

Regeneration and Potential Functional Differentiation of Arms in the Brittlestar, *Ophiocoma scolopendrina* (Lamarck) (Echinodermata: Ophiuroidea)

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Keryea Soong, Yen Shen, Shu-Hsien Tseng and Chang-Po Chen (1997) Regeneration and potential functional differentiation of arms in the brittlestar, *Ophiocoma scolopendrina* (Lamarck) (Echinodermata: Ophiuroidea). *Zoological Studies* 36(2): 90-97. Arm breakage and regeneration in the brittlestar, *Ophiocoma scolopendrina* (Lamarck), were surveyed in southern Taiwan from July 1991 to April 1992. A total of 618 individuals were examined, revealing that in 56% of individuals, or 19% of arms, were undergoing the process of regeneration. Breakage occurred mainly at the distal 1/3 of the arm. The number of individuals with 3 or more regenerating arms exceeded that of expectation from a binomial distribution, suggesting that individual arm breakage might be dependent on the status of the other arms. The arms, according to their position relative to the madreporite, have different probabilities of being protruded, and they also have different probabilities of breakage in the field. The arms most frequently protruded tend to be the most frequently injured. This phenomenon suggests that functions of arms may have differentiated despite the similar morphology of the various arms in the brittlestar.

Laboratory experimental results indicate that the rate of regeneration per broken arm averages 0.4 mm/day, whether 1 or 3 arms were injured. Arm position, relative to the madreporite, however, made no difference in regeneration rates when all 5 arms were cut. Nevertheless, when 3 adjacent arms were severed, the center arm regenerated faster than the 2 side arms; this did not happen when the 3 injured arms were not all adjacent. The faster regeneration of the center arm may provide the advantage of restoring arm functions sooner.

Key words: Brittlestar, Regeneration.

Arm breakage is common in brittlestars and may be caused by wave action, intraspecific aggression and predation by crabs, asteroids, and fishes (Emson and Wilkie 1980, Woodley 1981, Aronson 1985, Duineveld 1986, Aronson 1988 1989 1991 1992, Stancyk et al. 1994). The incidence of arm regeneration in individuals is high, e.g., 84%-93% of individuals in 2 species of amphiuroids in the North Sea (Buchanan 1964, Bowmer and Keegan 1983), and 66%-100% of individuals in 8 ophiuroid species in the Caribbean (Sides 1987, see also Aronson 1991) had 1 or more regenerating arms.

Arm breakage in brittlestars is considered an adaptation in which part of an arm (or arms) is sacrificed to make possible the survival of the individual. The amount of energy spent in arm regeneration is high (Bowmer and Keegan 1983). In *Amphiura filiformis*, for example, energy spent in arm regeneration was estimated to exceed twice that spent in reproduction; and somatic growth was almost entirely restricted to arm regeneration (O'Connor et al. 1986).

It is obvious that arms of brittlestars must serve other vital functions besides autotomy. Arms of a brittlestar may be used for locomotion, digging,

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grasping, and feeding (Woodley 1975, Clements 1984). All arms of an individual appear similar, although their positions relative to the madreporite are different. Some arms may probe outside caves or crevices more often than others which hold the brittlestar to the substratum. The frequencies of breakage may differ among these arms since they are exposed to a different extent. Moreover, the rate of regeneration may also differ for different arms. Arms with more important functions may regenerate faster as an adaptation for increased survival (Reichman 1984). Thus the potential differences in the frequencies of breakage and in the rates of regeneration would suggest differentiation in arm functions within individuals. So far, there has been no data indicating that different arms may vary in relative frequency of breakage or differ in rate of regeneration.

In this study, we investigated the frequency of arm breakage of *Ophiocoma scolopendrina* in southern Taiwan with a focus on different arms within individuals. Experiments were conducted in the laboratory to compare the rates of regeneration of different arms. The effects of both the absolute position (relative to the madreporite) and the relative position (relative to other injured arms) of arms on regeneration were investigated. The results suggest that, despite the pentasymmetric morphology, arms of a brittlestar may have potential functional differentiation.

MATERIALS AND METHODS

Ophiocoma scolopendrina (Lamarck), common along the Taiwanese coast (Wu 1982, Applegate 1984), is abundant in the intertidal areas at Lonshaton (N22°20.5', E120°22.3') and Gerban (N22°20.3', E120°21.2') of Hsiaoliuchiu island, and at Nanwan (N21°56', E120°48') in southern Taiwan. The brittlestars occur under boulders or coral fragments, or in crevices, with 1 or several arms protruding and sweeping the substratum, which is a mixture of sand and coral fragments. Disc autotomy, which occurs in some amphiriid species (Dobson 1985, Clements et al. 1988, Dobson and Turner 1989, Dobson et al. 1991), has not been observed in this species.

Arm breakage

Arm breakage of *O. scolopendrina* was investigated at Gerban in July 1991 and at Lonshaton in July and November 1991 and April 1992. About

150 individuals were collected at each time. Arms showing obvious signs of regeneration parts, i.e., discontinuous change in arm width, were recorded as regenerating arms in this study. The numbers of regenerating arms, the points of breakage in the arms, and the relative positions of regenerating arms were recorded for each individual. Fresh wounds on arms with no regenerating parts may have been caused by the collection itself, and so these individuals were not counted.

The point of breakage in each regenerating arm was recorded as "tip", "middle", or "base" using the longest intact arm of each individual as an index. For example, a break point located between 1/3 and 2/3 of the full length of an intact arm was recorded as "middle". Each arm was assigned a letter (from A to E) according to its position relative to the madreporite. The arm opposite the madreporite was designated A, and others were named B-E in a clockwise direction respectively when viewed from the oral side (Figure 1).

Arm protrusion

In order to compare frequencies of arm protrusion, the protruded arms of 50 individuals at Nanwan in July 1993 were nipped in situ by use of a pair of forceps to make a mark, and then the individuals were collected for identification of arm position.

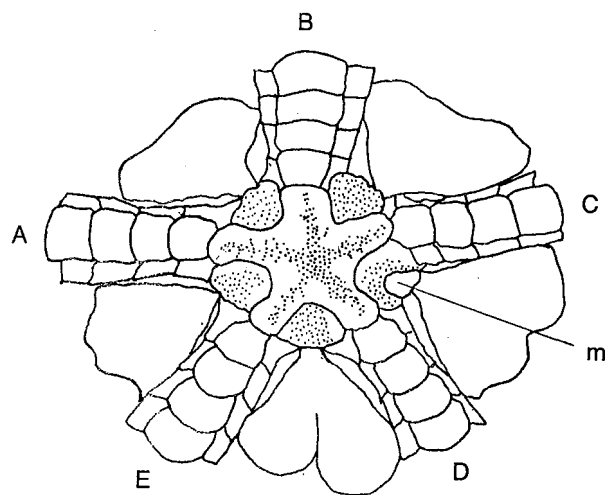


Fig. 1. Oral side of a brittlestar, *Ophiocoma scolopendrina*, showing the position of the madreporite (m), and the designation (A to E) of each arm, after Moore (1966). Only 4 segments of each arm are shown.

Arm regeneration

About 210 individuals were brought to the laboratory from collection sites at Gerban, Lonshaton, and Nanwan, and were kept in tanks with circulating sea water at 24-26 °C, 3.0%-3.5% salinity for 1 month before conducting experiments on the rate of regeneration. Arms were severed by cutting near their base using scissors. Individuals were kept separately in 10-cm diameter cylindrical plastic cages (2 mm mesh size) in the same water tank. The regenerated lengths of arms were measured with a pair of plastic vernier calipers after anesthetizing the animals with 6.5% MgCl₂. In the 1st experiment, from September 4 to November 6, 1991, 2 treatments, i.e., 1-arm cuts vs. 3-arm cuts were conducted to compare regeneration rates. The regenerated arm lengths were measured six times during this period at approximately 10-day intervals. The following experiments were done under the same conditions as above unless otherwise specified.

In the 2nd experiment, individuals were divided into 2 groups, i.e., 3-arm-cut and 5-arm-cut groups, to determine if the positions of injured arms affect regeneration rate. In the 3-arm-cut group, 2 treatments were applied: (1) 3 adjacent arms (arms -D, -E, -A) were cut; and (2) 3 non-adjacent arms (arms -A, -B, -D) were cut, at the same position near the basal segment. In the 5-arm-cut group, all 5 arms were cut at the same position near the base of each arm. In the 3rd experiment, 4 other combinations of 3 adjacent arms, i.e., ABC, BCD, CDE, and EAB were tested 2 mo later in November 1993. All statistical methods used are described in Sokal and Rohlf (1981).

RESULTS

Regenerating arms in nature

More than half (56%) of 618 individuals examined had regenerating arms; while 19% of arms were regenerating, i.e., the mean number of regenerating arms per individual at Hsiaoliuchiu was 0.95 (Table 1). For the Lonshaton area, the frequency of individuals with regenerating arms was not independent of time (G-test, $G = 9.03$, $p < 0.05$); more individuals with regenerating arms were found in July (60%) than in November (43%, Table 1).

The frequency distribution of the numbers of regenerating arms within individuals was compared to the expected values from a binomial distribution to determine whether or not arm breakage events were independent of one another. To make the sample sizes more appropriate for the G-test, consistently small values for 4- and 5-arm breakage groups were combined. A significant deviation from independence was found when all data from different sites and different months in Hsiaoliuchiu were pooled (Table 2). Numbers of individuals with no, 3, or more regenerating arms tended to be greater than expected; whereas numbers of individuals with 1 or 2 regenerating arms tended to be smaller than expected. In individual surveys, significant deviations from expectation were found at Lonshaton in July 1991 and April 1992 (Table 2).

Breakage occurred mostly at arm tips (53%); while basal breakage accounted for only about 20% of the cases (Table 3).

Occurrence of arm regeneration was dependent on arm position, with arm-B having the lowest

Table 1. Frequencies of regenerating individuals and regenerating arms of *Ophiocoma scolopendrina* at Hsiaoliuchiu, Taiwan

Date site	No. of individuals examined	No. of individuals with regenerating arms	No. of arms examined	Total number of regenerating arms
July 1991				
Gerban	154	103 (67%)	770	155 (20%)
Lonshaton	156	94 (60%)	780	186 (24%)
November 1991				
Lonshaton	144	62 (43%)	720	88 (12%)
April 1992				
Lonshaton	164	88 (54%)	820	159 (19%)
Total	618	347 (56%)	3 090	588 (19%)

frequency (all surveys pooled) (Table 4). In the observation of arm protrusion, most individuals protruded 1 to 3 arms (except 1 individual, with 4 arms protruded). The frequencies of protrusion were dependent on arm position, with arm-B having the lowest frequency (Table 5). Protrusion frequency was also dependent on whether the arm was adjacent to arm-B, or non-adjacent to arm-B ($p < 0.01$, G-test); arms adjacent to B had lower frequencies of protrusion.

Regeneration of arms broken experimentally

In the laboratory, the brittlestar arms regenera-

ted at an average rate of about $0.4 \text{ mm day}^{-1} \text{ arm}^{-1}$. No significant difference was found between the regeneration rate (per arm) of the 1-arm-cut and that of the 3-arm-cut groups (Figure 2).

In the 2nd experiment, no significant difference was found in the rates of regeneration among arms in the non-adjacent, ABD, group (Table 6). In the adjacent, DEA group, the 3 arms did not regenerate at the same rate within an individual (Friedman test, $p = 0.02$); arm E, the center arm, regenerated faster than the other two (Table 6). Arm-D and arm-A did not differ significantly in this experiment (Wilcoxon signed rank test, $p = 0.92$, $n = 38$).

Table 2. Frequencies of individuals of *Ophiocoma scolopendrina* with different numbers of regenerating arms at Hsialiuchi, Taiwan. Expected frequencies were calculated based on a binomial distribution, assuming independence between arms

Date site		No. of regenerating arms in an individual					G-test
		0	1	2	3	4+5	
July 1991							
Gerban	observed	51	66	23	13	1	7.5 ^{ns}
	expected	50.1	63.1	31.8	8.0	1.1	
Lonshaton	observed	62	42	25	18	9	39.0**
	expected	40.0	62.6	39.2	12.3	2.0	
November 1991							
Lonshaton	observed	82	42	15	4	1	6.4 ^{ns}
	expected	75.1	52.2	14.5	2.0	0.1	
April 1992							
Lonshaton	observed	76	47	23	10	8	36.6**
	expected	55.8	67.1	32.3	7.8	1.0	
Total	observed	271	197	86	45	19	79.5**
	expected	215.1	252.7	118.8	27.9	3.4	

^{ns} $p > 0.05$, ** $p < 0.01$.

Table 3. Frequencies of regenerating arms of *Ophiocoma scolopendrina* with breakage at each of 3 positions. G-test for goodness of fit to 1:1:1

Date site	Position of breakage			G-test
	Tip	Middle	Base	
July 1991				
Gerban	79	47	29	24.7**
Lonshaton	116	49	21	76.8**
November 1991				
Lonshaton	45	20	23	12.0**
April 1992				
Lonshaton	70	46	43	7.9**
Total	310 (53%)	162 (27%)	116 (20%)	100.8**

** $p < 0.01$.

Table 4. Frequencies of regenerating arms at different positions, relative to the madreporite, of individuals of *Ophiocoma scolopendrina*

Date site	Arm position					G-test
	A	B	C	D	E	
July 1991						
Gerban	44	15	33	30	33	15.3**
Lonshaton	37	27	44	37	41	4.6 ^{ns}
November 1991						
Lonshaton	17	19	13	13	26	6.3 ^{ns}
April 1992						
Lonshaton	27	23	32	39	38	6.1 ^{ns}
Overall	125	84	122	119	138	14.7**

^{ns} $p > 0.05$, * $0.01 < p < 0.05$, ** $p < 0.01$.

Fifty-nine individuals were tested in the other 4 combinations of adjacent 3-arm-cut experiments, ABC, BCD, CDE, and EAB. These individuals were measured twice, 34 and 60 d after severing. In both measurements, the center arms of the trios had regenerated significantly faster than the other 2 side arms (Friedman test, $p = 0.03, 0.05$ respectively, Table 6). Comparison of the 2 side arms showed no significant difference in either measurement (Wilcoxon signed rank test, $p = 0.30, n = 59$ for the 1st measurement 34 d after severing; $p = 0.39, n = 40$ for the 2nd measurement 60 d after severing. The number of individuals decreased in the 2nd measurement due to extra arm breakage after the 1st measurement).

The rate of regeneration was not significantly different among the 5 arms of an individual in the 5-arm-cut group (Table 7-A). When any 3 adjacent arms in this experiment were compared, none of the 5 possible combinations indicated any significant differences (Table 7-B).

DISCUSSION

Frequency of breakage

Individuals of *Ophiocoma scolopendrina* in this study were found to have relatively fewer arms undergoing regeneration (56%, Table 1) than brittlestars in other reported studies. For example, besides the studies mentioned previously, 80%-100% of 7 Scottish ophiuroids (except one population of *Ophiura albida* with only 46%, Emson and Wilkie 1980), and 64%-72% of 3 Floridian amphiurids (Singletary 1980) were in the process of

regenerating at least 1 arm. When the percentages of total numbers of regenerating arms were compared, only *O. albida* mentioned above had a lower rate (14%) than the findings in this study (19%); all others had much higher rates of between 28% and 89% (Emson and Wilkie 1980, Singletary 1980, Sides 1987).

The causes of different frequencies of regenerating arms among species may be complicated. However, difference in mode of life may have an important influence. For example, *Amphipholis kochii*, a species burrows in soft sediments with its arms exposed, discards arms readily, whereas, *Ophiura sarsi vadicola*, an epibenthic species, does not seem to autotomize its arms at all (Emson and Wilkie 1980). Abundance of predators, specific behavioral features, and palatability of brittlestars must also be important factors; direct estimates of predator pressure are difficult to make (Sides and Woodley 1985, Sides 1987). *O. scolopendrina* lives under rubble and between crevices, and individuals shed arms readily upon capture. This hiding behavior may protect the brittlestars from predators and may have resulted in low frequencies of arm breakage and regeneration.

The extent of damage to each arm differs among species. Arms of *Amphiura filiformis*, for example, usually broke in the proximal and midarm regions (Bowmer and Keegan 1983); arms of *O. scolopendrina* in this study broke at the tip most frequently (Table 3). Since breakage usually occurs near the point of stimulation (Wilkie 1978), differences

Table 5. Frequencies of protruded arms of *Ophiocoma scolopendrina* examined at Nanwan. Arms are designated according to their position relative to the madreporite (see text). G-tests are based on the assumption that arms at different positions had the same probability (0.46:0.54, estimated from overall probability) of being protruded

Numbers with arm	Arm position				
	A	B	C	D	E
Protruded	20	15	23	30	27
Hidden	30	35	27	20	23
G-test	0.73 ^{ns}	5.34*	0 ^{ns}	3.93*	1.28 ^{ns}

^{ns} $p > 0.05, *p < 0.05.$

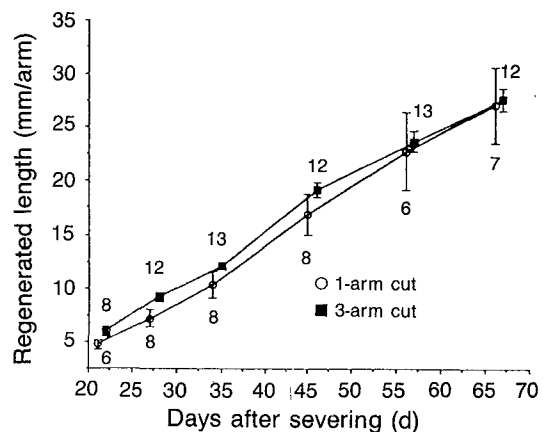


Fig. 2. Average length of regenerated arms of *Ophiocoma scolopendrina* in 67 days of monitoring. Arms were cut on September 4, 1991. The data for 3-arm cut represent the average of all 3 arms, and are shifted 1 day to the right for clarity. Numbers under or above error bars (1 standard error) indicate no. of individuals measured each day.

Table 6. Comparisons of relative rates of arm regeneration within individuals of *Ophiocoma scolopendrina* with non-adjacent or adjacent 3-arm-cut groups

Treatment (position ^a of arms cut)	Test period (interval)	<i>n</i>	Mean ranks ^c of 3 cut arms	<i>p</i>
Non-adjacent (ABD)	Sept. 13-Oct. 26, 1993 (43 d)	27	A = 1.81 B = 2.22 D = 1.96	0.24
Adjacent (DEA)	Oct. 4-Nov. 2, 1993 (29 d)	38	D = 1.86 E = 2.32 A = 1.83	0.02
Adjacent (ABC, BCD, CDE, EAB combined)	Nov. 16-Dec. 20, 1993 (34 d, 1st measurement)	59	side 1 = 1.99 center = 2.24 side 2 = 1.77	0.03
	Nov. 16, 1993-Jan. 15, 1994 (69 d, 2nd measurement)	40 ^b	side 1 = 1.90 center = 2.30 side 2 = 1.80	0.05

^aArm positions (A-E) designated according to their position relative to the madreporite (see text). *p* indicates results of Friedman tests.

^bNineteen individuals had additional arm breakage after the 1st measurement, and were not used later.

^cThe fastest among the 3 was ranked 3; the intermediate, 2; and the slowest, 1.

Table 7. Comparisons of rates of arm regeneration in 30 individuals of *Ophiocoma scolopendrina* with all 5 arms cut. (A) All 5 arms compared together; (B) Sub-comparisons of 3 adjacent arms in the same experiment

(A)

Arm ^a position	Regenerated length Mean ± se, cm	Mean rank ^b
A	0.54 ± 0.05	2.77
B	0.61 ± 0.07	2.90
C	0.63 ± 0.07	3.40
D	0.59 ± 0.06	2.85
E	0.60 ± 0.07	3.08

Friedman Test, *p* = 0.50 (corrected for ties)

(B)

Position ^a of the 3 adjacent arms	Mean ranks ^c			<i>p</i> , Friedman Test (corrected for ties)
ABC	1.85	1.95	2.20	0.31
BCD	1.95	2.18	1.87	0.38
CDE	2.20	1.80	2.00	0.31
DEA	1.98	2.10	1.92	0.75
EAB	2.12	1.93	1.95	0.71

^aArm positions designated according to their relative positions to the madreporite (see text). The experiment was conducted between May 8-31, 1993.

^bThe fastest was ranked 5, and the slowest was ranked 1, others were intermediate from 2 to 4.

^cThe fastest among the 3 was ranked 3; the intermediate, 2; and the slowest, 1.

among species in breakage point may indicate different behavior of the brittlestars or their predators. *A. filiformis*, mentioned above, inhabits soft sediments whereas *O. scolopendrina* lives in crevices or among coral rubble; a hard substratum may protect the brittlestars and limit the extent of each injury to the tips of the arms. Injuries at the tips are more quickly regenerated to full length than those in the proximal region of the arm, so breakage frequency at the tip must be higher than the data of regenerating points suggests. Rates of regeneration also determine how many regenerating arms can be observed at any one time (Sides 1987, Stancyk et al. 1994).

Dependency of arm breakage

In *O. scolopendrina*, multiple arm breakage occurred more frequently than expected (Table 2), suggesting that several arms may break dependently. A similar pattern also occurred in all 8 ophiuroids in Sides' (1987) study in the Caribbean. In her study, the estimated numbers of individuals with no arms broken, or with 3 or more arms broken were more than expected from a binomial distribution, whereas the numbers of individuals with 1 or 2 arms broken were fewer than expected. It is possible that once injured, an individual may be predisposed to be injured again (Aronson 1991). Since predation may cause a majority of arm damage in brittlestars, the "dependency" pattern of

arm breakage may be related to persistence of predators, or alternatively, habitat quality of individual brittlestars. Some brittlestars may be confined to poor habitats, e.g., shallow or small crevices, and thus suffer frequent damage.

Effect of arm position and possible differentiation

Possible differentiation of arms was first observed in juveniles of the burrowing species *Ophiophragmus filograneus* in Florida (Turner 1974). Two non-adjacent arms grew at a faster rate than the other 3 arms, and Turner suggested that this might be an adaptation, enabling small individuals to bury their discs into soft sediment while maintaining the ability to feed by protruding 2 long arms to the surface. These 2 non-adjacent long arms could occur at any position relative to the madreporite, although frequencies varied (8:1:5:4:1, frequencies of the location of the unpaired short arm). In this case, the 2 long arms obviously function differently from the short ones. The frequency, 8:1:5:4:1, deviated significantly from what might be expected from a random pattern (our analysis for goodness of fit to 1:1:1:1:1 ratio, $G = 9.72$, $p < 0.05$). Since the arms were designated according to their position relative to the madreporite, and the madreporite seems to be the only organ not in pentamerous symmetry in brittlestars, the determination of arm function might be related to the function of the madreporite. The differentiation in *Ophiophragmus filograneus* was not fixed on certain arms, it is likely that other factors, e.g., early arm breakage, may affect which two arms grow faster than others.

The 5 arms of *O. scolopendrina* broke at different probabilities, as indicated from their respective frequencies of being regenerated in nature (Table 4). This implies that particular arms may serve different functions. For brittlestars which inhabit crevices or holes, only some arms protrude at a time, other arms may be holding the substratum to anchor the organisms. If the madreporites are consistently oriented at certain spatial relationship to the opening of the crevices, then the functions of the arms may be differentiated according to their position relative to the madreporite.

The above hypothesis is supported by the fact that in nature Arm-B of *O. scolopendrina* had both the lowest frequency of protrusion and the lowest frequency of breakage among the 5 arms in nature (Tables 4, 5). A tentative analysis of the relationship between protrusion frequency and breakage frequency among arm positions indicates a positive

correlation coefficient of 0.80 ($p = 0.10$, $n = 5$). Arms protruded more often tend to suffer more frequent breakage.

Differences in arm regeneration rate

When arm differentiation does occur, one possible phenomenon to be expected is that the regeneration rates may differ among arms, assuming that their relative importance to the survival of the individual is different (see theory of Reichman 1984). Present experimental data, however, do not support this hypothesis: no particular arm regenerated faster than others when all 5 arms were cut (Table 7). Most natural injuries to arms of *O. scolopendrina* occurred at the tips (Table 3), thus injured arms may still remain functional. Arm function may also be substituted totally or partially by other arms when injury occurs, thus the relative importance of any specific arm is likely to be small and thus not reflected in differential regeneration rates.

The present study, nevertheless, revealed that the regeneration rate of arms might be influenced by the status of neighboring arms when only some arms are broken. Significant differences occurred when 3 adjacent arms were cut in an individual, with the center arm of the trio regenerating faster than the 2 side arms. No such difference in regeneration rates was found when non-adjacent arms were cut (Table 6). Previously, Fielman et al. (1991) suggested that in *Microphiopholis gracillima* in nutrient-free sea water, materials were allocated to the disc and/or arm regeneration until a gut and 3 complete arms were achieved; thereafter the rate of regeneration slowed down. They suggested that this "minimal functional configuration" (a gut and 3 complete arms) allows the brittlestars to reestablish respiration, feeding, and digestion capabilities. Both "minimal functional configuration" in *M. gracillima* and the faster regeneration of the central injured arm in *O. scolopendrina* of this study may have the effect of restoring basic functions in the shortest time. It remains to be investigated whether these are adaptations of brittlestars which suffer frequent injuries.

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蜈蚣櫛蛇尾陽燧足之腕再生及功能分化

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民國八十年七月至八十一年四月間在南臺灣研究了蜈蚣櫛蛇尾陽燧足 (*Ophiocoma scolopendrina*) 之腕的斷落及再生，在 618 隻樣品中 56% 的個體有斷落而再生的腕 (佔全部腕數 19%)，斷腕多發生在靠近尖端處。斷三腕以上之隻數超過逢機之預期，斷腕之間可能互相並不是獨立的。每隻腕可依對水孔 (madreporite) 之相對位置定出腕號，五隻不同腕號發生再生之機率顯著不同，在野外觀察中，其伸出岩隙的機率也顯著不同。較少伸出之腕有較少受傷而再生之現象，此點顯示輻射對稱的陽燧足五隻腕外形上雖然沒有差別，但功能上可能已有分化。

腕再生速率為 1.2 公分 / 月，與斷腕隻數無關。不同腕再生速率未發現不同。但再生速率可能受到鄰腕狀況之影響，當三隻相鄰腕均切斷時，中間斷腕再生較快；但若三隻斷腕不全相鄰，則並無此現象。

關鍵詞：陽燧足，再生。

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