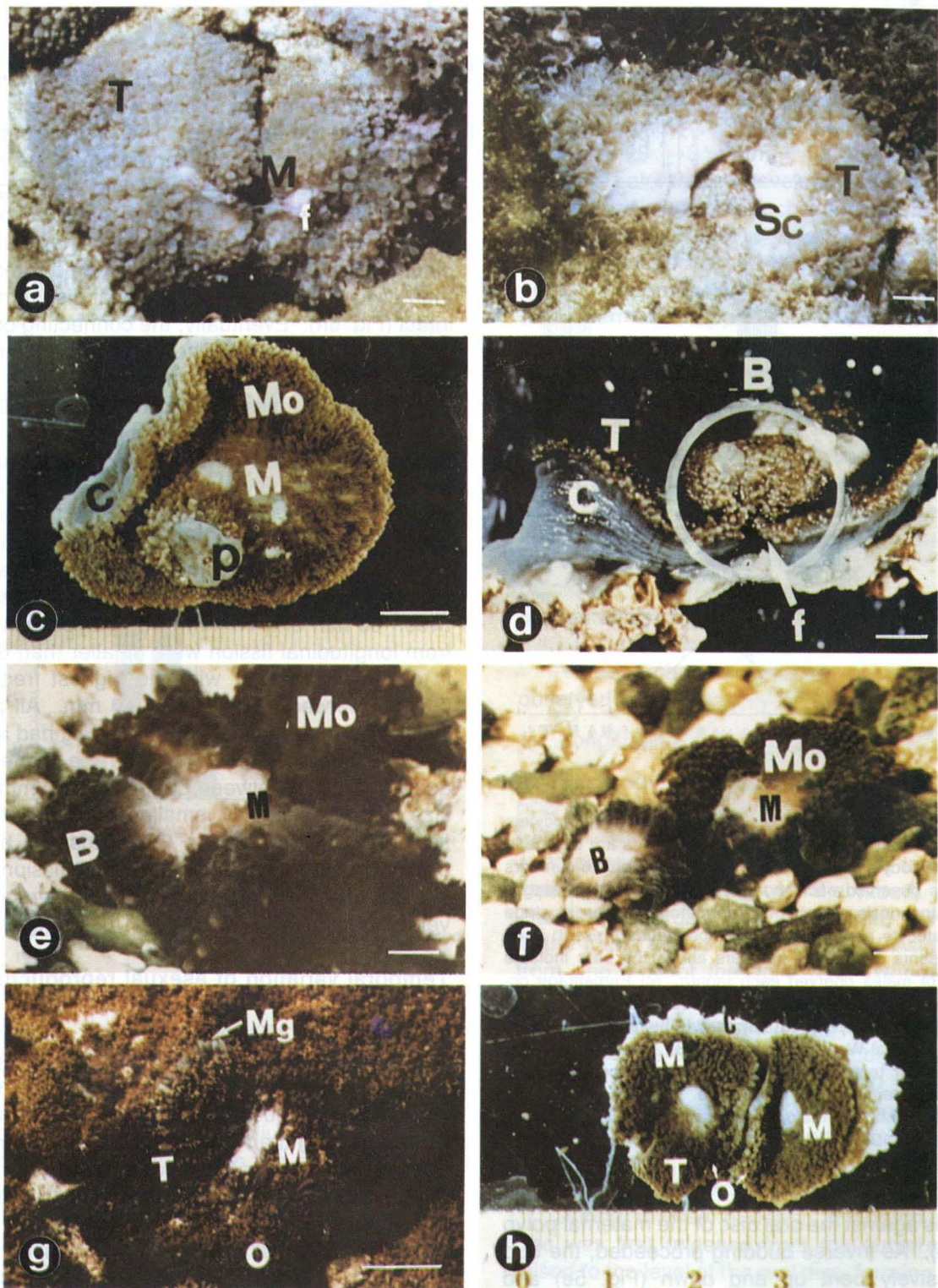
### 3) Two-mouth fission

The three specimens of *R. indosinensis* that underwent two-mouth fission were collected and observed in the aquarium. The first indication of two-mouth fission was observed when the mouth pinched in and began to split into two (Fig. 5g). Two mouths were formed and remained on the oral disc for about two weeks. The oral disc pinched in from the margins between the mouths, then divided into two, but the pedal disc remained intact (Fig. 5h). Eventually, the connecting column divided longitudinally. The process of two-mouth fission took more than two months.

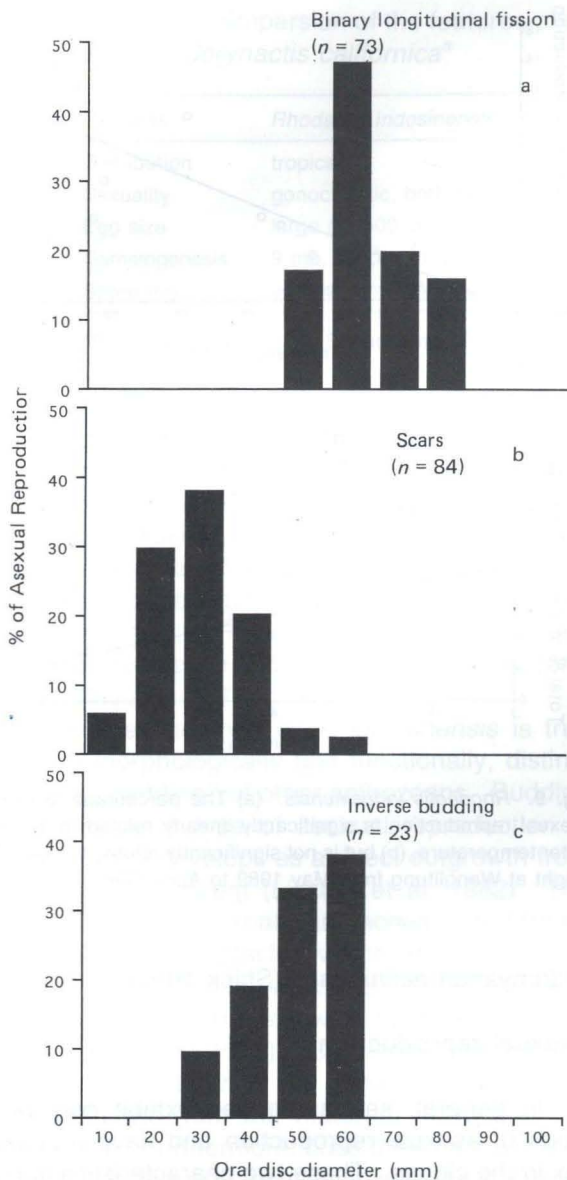
Longitudinal fission occurred in 73 (73.9%) of the 99 polyps observed undergoing asexual reproduction during the one-year survey, inverse budding occurred in 23 polyps (23.2 %), and two-mouth fission occurred in only three polyps (2.9%). Of the 73 individuals undergoing longitudinal fission, all polyps were larger than 50 mm in oral disc diameter with the highest frequency (47.4%) between 60 mm and 70 mm. The polyps with scars from longitudinal fission were smaller than 60 mm in oral disc diameter with the highest frequency (38.1%) between 30 mm and 40 mm. All polyps which had undergone inverse budding had an oral disc diameter of 30-60 mm with the highest frequency (38.1%) between 60 mm and 70 mm. The size was significantly smaller after longitudinal fission ( $X^2 = 66.80$ ,  $p \leq 0.05$ ; Figs. 6a, b), and the polyps undergoing longitudinal fission were significantly larger than the ones undergoing inverse budding ( $X^2 = 51.55$ ,  $p < 0.05$ ; Figs. 6a, c).

### Temporal variation of asexual reproduction

More than 220 specimens of *R. indosinensis* were surveyed monthly between May 1989 to April 1990. Longitudinal fission occurred at a significantly higher frequency during the summer (highest [7.6%] in July) than during the winter, but inverse budding occurred mainly between winter and spring (highest [3.1%] in March) not during the summer (Figs. 7a, b;  $X^2 = 45.63$ ,  $p < 0.05$ ). The occurrence of all modes of asexual reproduction combined peaked in June-July for aggregation A (20%), in July for aggregation B (24.5%), and in August for aggregation C (18.2%) (Fig. 8). The appearance of the asexual reproductive peaks differed significantly among these three monitored aggregations (Fig. 8;  $H = 5.63$ ,  $p < 0.06$ ). The total frequency of asexual reproduction was sig-



**Fig. 5.** *Rhodactis indosinensis*. Modes of asexual reproduction, (a) Longitudinal fission, polyp with a split through its mouth, bar = 100 mm. (b) Longitudinal fission, polyp totally bisected, bar = 100 mm. (c) Inverse budding, fusion of column and oral disc, bar = 50 mm. (d) Inverse budding, form of a bud. (e) Inverse budding, the behavior of bud detachment from maternal polyp, bar = 100 mm. (f) Inverse budding, the detached bud and maternal polyp, bar = 100 mm. (g) Two-mouth fission, mouth splitting (in the field), bar = 100 mm. (h) Two-mouth fission, formation of two polyps still connected by their pedal discs. Abbreviations - B: bud; C: column; f: fission in (a); M: mouth; Mg: marginal tentacle; Mo: Maternal polyp; o: oral disc; p: pedal disc; Sc: scar; T: discal tentacle.



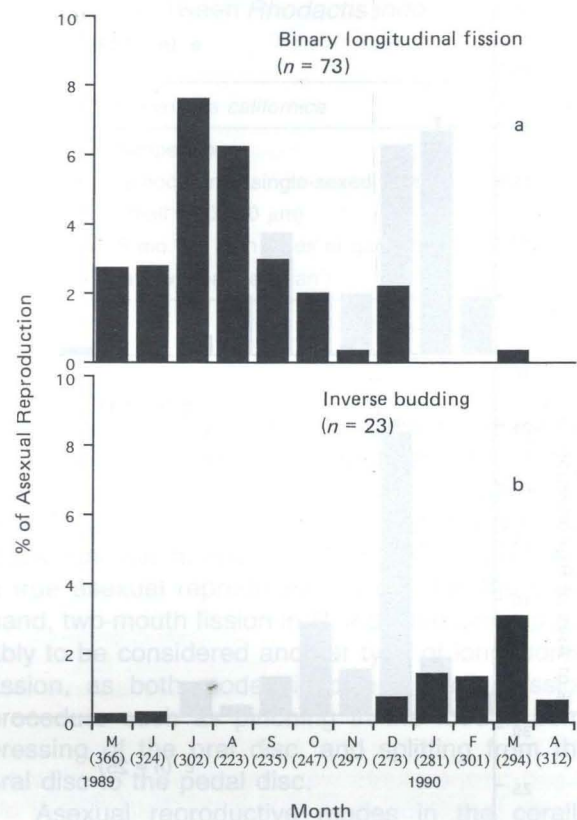
**Fig. 6.** *Rhodactis indosinensis*. Histogram showing the oral disc diameters in polyps that (a) were undergoing longitudinal fission, (b) had scars after longitudinal fission and (c) were undergoing inverse budding.

nificantly linearly related to the in situ water temperature ( $y = 0.934x - 17.887$ ,  $n = 12$ ,  $r = 0.65$ ,  $p < 0.05$ ; Fig. 9a), but was not significantly related to the local tidal height ( $y = -10.798x + 12.064$ ,  $n = 12$ ,  $r = 0.41$ ,  $p < 0.05$ ; Fig. 9b).

## DISCUSSION

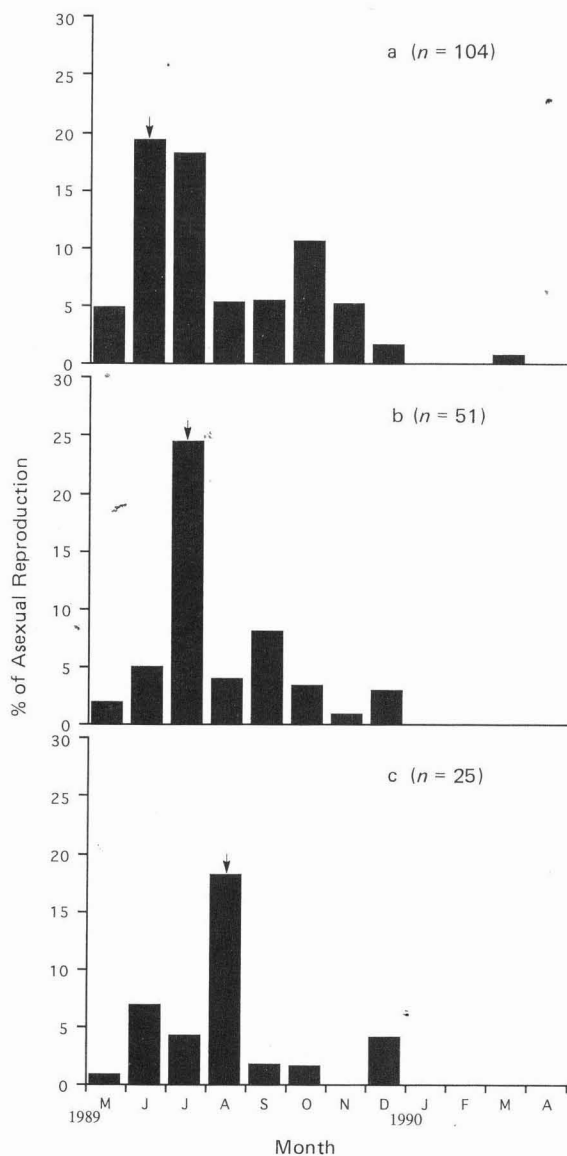
### Sexual Reproduction

The synchronous gametogenesis observed in



**Fig. 7.** *Rhodactis indosinensis*. Percentage occurrence of (a) longitudinal fission and (b) inverse budding in the monitored aggregations at Wanglitung from May 1989 to April 1990. Numbers under the months along the X-axis are the total numbers of polyps surveyed during the lowest tide in that month.

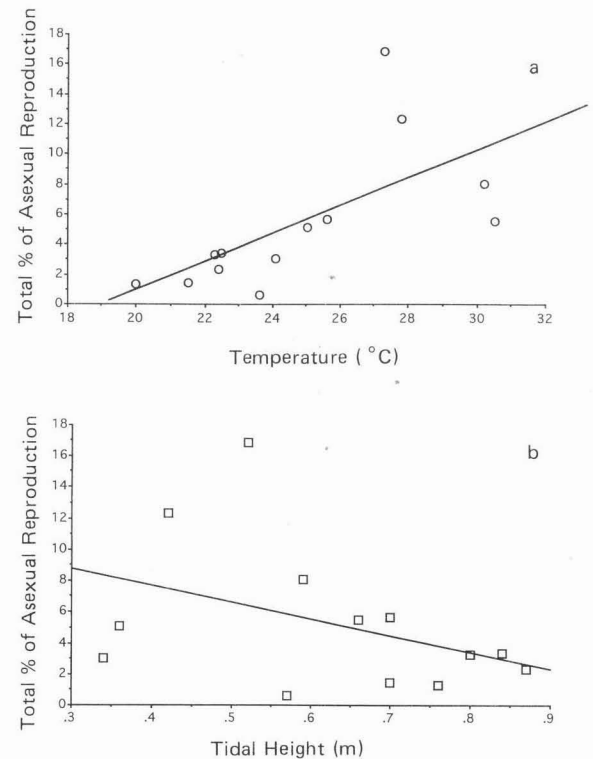
*R. indosinensis* provides the first evidence of an annual cycle of sexual reproduction in a tropical corallimorpharian. *R. indosinensis* has characteristic features of sexual reproduction which are different from those of the temperate corallimorpharian, *C. californica* (Table 1): (1) *R. indosinensis* is gonochoristic with male and female polyps occurring together in an aggregation. Though *C. californica* is gonochoristic some of its aggregates formed monosexual clones. (2) *R. indosinensis* has large eggs ( $> 500 \mu$ ), whereas the fully grown oocyte of *C. californica* is relatively smaller (120 to  $140 \mu$ m). (3) *R. indosinensis* takes nine months to complete oogenesis, and three to four months to complete spermatogenesis, while *C. californica* takes five months to develop either the eggs or sperm. (4) *R. indosinensis* spawns between late spring and early summer while *C. californica* spawns in the late winter (Holts and Beauchamp 1993). These contrasting characteristics suggest



**Fig. 8.** *Rhodactis indosinensis*. Percentage occurrence of asexual reproduction (longitudinal fission + inverse budding) in the three monitored aggregations at Wanglitung from May 1989 to April 1990.

that the corallimorpharians have adopted different life history traits between tropical and temperate environments.

The egg size and fertilization mode (external vs. internal) were interpreted as ecological indices in sea anemones (for review see Chia 1976, Shick 1991). *R. indosinensis* spawns relatively large eggs ( $> 500 \mu\text{m}$ ). These characters suggest that development in *R. indosinensis* may be categorized as oviparous-planktonic-lecithotrophic (cf. Chia 1976), implying that a similar trend of sexual reproductive patterns exists among the tropical



**Fig. 9.** *Rhodactis indosinensis*. (a) The percentage level of asexual reproduction is significantly linearly related to in situ water temperature, (b) but is not significantly related to low-tide height at Wanglitung from May 1989 to April 1990.

endomyarian actiniarians (Shick 1991).

### Asexual reproduction

In general, sea anemones exhibit only one mode of asexual reproduction and have a single sex in the clones. These two characteristics imply that certain species of clonal sea anemones are genetically determined. However, both longitudinal fission and pedal laceration occur regularly within a single clonal population of *Haliplanella lineata* (Johnson and Shick 1977). Moreover, a transverse fission which occurred in *Anthopleura stellula* was surmised to not be an ordinary nature mode of proliferation but appeared to be induced by abnormal salinities (Schmidt 1970, for review see Shick 1991). By contrast, three modes of asexual reproduction occur regularly in the corallimorpharian *R. indosinensis* and, furthermore, both sexes occur in a single aggregation. The data suggest that the clonality of *R. indosinensis* aggregations is questionable, when compared to the clonal, genetically determined asexual reproductive modes in sea anemones.

**Table 1.** Comparison of the features of sexual reproduction between *Rhodactis indosinensis* and *Corynactis californica*<sup>a</sup>

Features	<i>Rhodactis indosinensis</i>	<i>Corynactis californica</i>
Distribution	tropical	temperate
Sexuality	gonochronic, both sexes occur in an aggregation	gonochronic, single-sexed clone
Egg size	large (> 500 $\mu\text{m}$ )	small (120-140 $\mu\text{m}$ )
Gametogenesis	9 mo. for oogenesis, 3 mo. for spermatogenesis	5 mo. for both types of gametogenesis
Spawning	early summer (May-June)	late winter (Dec.-Jan.)

<sup>a</sup>Data source: Holts and Beauchamp 1993.

Longitudinal fission is the main mode of asexual reproduction in *R. indosinensis* as compared to the other two modes. Each offspring of longitudinal fission retains the major structures, such as the actinopharynx and gonads, which are functional immediately after recovery, ensuring that clonemates of *R. indosinensis* can successfully occupy a space in a short time (Strawberry-coral model, Williams 1975).

"Inverse budding" in *R. indosinensis* is true budding morphologically and functionally, distinct from the "budding" of other anthozoans. Budding is defined as a type of asexual reproduction in which a polyp develops as a direct outgrowth from the body of a parent (Lincoln et al. 1982). The buds of boloceroidarian anemones are formed by autotomizing tentacles which are shed when escaping from predators (Robson 1966, Lawn and Ross 1982) or when swallowed incidentally during feeding (Cutress 1979). Contrarily, the inverse buds of *R. indosinensis* are generated by a series of fused parts from the maternal polyp (i.e., regeneration). Furthermore, buds grew on the maternal polyp in the aquarium, indicating that inverse budding in *R. indosinensis* is true budding. Inverse budding of *R. indosinensis* may also function as a dispersal mechanism, as the small bud is easily carried away by water currents (personal observation). Since corallimorpharians lack basal muscles and move more slowly than some sea anemones (Chadwick and Adams 1991), inverse budding in *R. indosinensis* may play a role in reducing spacial competition between the maternal polyp and its increasingly dispersed clones of the same genotype.

In his survey of Caribbean corallimorpharians, den Hartog (1980) observed corallimorpharians with two mouths, but considered them abnormal. However, during two-mouth fission in *R. indosinensis*, each of the two intact oral discs will enfold its oral disc, conducting upon itself the ty-

pical "enveloping feeding behavior" (personal observation), as described in other tropical corallimorpharians (Hamner and Dunn 1980, Elliott and Cook 1989). This implies that the two oral discs function normally and two-mouth fission is a true asexual reproductive mode. On the other hand, two-mouth fission in *R. indosinensis* is probably to be considered another type of longitudinal fission, as both modes involve a similar fission procedure such as pinching in the mouth, compressing of the oral disc, and splitting from the oral disc to the pedal disc.

Asexual reproductive modes in the corallimorpharians are summarized in Table 2. The following characteristics are revealed. (1) There are four modes of asexual reproduction in corallimorpharians. (2) Pedal laceration occurs in three families. (3) Longitudinal fission occurs in the families Corallimorphidae and Discosomatidae, but not in the Ricordeidae. (4) *Discosoma* (= *Rhodactis*) *sanctithomae* may have more than two modes of asexual reproduction. Further studies of the modes of asexual reproduction should be conducted to confirm the relationships between modes of asexual reproduction and taxa within the Order Corallimorpharia.

### Environmental factors and reproduction

Environmental factors controlling reproductive activities (sexual and asexual) have been frequently documented for anthozoans in the past decade (for review, see Harrison and Wallace 1990, Shick 1991). In sexual reproduction of *Corynactis californica*, high temperature was suggested as a cue triggering the onset of gametogenesis, and food availability also was thought to possibly play a role in initiating gametogenesis and spawning (Holts and Beauchamp 1993). In *Anthopleura dixoniana*, a long photoperiod significantly enhanced the growth of oocytes under laboratory conditions, and

**Table 2.** Summary of modes of asexual reproduction in the corallimorpharians (Order Corallimorpharia)

Taxa	Mode	References
Family Corallimorphidae		
<i>Corynactis australis</i>	Longitudinal	Carlgren (1949)
<i>C. californica</i>	Longitudinal	Chadwick & Adams (1991)
<i>C. parvula</i>	Pedal	den Hartog (1980)
Family Ricordeidae		
<i>Ricordea florida</i>	Pedal	den Hartog (1980)
<i>R. c.f. yuma</i>	Pedal	pers. obser. <sup>a</sup>
Family Discosomatidae		
<i>Discosoma</i> (= <i>Paradiscosoma</i> ) <i>sanctithimae</i>	Pedal, Longitudinal	den Hartog (1980)
<i>D. (=P.) carlgreni</i>	Pedal	den Hartog (1980)
<i>D. (=P.) neglecta</i>	Pedal	den Hartog (1980)
<i>Rhodactis</i> (= <i>Discosoma</i> ) <i>indosinensis</i>	Longitudinal, Inverse budding, Two-mouth fission	present study
<i>R. (=D.) howesii</i>	Longitudinal	pers. obser. <sup>a</sup>
<i>R. (=D.) bryoides</i>	Longitudinal	pers. obser. <sup>a</sup>
<i>R. (=Platyzoanthus) mussoides</i>	Longitudinal	pers. obser. <sup>a</sup>
<i>Actinodiscus</i> (= <i>Discosoma</i> ) <i>nummiformis</i>	Pedal	pers. obser. <sup>a</sup>

<sup>a</sup>personal observation in the Great Barrier Reefs.

raised temperatures was suggested to be the inducing factor for spawning in the field (Lin et al. 1992). In the present study, the three aggregations of *R. indosinensis* were located each in a bowl-like tidal pool, where environmental factors, e.g., temperature and tidal exposure, fluctuate seasonally (Figs. 4d, e). Thus, more detailed studies could be conducted here to possibly understand the relationship between environmental factors and sexual reproduction in *R. indosinensis*.

Frequency of asexual reproduction which varies monthly and peaks in one season has been documented in a number of sea anemones (Sebens 1982, Bucklin 1987, Lin et al. 1992; for a review see Shick 1991). This temporal variation of asexual reproduction has been attributed to abiotic factors that affect the energy budget (Lin et al. 1992; for a review see Shick 1991). In *R. indosinensis*, the highest percentage of asexual reproduction occurs during times of high water temperatures (Figs. 4c, d). In addition, the peaks of asexual reproduction in each of the three monitored aggregations were staggered a month apart from near shore to off shore (Fig. 8). These results suggest that temperature plays an important role in the induction of asexual reproduction in *R. indosinensis*.

The sea anemone *Anthopleura elegantissima* divides during periods of starvation, and undergoes gametogenesis and spawns during the growth

season (Sebens 1979 1980 1982). In contrast, in *A. dixoniana* there is no interruption of gametogenesis by division in the field, but the oocyte diameter is influenced by the division rate under laboratory conditions (Lin et al. 1992). In *R. indosinensis*, oogenesis occurs from August to May of following year, with spawning in May to June, while asexual reproduction peaks in July and remains high during the following two months (Figs. 4c, 7). We postulate that *R. indosinensis* may allocate energy to sexual reproduction during the period of high-water immersion and moderate temperatures (24°C to 26°C, Fig. 4e), and asexual reproduction occurs sequentially in periods of low-water exposure and higher temperature (28°C to 32°C, Fig. 4e). Further study is needed to confirm this.

**Acknowledgements:** We thank Drs. D. G. Fautin, J. L. Simon, K. Soong, L. L. Liu, and L. S. Fang for encouragement and for reviewing the manuscript; Dr. B. L. Willis, Ms. G. Brodie, B. J. Norris, Mr. B. Stobart, K. Martin-Smith, P. Spencer (James Cook University, Australia) and Dr. N. E. Chadwick-Furman (Israel) for final revisions; Ms. M. L. Chang-Lai for helping with field collection; and Ms. L. Chen for the typing and correcting the manuscript. Thanks also to Dr. D. G. Fautin for her advice on the species name. This paper is adapted from a thesis submitted to National Sun

Yat-sen University by C. A. Chen in partial fulfillment of the requirements for a MSc degree.

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## 台灣產印支圓盤擬珊瑚海葵之有性及無性生殖

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從1988年到1990年在台灣南部萬里桐低潮線附近淺水域研究印支圓盤擬珊瑚海葵生殖學。印支圓盤擬珊瑚海葵為群集性生物，在研究地點形成3個大群集。在有性生殖方面：印支圓盤擬珊瑚海葵為雌雄異體，卵發育需要9個月，精子發育需要3個月。成熟卵直徑為850微米。卵與精子皆在5月成熟，而在5~6月間釋放配子。

本研究記錄印支圓盤擬珊瑚海葵三種無性生殖方式：縱分裂、反口出芽及雙口裂。其中後兩種無性生殖方式未曾在花蟲網報導過。縱分裂為印支圓盤擬珊瑚海葵主要的無性生殖方式，發生在口盤直徑大於50毫米的個體，生殖高峰在夏季。反口出芽為次要的無性生殖方式，發生在口盤直徑大於30毫米的個體，生殖高峰在冬、春之際。雙口裂只偶然發生。無性生殖起始於高潮位的群集及無性生殖頻度高峰出現在水溫回昇時，是以推測環境因子中水溫可能影響無性生殖的發生。

關鍵詞：生殖周期，配子發生。

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