

## Morphological and Life History Divergence of the Zoanthid, *Sphenopus marsupialis* off the Taiwanese Coast

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**Keryea Soong, Yuh-Saint Shiau and Chang-Po Chen (1999)** Morphological and life history divergence of the zoanthid, *Sphenopus marsupialis* off the Taiwanese Coast. *Zoological Studies* 38(3): 333-343. The morphology and life history of the solitary zoanthid, *Sphenopus marsupialis*, were studied. Individuals were collected by periodic bottom trawling at about 10-25 m depth at 5 localities along the coast of Taiwan from 1989 to 1995. The sizes (column length) of individuals from 2 southern localities were about twice as great as those from 3 relatively more northern localities. The size of mature specimens was also significantly larger at Linbien (south) than at Chadin (relatively north). The sizes of cnidae occurring on tentacles, actinopharynx, mesenterial filaments, and body columns of the zoanthids were not significantly different between the 2 sites. The seasonal change of oocyte diameters revealed that spawning occurred in August at Linbien, but later at Chadin, between October and November. At Linbien, individuals were strictly gonochoristic, whereas 22% of mature individuals were hermaphroditic at Chadin. Transverse division, the first such case reported in Zoanthidea, occurred in about 7% of more than 8000 examined individuals from the 3 relatively northern localities. In contrast, no evidence of asexual division was observed in more than 500 individuals from the 2 southern localities. Asexual division reduced the size of the organisms to below the normal maturation size. The relative frequencies of dividing individuals were lower between May and October, prior to the presumed spawning, than at any other time of the year. The populations from southern and northern localities are obviously different in their reproductive and life history characteristics, although they cannot be separated by cnidom or septa numbers, which have been traditionally used as taxonomic characteristics. These results suggest that what was considered *Sphenopus marsupialis*, with worldwide distribution, might actually be comprised of 2 sibling species off the Taiwanese coast.

**Key words:** Zoanthid, Size, Reproduction, Asexual, Cnida.

Since local populations cannot be distinguished easily on the basis of simple morphological traits, many marine species have long been assumed to have wide distributions (see Knowlton et al. 1992). Nevertheless, more detailed investigations have provided evidence that reproductive isolation and genetic differentiation do occur among widely distributed populations, and speciation might be complete in some resultant sibling species (see review by Knowlton 1993). The vast dimensions of the ocean, with potentially complicated patterns of currents, bottom topography, gradients of environmental factors, as well as historical events, might all provide opportunities for biological divergence (see review by Palumbi 1994). Nor is the sea a homo-

geneous habitat, especially for benthic species which have dispersal ability limited to a part of their life cycles. Indeed, opportunity for reproductive isolation may be higher than previously thought for these organisms. The morphological stasis within species complexes might reflect constraints on external morphology, recent common ancestry, and/or the decoupling of physiological and ecological divergence from morphological changes (Knowlton 1993).

*Sphenopus marsupialis* (Gmelin, 1827), a free-living solitary zoanthid, is known to have a worldwide distribution, e.g., Indian Ocean (Gravelly 1941, Nagabhushanam and Jothinayagam 1982); "Fulo Faya" in the China Sea, Massachusetts Bay in North

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America (Gray 1867), and the Great Barrier Reef in Australia (Burnett et al. 1997). Like many zoanthids, *S. marsupialis* has a thick coating of sand grains embedded in the mesoglea, which might help anchor the organism on sandy or muddy bottoms. Unlike most other zoanthids (Hyman 1940), which are colonial and are either encrusting or epizoic, *S. marsupialis* can move slowly on the bottom of an aquarium (Nagabhushanam and Jothinayagam 1982, and pers. obser.).

*S. marsupialis* has often been collected as a by-catch by shrimp boats using bottom trawlers in Taiwan. These by-catches of *S. marsupialis* seemed to vary in size and color depending on the locality. In this study, specimens from several localities along the coast of Taiwan were compared. The results reveal that they do not differ in external morphology, cnidom composition, or septal arrangements, but they do vary greatly in their body sizes and reproductive characteristics.

## MATERIALS AND METHODS

In the present study, specimens were collected monthly from October 1989 to September 1991 at Linbien (22°24'N, 120°30'E), and from April 1991 to February 1992 at Chadin (22°40'N, 120°09'E) in southwestern Taiwan (Fig. 1), by means of a bottom trawler with a mesh size of about 1.1 cm at depths between 10 and 25 m. Specimens were not obtained in certain months despite similar sampling efforts. Individuals were fixed in 10% neutral formalin for about 3 d, and later preserved in 70% ethyl alcohol. Due to a thick coating of sand grains, preserved specimens were rigid and had a relatively constant length and width. The column lengths, i.e., the distance between the oral and aboral ends, were measured with a pair of vernier calipers and were used to represent the size of the individuals. In addition, specimens from Dashi (24°55'N, 121°50'E), Masago (also known as Mashakou) (23°15'N, 120°05'E), and Chunyun (also known as Chungyun) (22°30'N, 120°22'E, see Fig. 1) collected between 1994 and 1995, using a similar method at the same depth ranges, were available in the collections of the National Museum of Natural Science (NMNS), Taiwan. Their size distributions were also analyzed in this study.

Individuals near the end of transverse division could be identified by their elongated shape, which resembled an unshelled peanut. For individuals in the intermediate stages of transverse division, a ridge in the inner wall of the coelenteron could be

detected after the organism was cut open. These were categorized as dividing individuals (Fig. 2), and their frequencies and sizes were recorded. In collections with many specimens, only subsets were used to estimate the frequency of the dividing individuals as well as their size structures. In addition, some specimens were reared in aquaria to observe the sequence and the time span of the transverse division.

Nine individuals, ranging from 2.4 to 9.1 cm in length, from Linbien, and 4 individuals, 1.6 to 2.9 cm in length, from Chadin were examined for their cnidom by macerating fresh tissues from tentacles, actinopharynx, mesenterial filaments, and body walls of fresh specimens. The nomenclature of cnidae mainly followed Carlgren's (1949) scheme. The lengths and widths of up to 20 cnidae of each type were measured for each kind of tissue in an individual.

About 10 specimens from each collection at Linbien and Chadin were cut open, fixed, and preserved. Macromesenteries were dissected from the organisms under a stereo microscope and then processed for histological gonad analysis. The 5- $\mu$ m thick sections were stained with basic fuchsin-picro-indigocarmine (Mohr 1981). Diameters of oocytes with a germinal vesicle in each section were measured. The average of the longest diameter and the maximal diameter perpendicular to it was used if the ova were not round. Further, numbers of both the tentacles and mesenteries near the mid-portion of the column were counted in some specimens from Linbien and Chadin. It should be noted that speci-

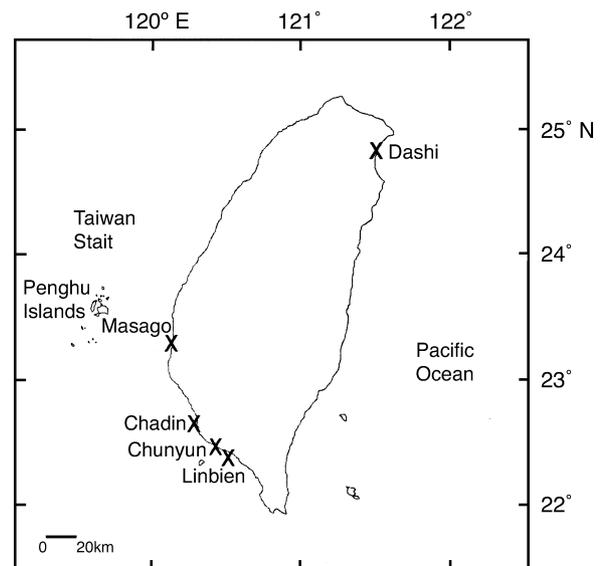


Fig. 1. Five collection sites in Taiwan.

mens from the NMNS were not analyzed histologically since specimens were preserved whole, and thus not fixed properly due to the thick coating of sand grains.

**RESULTS**

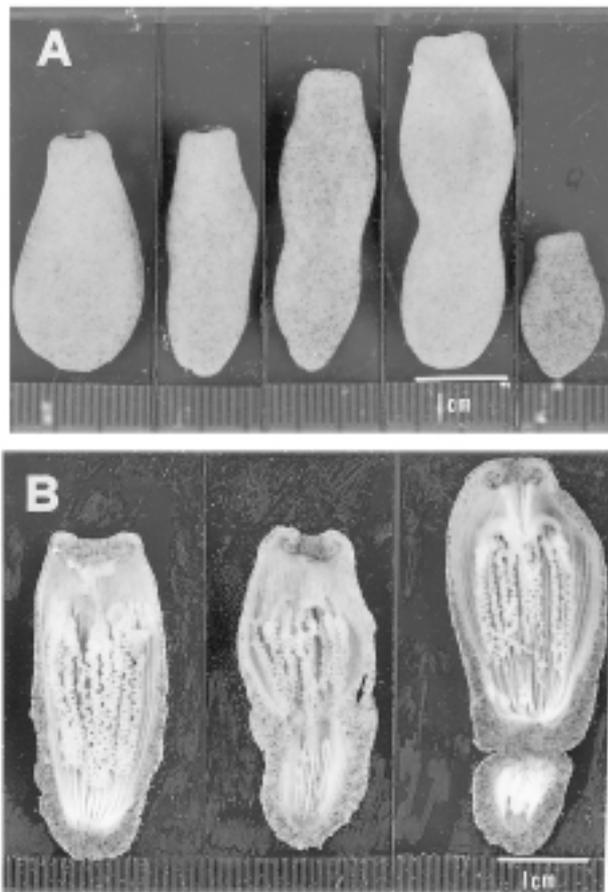
**General morphology**

The color of specimens was either dark gray (at Linbien, Masago, Dashi, and Chunyun) or mustard yellow (at Chadin). However, after long periods of rearing in aquaria without sediment, the aboral ends of live individuals became semi-translucent, like the oral ends where there are few sand grains under natural conditions. Such a phenomenon suggests that body color variation was determined, at least partly, by the color of the sediment on which the animal lived.

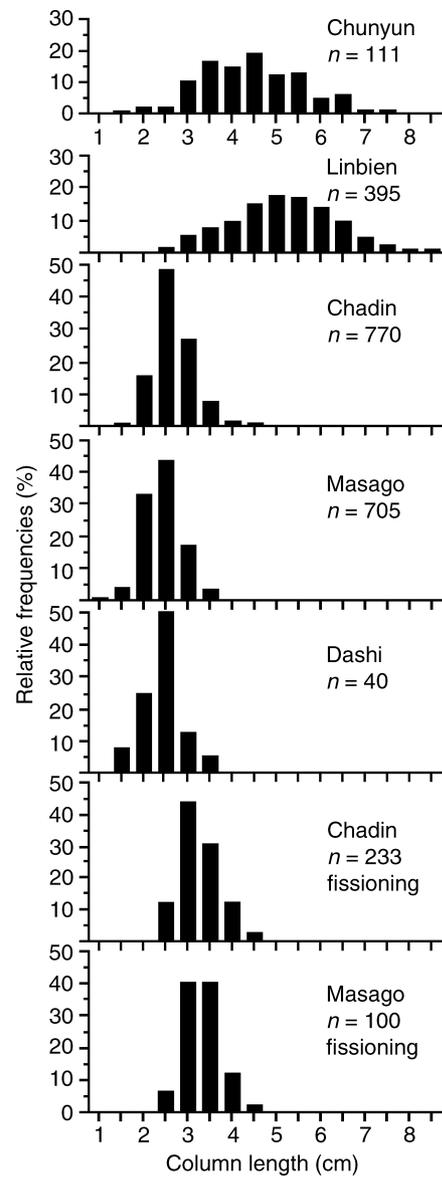
Non-dividing individuals from the 3 relatively

northern localities (Chadin, Dashi, and Masago) had almost identical mean column lengths ( $2.4 \pm 0.4$  cm [SD] for each of 3 localities). On the other hand, specimens from Chunyun ( $4.4 \pm 1.1$  cm) and Linbien ( $4.9 \pm 1.2$  cm) were significantly larger (Anova,  $p < 0.01$ ), with the largest reaching 8.5 cm in column length (Fig. 3).

Tentacle numbers and column lengths have a significant positive relationship at Linbien ( $r = 0.79$ ,  $n = 30$ ,  $p < 0.01$ ), but not at Chadin ( $r = 0.16$ ,  $n = 38$ ,  $p > 0.05$ ). A similar geographical trend was found in



**Fig. 2.** *Sphenopus marsupialis*. Asexual fission. A: External morphology of individuals in different stages of fission; B: Longitudinal sections of individuals in different stages of fission.



**Fig. 3.** *Sphenopus marsupialis*. Column length frequency distributions of individuals at the 5 localities. Normal individuals and individuals undergoing asexual division at Chadin and Masago are depicted separately; dividing individuals at Dashi are not depicted due to small sample size.

the relationship between the numbers of mesenteries and column length: being positive at Linbien ( $r = 0.72$ ,  $n = 23$ ,  $p < 0.01$ ,  $b = 3.25$ ), but not at Chadin ( $r = 0.04$ ,  $n = 33$ ,  $p > 0.05$ , Fig. 4). When samples from Linbien and Chadin were combined, the slope ( $b = 4.40$ ) of the relationship was not significantly different from that at Linbien alone.

A total of 4 cnida types (namely, holotrich, spirocyst, microbasic b-mastigophore, and microbasic p-mastigophore) was found; and each kind of tissue examined contained 2 to 3 types. The ranges of cnida length and width from comparable tissues overlapped between Linbien and Chadin individuals. However, no difference in the mean lengths or mean widths of various types of cnidae within each kind of tissue was found between the 2 sites (Table 1).

### Asexual reproduction

Transverse fission was found only in individuals

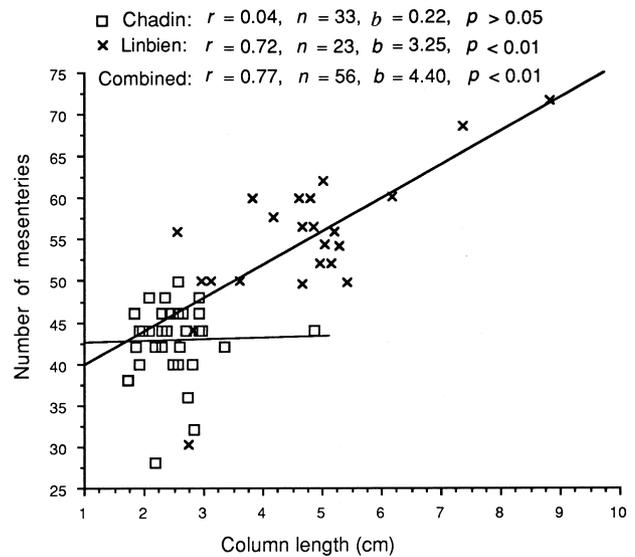


Fig. 4. *Sphenopus marsupialis*. Relationship between number of mesenteries and column length.

Table 1. *Sphenopus marsupialis*. Mean length, mean width, and range of cnida capsules at Linbien and Chadin (units:  $\mu\text{m}$ )

Tissue type	Mean length $\times$ Mean width	
	Linbien	Chadin
<b>Tentacle</b>		
Holotrich	34 (20-44) $\times$ 15 (10-21) $n = 160$	28 (20-42) $\times$ 13 (9-18) $n = 65$
Spirocyst	22 (13-32) $\times$ 4 (2-6) $n = 180$	20 (13-29) $\times$ 4 (3-6) $n = 80$
Microbasic b-mastigophore	32 (24-41) $\times$ 4 (2-6) $n = 140$	29 (20-40) $\times$ 4 (2-7) $n = 80$
<b>Actinopharynx</b>		
Holotrich	37 (24-49) $\times$ 18 (13-25) $n = 180$	32 (22-40) $\times$ 13 (11-16) $n = 60$
Microbasic b-mastigophore	36 (26-44) $\times$ 5 (3-6) $n = 180$	31 (25-38) $\times$ 5 (4-6) $n = 80$
<b>Mesenterial filament</b>		
Holotrich	37 (28-46) $\times$ 16 (13-22) $n = 180$	33 (25-40) $\times$ 13 (10-17) $n = 80$
Microbasic p-mastigophore	20 (11-25) $\times$ 6 (4-6) $n = 160$	16 (11-21) $\times$ 5 (4-7) $n = 80$
Microbasic b-mastigophore	44 (29-59) $\times$ 5 (3-6) $n = 180$	38 (27-47) $\times$ 5 (3-6) $n = 80$
<b>Column</b>		
Holotrich	42 (29-60) $\times$ 19 (14-25) $n = 180$	34 (29-40) $\times$ 16 (12-19) $n = 74$
Microbasic p-mastigophore	53 (30-74) $\times$ 8 (5-10) $n = 108$	35 (27-50) $\times$ 7 (5-17) $n = 80$
Microbasic b-mastigophore	16 (11-22) $\times$ 3 (2-4) $n = 140$	14 (10-21) $\times$ 3 (2-4) $n = 80$

Numbers in parentheses indicate ranges.  $n$ : total number of cnidae measured. No significant difference between Linbien and Chadin was found (Nested ANOVA,  $p > 0.05$  in all cases).

collected from the northern localities of Chadin, Dashi, and Masago. Asexual division started with the development of filaments in the lower part of the originally filament-free septa. A constriction was then formed in the body column (Fig. 2), which unequally separated the organisms into larger upper ( $1.7 \pm 0.3$  cm) and smaller lower ( $1.3 \pm 0.2$  cm) parts ( $n = 233$ , paired  $t$ -test,  $p < 0.01$ ). Sometimes, new mouths and tentacles developed for the lower parts before complete separation of the zoanthids into 2 independent organisms. In this study, the whole process of division is estimated to have taken 1-2 wk for the individuals observed in the aquaria. Individuals undergoing asexual fission had greater column length ( $3.0 \pm 0.5$  cm,  $n = 233$ , at Chadin; and  $3.3 \pm 0.4$  cm,  $n = 100$  at Masago; Fig. 3) than did non-dividing individuals ( $2.4 \pm 0.4$  cm, at each of the 3 localities) ( $t$ -test,  $p < 0.01$ , in both cases).

The relative frequencies of individuals undergoing asexual division ranged from 0% to 22.3% in the different collections. Low frequencies of dividing individuals occurred from August to October at Chadin (1.9%, pooling 3 collections,  $n = 53$ ) and from May to October at Masago (1.8%, pooling 4 collections,  $n = 3320$ ). Occurrence of transverse division was dependent on season in both localities ( $\chi^2$ -test,  $p < 0.05$  at Chadin,  $p < 0.01$  at Masago). On the other hand, high frequencies of dividing individuals occurred from November to May at Chadin (10.4%, pooling 6 collections,  $n = 751$ ), and from November to March at Masago (11.5%, pooling 3 collections,

$n = 4452$ ). Only 2 collections were available at Dashi, where the frequencies of dividing individuals were 22.7% and 8% in November and December, respectively (Table 2).

### Sexual reproduction

Gonads were found only on macro-(or complete) mesenteries, and the gender of the individuals could be identified in histological sections. The population at Linbien was strictly gonochoristic; a total of 39 males, 17 females, and 51 immature individuals were observed in the breeding season. At Chadin, 27 males, 18 females, 13 hermaphrodites, as well as 29 immature individuals were found. Both oocytes and spermaries occurred in the same mesenteries in the hermaphroditic individuals (Fig. 5).

Larger individuals were more likely to be sexually mature at both localities (Fig. 6). However, more than 60% of individuals in size groups above 2 cm were mature at Chadin, whereas individuals at Linbien had to reach 5 cm to achieve a comparable probability (Fig. 6). These results indicate that individuals had a smaller mature size at Chadin than at Linbien.

At both localities, early female germ cells, with diameters of 6-15  $\mu$ m, first occurred in February; oocytes with diameters of 10-15  $\mu$ m entered the mesoglea in April. The germinal vesicles moved toward the periphery of the oocytes, while their diameters were maintained at about 40  $\mu$ m during vitellogenesis. Trophonema, the connecting trophic cells between oocytes and endodermal cells, could be observed for oocytes less than 180  $\mu$ m in diameter. Mature oocytes reached an average diameter of about 200  $\mu$ m. Early spermatogonia measuring 3-4  $\mu$ m first appeared in April. Later, spermaries, with sperm tails directed toward the center, increased in diameter and occupied almost the entire width of the mesenteries (Fig. 5).

At Linbien, oocyte diameter reached its maximum between June and August. Indications of egg release, i.e., empty vacuoles scattered in the mesenteries, were observed in August 1990, and oocytes were not present in October 1990 (Fig. 7) and 1991. A similar seasonal pattern also occurred in males in which mature spermaries occurred in August and September, with only 1 individual found to have spermaries in October. These results indicate that spawning occurred between August and October in the Linbien population.

At Chadin, oocyte diameter reached its maximum between August and November; signs of egg release were observed in November when the num-

**Table 2.** *Sphenopus marsupialis*. Relative frequencies of dividing individuals collected at northern localities (numbers in parentheses indicate total numbers examined)

Month	Percentages of individuals dividing		
	Chadin	Masago	Dashi
January	11 (31)		
February	6 (16)	21.2 (298)	
March		9.2 (3525)	
April	10 (338)		
May	11 (338)	2.7 (1036)	
June		0.7 (1696)	
July			
August	0 (13)	9.0 (11)	
September	3 (35)		
October	0 (5)	3.0 (577)	
November	10 (20)	8.3 (629)	22.7 (22)
December	13 (8)		8.0 (25)

Samples from Chadin were collected from January 1991 to February 1992; samples from Masago were collected from August 1994 to June 1995; samples from Dashi were collected in 1994.

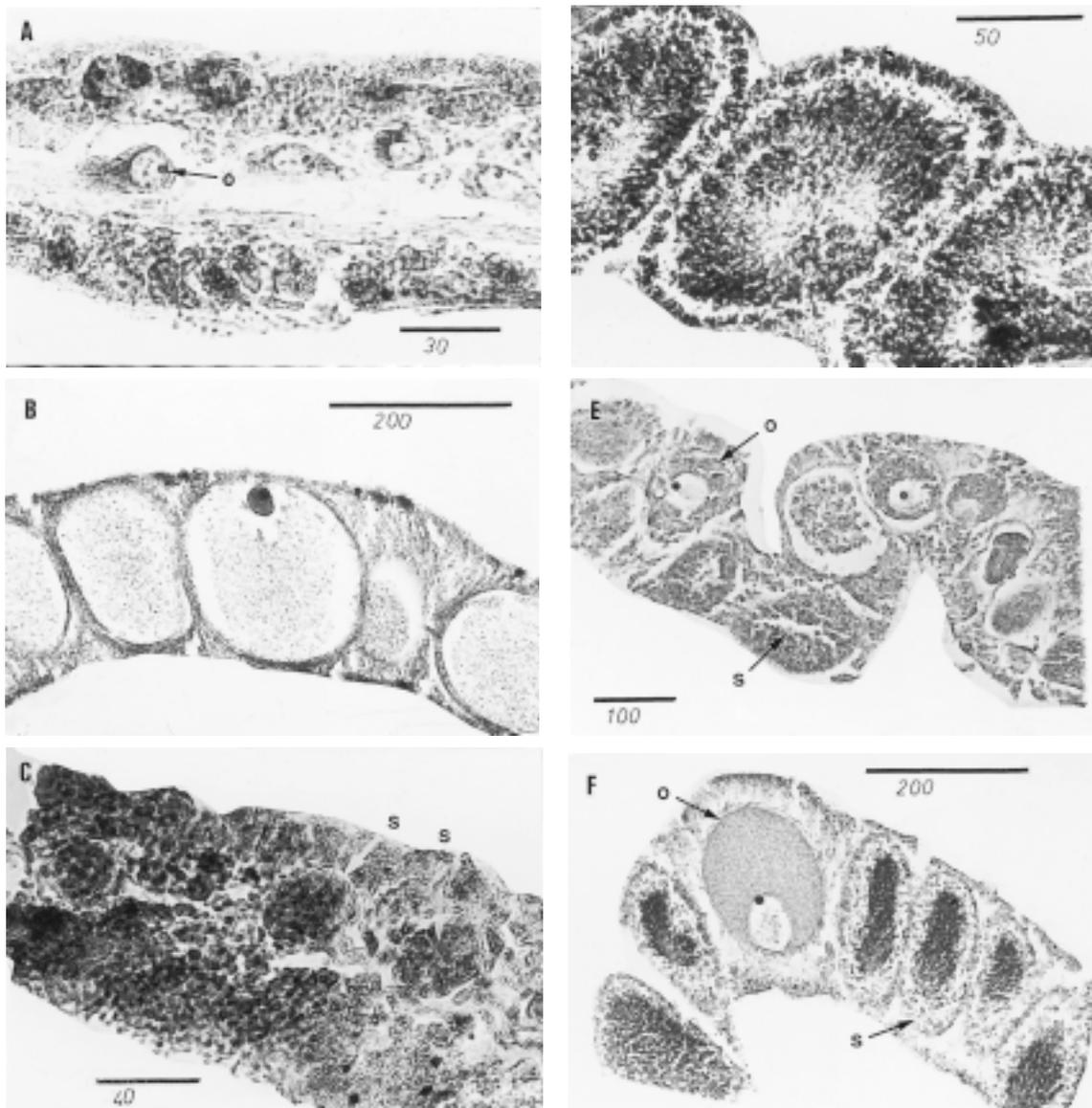
ber of oocytes decreased and empty vacuoles appeared. No oocytes were found in December (Fig. 7). Spermaries matured in October, and most males released gametes by November. Spawning in the Chadin population had apparently occurred between October and December.

No larvae, either within individuals or in the water column, were observed.

## DISCUSSION

Undoubtedly, individual size is the most obvious

difference among *S. marsupialis* collected from different localities (Fig. 3). One possible explanation for the relatively smaller size of individuals in the relatively more northern populations (Chadin, Dashi, and Masago) is that they exhibited transverse fission (Fig. 2), which is the first such case reported in Zoanthidea. This phenomenon, however, was not found in the southern populations at Chunyun and Linbien. Transverse fission not only reduced the size of individuals but also might have decreased their potential for sexual reproduction. After division, both the upper and lower parts were reduced to an average length of less than 2 cm. This size category is



**Fig. 5.** *Sphenopus marsupialis*. Gametogenesis. A: Early oocyte in the mesenterial endoderm; B: Mature oocytes; C: Spermatogonia in the endoderm; D: Mature spermary; E, F: Hermaphroditic individuals at Chadin. s: spermatogonia, o: oocyte; units of scale bars:  $\mu\text{m}$ .

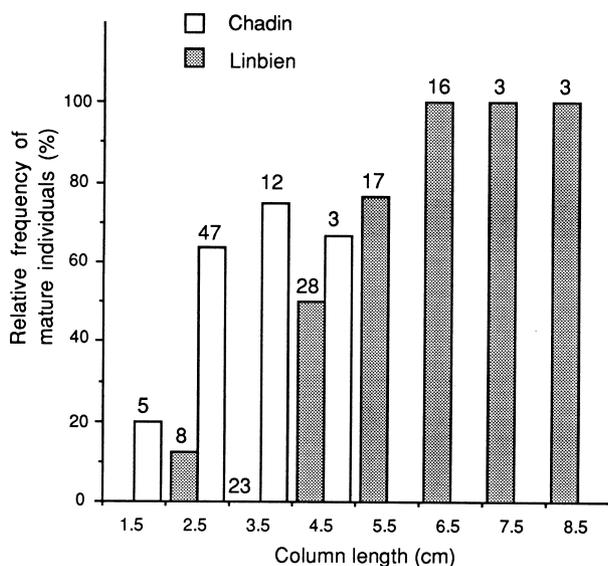
unlikely to be sexually mature even for the northern population (only 20%, compared to more than 60% for individuals longer than 2 cm, Fig. 6) which has a smaller mature size than the southern population. Unequal division, with the upper part being larger than the lower part, however, might allow one of the descendants to reach maturity size earlier than if both descendants were of equal sizes.

The relative frequencies of dividing individuals were not consistent throughout the year, being lower before October, and higher between November and May (Table 2). These results suggest that there might be a conflict between sexual reproduction and asexual fission of an individual, since fission mainly occurs in the period when gametogenesis takes place (Fig. 7). On the other hand, seasonal fluctuation of the frequency of asexual fission (Table 2) may result in an annual polyp size fluctuation which may be an adaptation for feeding if food particle size changes through the seasons (Sebens 1979). The lack of correlation between body lengths and the number of tentacles and mesenteries at Chadin might also be a result of transverse fission. Individuals elongated and became peanut-shaped, while the diameters of the columns remained relatively unchanged before fission. However, after fission, the column length was drastically reduced, but the column diameter remained almost the same.

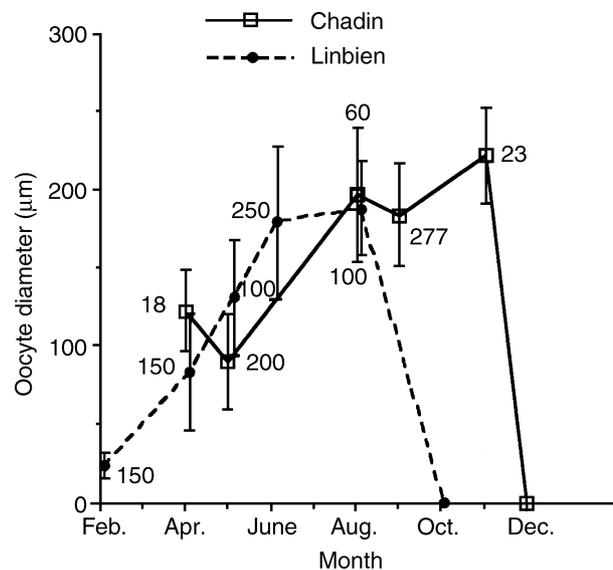
Most colonial zoanthids increase polyp numbers by budding or longitudinal fission (Ryland 1997).

Transverse fission of the solitary *S. marsupialis* is obviously not suited to the formation of colonies in which polyps remain horizontally connected. A colonial mode of growth may not confer much benefit to organisms which are capable of inhabiting soft sediments, because substrate availability is not a limiting factor. A similar transverse mode of fission also occurs in a few species of the order Actiniaria (Shick 1991, Hand and Uhlinger 1995) and Fungiidae of the order Scleractinia (see Hoeksema 1989); none of these species exhibits longitudinal fission, which is common in other members of the taxa. Formation of independent polyps, instead of colonies, may help by spreading the risk of mortality when separated polyps are far apart from each other (Janzen 1977).

Both hermaphroditism and gonochorism occur in zoanthids. A species is considered hermaphroditic when a certain percentage of individuals is found to develop the gonads of both sexes (e.g., 16%-66% in *Zoanthus* spp. and *Palythoa caribaeorum*, see Fadlallah et al. 1984). Hermaphroditic colonies (with either dioecious or monoecious polyps, e.g., Karlson 1981, Fadlallah et al. 1984) can sometimes only be identified late during gametogenesis due to the fact that the development of spermaries often starts later than that of oocytes in anthozoans (Soong 1991). However, repeated sampling of the same individuals in colonial species indicated that in some species a mixed mode does exist in



**Fig. 6.** *Sphenopus marsupialis*. Relative frequencies of mature individuals in each size class collected at Linbien and Chadin. Numbers above bars indicate sample sizes.



**Fig. 7.** *Sphenopus marsupialis*. Seasonal changes in the average oocyte diameter at Linbien (1990 samples) and Chadin (1991 samples). Vertical bars indicate 1 standard error; numbers indicate the number of ova measured.

which both gonochoristic and hermaphroditic colonies occurred (Yamazato et al. 1973, Ryland and Babcock 1991). Whether an individual might express different genders at different times remains to be investigated. The present study reveals clearly that the mixed-mode Chadin population, with both hermaphroditic (22% of fertile individuals,  $n = 58$ ) and gonochoristic individuals occurring late in the reproductive season, obviously differed from the strictly gonochoristic (56 fertile individuals) Linbien population.

Reproductive investment in Anthozoa does not involve sex-specific costs in non-gametic tissues (see Harrison and Wallace 1990). Thus, allocation of resources to gametes of both sexes may incur few extra costs to hermaphroditic individuals (Charnov 1982). The mechanism determining individual expression of either gonochorism or hermaphroditism remains unresolved.

Although direct observation of broadcasting has been made for only 2 species of zoanths (Ryland and Babcock 1991, Burnett 1995), spawning of gametes has been presumed to be the mode of reproduction for most zoanths studied, since no embryos have been found in their gastrovascular cavities (e.g., Yamazato et al. 1973, Cooke 1976, Fadlallah et al. 1984, Muirhead et al. 1986). The only known exception is *Isozoanthus gigantea*, in which brooded larvae were found (Carlgren 1923, cited in Ryland, [1997]). The annual cycle of gametogenesis also suggests that the 2 populations studied here are likely to be broadcasters (see Soong 1993).

Evidence of divergence in many aspects of life history traits, namely mean size, size at sexual maturity, occurrence of hermaphrodites, and occurrence of asexual division (Table 3), strongly suggests that the species studied here belong to 2 isolated

populations. It is unlikely that the above variations are all caused by environmental factors. In fact, it is highly possible that they belong to 2 different species. It would be interesting to better understand the limits of each of their distributions, particularly since both inhabit very similar, if not identical, depth ranges and substratum and have the same external morphology. Both are likely to broadcast gametes and thus have an extended period of external development, which would result in a greater dispersal range than with brooding (e.g., Jackson 1986). Moreover, the 2 populations were only about 70 km apart from each other, with no obvious geographical barrier between them.

Both temperature and current pattern differences were invoked to explain differences in assemblages of marine fauna between northern and southern Taiwan (fishes: Shao et al. 1997; corals: Chen 1999). Temperature differences between Linbien and Chadin at depths of 10-20 m are about 0 to 2 °C (Hwang and Tang 1993), which may be too small a variation to have resulted in a clear-cut barrier as was observed in *S. marsupialis*. The hypothesis of dispersal barrier due to current pattern was also invoked to explain genetic differentiation of populations of a scleractinian coral *Mycedium elephantotus*. Yu et al. (1999) estimated that there is more gene flow between *M. elephantotus* populations in the Penghu Islands and northern Taiwan, whereas the southern Taiwan population is relatively isolated. The local current pattern changes seasonally, with stronger northbound water in the Taiwan Strait in summer. In winter, the northeasterly monsoon drives cold water into the southern Taiwan Strait (Jan 1995). In contrast to *M. elephantotus* which spawns in late spring to summer (Dai et al. 1992), *S. marsupialis* spawns in fall. Thus a more detailed current

**Table 3.** *Sphenopus marsupialis*. Summary of differences between the northern and southern populations

Character <sup>a</sup>	Northern	Southern
Color	mustard yellow (Chadin), dark gray (Masago and Dashi)	dark gray
Column length ± SD	2.4 ± 0.4 cm	4.9 ± 1.2 cm (Linbien) 4.4 ± 1.1 cm (Chunyun)
Column length and number of mesenteries	no correlation ( $r = 0.04$ )	positive correlation ( $r = 0.72$ )
Length of maturation	short	long
Transverse fission	present	absent
Spawning season	October-December	August-October
Sexuality	gonochoristic, with some hermaphroditic	strictly gonochoristic

<sup>a</sup>Except for color and column length, all other characteristics were based on comparisons between the collections at Chadin (north) and Linbien (south).

pattern, both temporally and spatially, is necessary before the role of current on the variation or differentiation of this zoanthid can be solved.

Given the present findings, we suspect that there is genetic differentiation between populations of *S. marsupialis* along the Taiwanese coast. It is possible that the *S. marsupialis* in the 3 oceans may consist of several sibling species (see "Introduction"). Contrary to the above speculation, no differentiation in allozymes was found for populations of *S. marsupialis* almost 1000 km apart in the Great Barrier Reef (GBR) and Torres Strait (Burnett et al. 1997). A study on the sedentary zoanthid, *Palythoa caesia*, a species with high external morphological variation, also revealed very limited allozyme variation among samples collected from various sites in the GBR (Burnett et al. 1994 1997).

Accepting that there are 2 species of *Sphenopus* occurring in Taiwan, cnidom and septal characteristics are obviously too similar to be used effectively in distinguishing different species of these solitary zoanthids (also see Sole-Cava and Thorpe 1992 for *Actinia* spp.). The previously held notion of a worldwide distribution of *S. marsupialis*, then, might have been based on the lumping together of some sibling species that did not diverge much morphologically. Extrapolating from this study, one would suspect that many different species in the order Zoanthidea, and even in the class Anthozoa, might have been inaccurately lumped together since the cnidom and septal characteristics (and other morphological traits) are normally used to define different species in these groups. On the other hand, many marine invertebrates were assigned new specific names based on locality differences with no other justifications. Weil and Knowlton (1994) have reported that what had long been considered a highly plastic colonial coral, *Montastraea annularis*, in the Caribbean actually consists of 3 (or more) different species that differ in corallite characteristics, colony morphology, depth distribution, competitive ability, allozyme patterns, etc. For anthozoan species, which do not deposit skeletons and are solitary, and for many other marine invertebrates as well, there are fewer morphological characteristics to inspect than in corals. Among the many available modern research approaches, examining life history characteristics (such as reproductive traits) may be a relatively inexpensive, but powerful method for investigating hidden diversities among species, owing to the fact that it does not necessitate maintaining live or fresh specimens. In addition, it also provides clues to the adaptation of organisms, which, along with genetic data, could reveal much about their

evolution.

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## 臺灣袋狀兔葵在形態及生活史上之分化

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本研究比較了單體型式的袋狀兔葵 (*Sphenopus marsupialis*) 在臺灣不同海域的形態及生活史上的變異。樣品由 1989 至 1995 年間以底拖網採自沿岸水深 10-25 米的五個地點。由南部二地點（中芸、林邊）採得的體柱長約是其他較北地點（大溪、馬沙溝、茄荳）的 2 倍。成熟體柱長也是南部的林邊大於北部茄荳的個體。經由卵徑分析，生殖季應以南部（林邊）在八月早於十至十一月間的北部族群。在南部，個體都是雌雄異體，而北部茄荳則有 22% 的成熟個體為雌雄同體。北部採得的個體中 7% 有正在進行橫分裂的現象，而南部的個體則全無此現象。進行分裂個體的比例以五至十月時較低，而以其他季較高，分裂後個體比成熟體柱長還小。臺灣南、北採得的袋狀兔葵顯然在外型及生活史多方面都有很大的差別，然而傳統上用作分類、鑑定依據的不同部位刺細胞上卻未見不同。本研究顯示在目前被認為有世界性分布的袋狀兔葵，在臺灣海岸可能已經有分化的現象。

**關鍵詞：**兔葵，體型，生殖，無性生殖，刺絲胞。

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