Zeitschrift: Eclogae Geologicae Helvetiae

Herausgeber: Schweizerische Geologische Gesellschaft

Band: 80 (1987)

Heft: 3

Artikel: Ophiurous oddities : deviation from pentamerous symmetry in non-fissiparous Ophiuroids : a comparison of recent and fossil species

Autor: Bomwer, T. / Meyer, C.A.

DOI: https://doi.org/10.5169/seals-166031

Eclogae geol. Helv.	Vol. 80	Nr. 3	Pages 897–905	Basel, Dezember 1987

Ophiurous oddities – deviation from pentamerous symmetry in non-fissiparous Ophiuroids: a comparison of recent and fossil species

By T. BOMWER[1]) and C. A. MEYER[2])

ABSTRACT

This paper reports on the incidence of deviant symmetry in a recent and a fossil ophiuroid, both of which are known to be non-fissiparous species. Tetramerous and hexamerous specimens are described, the living Amphiurid – *Amphiura filiformis* (O. F. MUELLER) and the fossil Ophiurid – *Ophiomusium gagnebini* (THURMANN). Isolated instances in other recent species are listed. In total, two principal deviant types are described. Those with entire deviant symmetries, i.e. four or six arms, jaws etc., are considered to result from genetic defects or abnormal development at the embryonic stage. Those with superficial or partial symmetry deviations and which exhibit growth irregularities are considered to be a result of injury and subsequent regeneration. An instance of disc regeneration in the fossil *Ophiomusium gagnebini* is also reported, where the half of the disc has regenerated in a non-fissiparous species.

RÉSUMÉ

Le présent travail résume l'apparition des déviations de symétrie chez une ophiure récente et une forme fossile, les deux ne reproduisent par schizogonie. Des espèces avec quatre et six bras sont présentés – une forme actuelle, *Amphiura filiformis* (O. F. MUELLER) et une forme fossile – *Ophiomusium gagnebini* (THURMANN). La répartition des déviations de symétrie dans des autres espèces vivants est donnée. En tout, deux types de déviations sont décrits. Ceux avec une déviation totale, p.e. quatre ou six bras, mandibules, etc., sont le résultat d'un développement anormal pendant le stage embryonal. Les formes assymétriques et ceux avec des irrégularités de croissance montrent des blessures qui sont suivies par une régénération. La régénération partielle du disque chez une forme fossile – *Ophiomusium gagnebini* – est raportée pour la première fois.

ZUSAMMENFASSUNG

Diese Arbeit beschreibt das Auftreten abweichender Symmetrien bei einer rezenten und einer fossilen Schlangensternart, beide sind nicht fissipar. Vier- und sechsarmige Exemplare der rezenten Art *Amphiura filiformis* (O. F. MUELLER) und der fossilen Art *Ophiomusium gagnebini* (THURMANN) werden beschrieben und abgebildet. Das vereinzelte Auftreten abweichender Symmetrien bei anderen rezenten Formen wird aufgeführt. Im ganzen werden zwei Formtypen mit einer abweichenden Symmetrie diskutiert. Formen mit einer deutlich abweichenden Symmetrie, z. B. vier- oder sechs Arme, Kiefer, etc., sind das Resultat einer anormal verlaufenden Embryonalentwicklung. Assymetrische Exemplare und solche mit Wachstumsunregelmässigkeiten zeigen Folgen einer Verletzung mit nachfolgender Regeneration. Die partielle Scheibenregeneration bei *Ophiomusium gagnebini* wird für fossile Formen erstmals nachgewiesen.

[1]) Zoology Department University College, Galway, Ireland.
[2]) Geologisches Institut, Universität Bern, Baltzerstrasse 1, CH–3012 Bern, Switzerland.

1. Introduction

Ophiurous ophiuroids with unusual symmetries, deviating from the normal pentamerous arrangement, have long been known. Such symmetrical oddities are frequent, if not the norm among fissiparous species which reproduce vegetatively by splitting across the disc; subsequently, the isolated halves regenerate the lost parts (viz. HYMAN 1955; EMSON & WILKIE 1980). However, reports on symmetry deviation among non-fissiparous species are few and far between in the literature.

This paper attempts to examine and explain the incidence of deviant symmetry among populations of shallow-water living and fossil ophiuroids which are not known for their fissiparity. The material for this report originated from two totally separate studies of size frequency and population dynamics, one, on the recent Amphiurid *Amphiura filiformis* (O. F. MUELLER) and the other on the fossil Ophiurid *Ophiumusium gagnebini* (THURMANN). The population dynamics of *A. filiformis* is described by BOMWER (1982a) and O'CONNOR et al. (1983), while its reproductive biology and regenerative ability have been reported by BOMWER (1982b) and BOMWER & KEEGAN (1983) respectively. MEYER (1984, 1985) has previously described the population dynamics and general palaeobiology of *O. gagnebini*, whose exceptional state of preservation is considered to result from smothering by 'storm' layers. Isolated records from other non-fissiparous, recent species are also included, e.g. *Amphipholis squamata* (D. CHIAJEI) and *Ophiotrix fragilis* (ABILDGAARD).

2. Material and methods

The burrowing amphiurid brittle-star *Amphiura filiformis* (O. F. MUELLER) occurs in high densities at the 'Margaretta' station in Galway Bay (53°13'16", 9°6'30"). Here, the sediment is composed largely of fine sand with some 15% silt-clay, at a depth of 17m. *Amphiura filiformis* has been collected on a monthly basis, by Van Veen grab, from 1974 to 1976 and from 1978 to the present day. The material reported here extends from 1974 to 1982. The brittle star *Ophiomusium gagnebini* (THURMANN) (Family: Ophiuridae LYMAN) is thought to be a vagile, epifaunal detritus/suspension feeder. It occurs in two populations separated in time by marl deposition but with similar age structure. This fossil material was collected from silty sandstone layers interbedded in the predominantly clayey sequence of Lower Effingen beds (middle Oxfordian, Upper Jurassic) in the Schofgraben area near Solothurn, Switzerland (MEYER 1984, 1985). The first population is accompanied by macrourous crustaceans (*Eryma ventricosa* VON MEYER) and another ophiuroid (*Sinosura wolburgi* HESS) whereas the second one is found together with the astropectinid sea star *Pentasteria (P.) longispina* HESS, *Eryma ventricosa* VON MEYER and the two brittle stars *Sinosura wolburgi* HESS and *Ophiopetra ? oertlii* HESS (MEYER 1985). All fossils are now collated at the Museum of Nature in Solothurn (Switzerland).

3. Results

Table 1 lists the number of *A. filiformis* and *O. gagnebini* symmetry deviants, giving the total number of specimens in each sample and a cumulative total for each time series sampling period. It is difficult to determine an overall ratio of non pentamerous to

Table I: List of symmetry deviants of *Amphiura filiformis* and *Ophiomusium gagnebini*.

Year	Month	No. of deviants	No. in sample	
Location: Margaretta Station, Galway Bay, Ireland.				
Type I, tetramerous individuals, *A. filiformis*				
1975	July	1	435	
1976	May	1	463	
	Sept.	1	616	
1979	July	1	155	
	Nov.	1	354	
1981	Jan.	1	486	
	Feb.	1	331	
	Oct.	1	360	
	Dec.	1	428	
1982	Jan.	1	354	
	Feb.	1	313	
Type IIa, superficially hexamerous individuals.				
1980	Feb.	1	255	
	Oct.	1	314	
Location: Kinsale Harbour, Co. Cork, Ireland.				
Type I, tetramerous individuals, *A. filiformis*.				
1980	Feb.	1	113	
	Mar.	1	116	
Location: Schofgraben, Lower Effingen Beds, Solothurn, Switzerland.				
Type I, tetramerous individuals. *O. gagnebini*.				
1979		1	100	NM20041
		1	100	NMS 20139 (Fig. 2)
Type 2b, tetramerous individual, *O. gagnebini*.				
		1	200	NMS 20043 (Fig. 4)
Type 2c, hexamerous individual, *O. gagnebini*.				
		1	200	NMS 20140 (Fig. 5)

normal individuals owing to the time series nature of the *A. filiformis* data and the comparatively small numbers of fossil *O. gagnebini*.

Out of the many thousands specimens of *A. filiformis* from Galway Bay examined for size frequency analysis, a total of thirteen were found to have symmetries which deviated from the normal pentamerous type. Two further *A. filiformis* individuals with deviant symmetries were also observed from a collection of recent material from Kinsale Harbour, Co. Cork. Four fossil *O. gagnebini*, from the Schofgraben area of Switzerland, out of a total of 200 examined for size frequency analysis were found to possess deviant symmetries.

Two main types of deviation were observed: 1, genuine alterations in total body symmetry (type I), and 2, partial changes due to accidental causes and influenced possibly by regeneration (Type II).

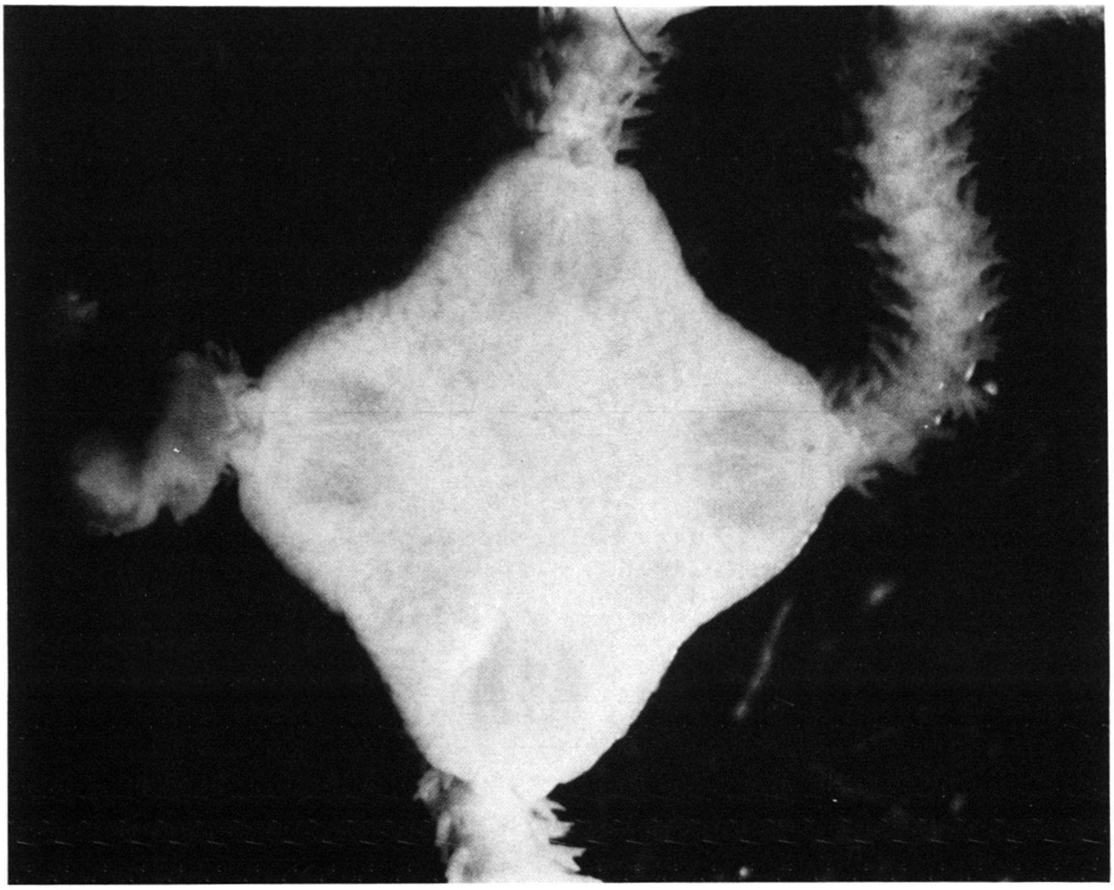

Fig. 1. *Amphiura filiformis* (O. F. MUELLER), Kinsale Harbour, Co. Cork, Ireland. Type I deviation (disc diameter = 5 mm).

3.1. Type I (Fig. 1, 2)

The first deviant type consists of individuals all of which are perfectly tetramerous or hexamerous and show no sign of accidental damage and regeneration.

All but two of these specimens are tetramerous, possessing four arms, four sets of jaw plates and four sets of radial and genital plates, etc. This applies to eleven *A. filiformis* from Galway Bay and to two from Kinsale Harbour (Fig. 1). Oddly, several of these *A. filiformis* specimens have two madreporic plates instead of the usual single structure. One four rayed example of *O. gagnebini* has already been figured by MEYER (1984, Fig. 9). Two ophiuroids have been found to have only four arms, one showing the aboral side, the other the oral side (Fig. 2) and are perfectly tetramerous.

In general, a normal adult *A. filiformis* has a disc diameter (viz. O'CONNOR et al. 1983) of 6 to 7 mm, while the tetramerous individuals vary from 4 to 6 mm across the disc. *O. gagnebini* also had an adult disc diameter of 6 to 7 mm and all deviant specimens are considered to have been full grown. The authors are of the opinion that all tetramerous specimens are adults and that any variation from the normal size may be accounted for by the missing ray. There was little evidence of gonad proliferation in those tetramerous *A. filiformis* collected during summer months, when this species is usually gravid. However, a more recent tetramerous specimen collected in 1983 was found to be fully gravid (not listed), indicating maturity.

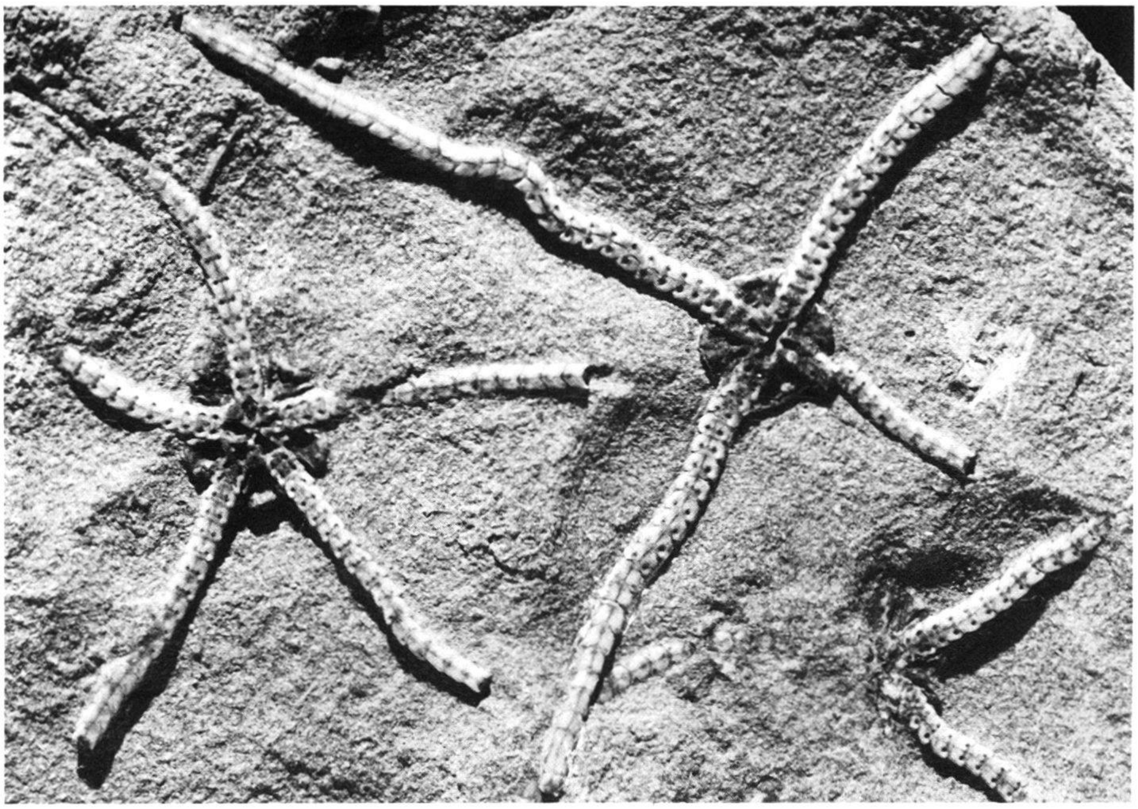

Fig. 2. *Ophiomusium gagnebini* (THURMANN), Lower Effingen beds, Schofgraben, Switzerland. Type I deviation (disc diameter = 6 mm).

Tetramerous individuals of *A. filiformis* from both Galway Bay and Kinsale Harbour occurred at frequencies ranging from 1:113 and 1:616 when individual samples are considered. However, when all the ophiuroids collected in monthly samples over a period are taken into account this ratio is much lower at 1:4662 and 1:1340 for the 1974 to 1976 and 1978 to 1982 sampling periods respectively. On the other hand *O. gagnebini* showed a much higher frequency of 1:100 in both populations. However, calculation of accurate ratios of incidence for tetramerous specimens is difficult for both species, as usually only a single individual turned up in any one sample, whether fossil or living.

A single collection in 1983 of some 300 living *Amphipholis squamta* (D. CHIAJEI) from Clifden, Co. Galway, Ireland, also yielded one perfectly tetramerous specimen.

Another collection of approximatively 900 living *Ophiotrix fragilis* (ABILDGAARD) from Kinsale Harbour Co. Cork, Ireland, yielded two perfectly hexamerous specimens, showing six of each plate series and no signs of accidental damage and regeneration to explain the extra ray.

3.2. Type II

The second type of symmetry variant is composed of individuals which at first sight appear to show symmetry deviation. Some, in particular *O. gagnebini*, genuinely have 4 or 6 rays, but its felt that the following type II deviants all arose from accidental causes during their post-metamorphic life.

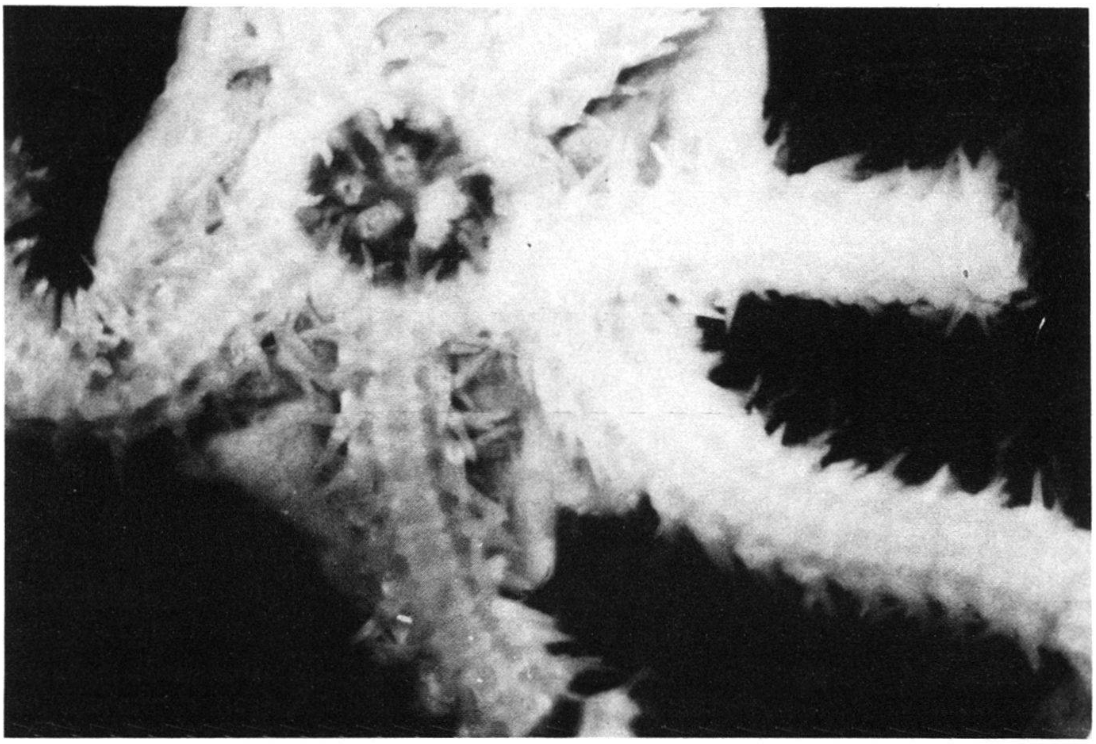

Fig. 3. *Amphiura filiformis* (O. F. MUELLER), Margaretta Station, Galway Bay, Ireland. Type IIa deviation (disc diameter = 6 mm).

Fig. 4. *Ophiomusium gagnebini* (THURMANN), Lower Effingen beds, Schofgraben, Switzerland. Type IIb deviation (disc diameter = 6 mm).

3.3. Type IIa (Fig. 3)

Only two specimens of *A. filiformis* were found with the following configuration. Close examination reveals that although they have six arms, they are otherwise entirely five rayed (Fig. 3), having five jaw structures etc. One of the arms of both these individuals possesses a basal bifurcation (from the first arm segment), thus, giving rise to two arms from one radius. The two specimens with the above configuration were both from Galway Bay material occurring at a frequency of 1:255 and 1:314 per sample or at a frequency of 1:5360 for the time series sampling period 1978 to 1982.

3.4. Type IIb (Fig. 4)

This four armed specimen (aboral side), with an assymmetric disc (Fig. 4), has one arm directly regenerating from the disc margin, whilst another arm shows a regeneration 2 mm away from the disc. Whether its symmetry abnormality was originally a result of predation is unknown, it nevertheless shows signs of disc and arm repair by regeneration. It is included at this point largely for the sake of convenience.

3.5. Type IIc (Fig. 5)

This single specimen of *O. gagnebini* possesses six arms (Fig. 5), three are normally grown and protrude from an apparently normal portion of disc with a radius of 3.5 mm.

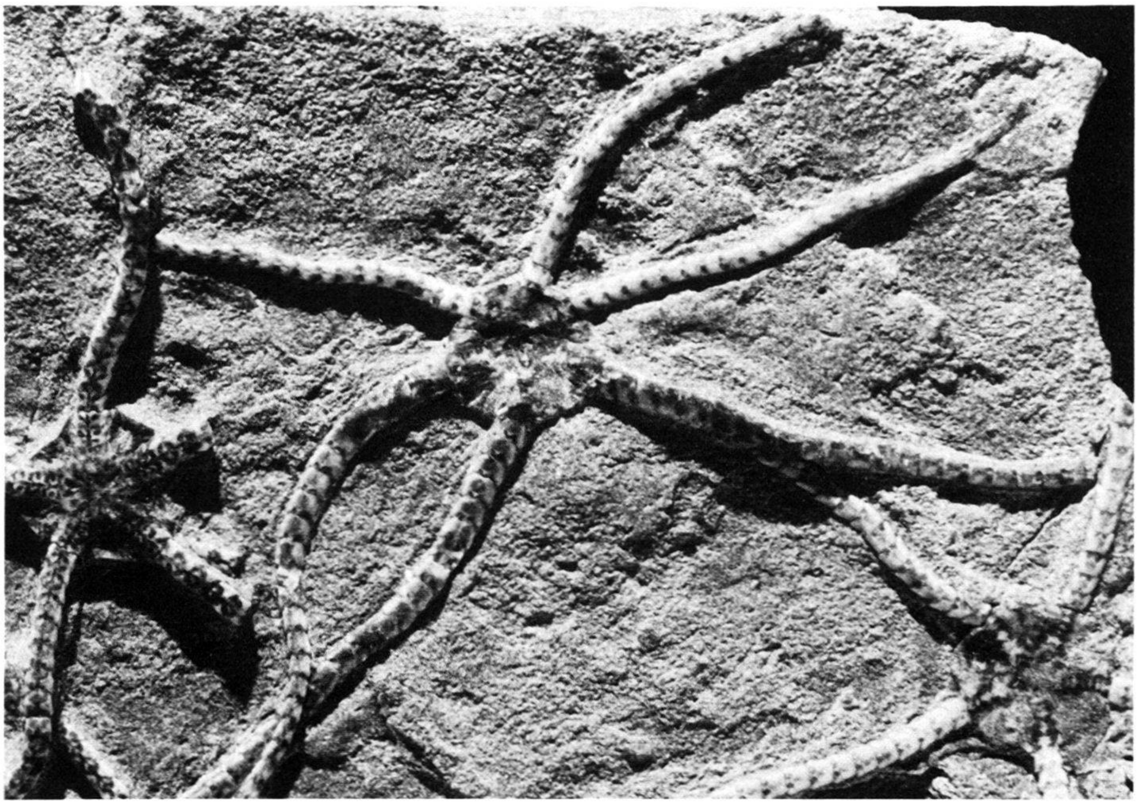

Fig. 5. *Ophiomusium gagnebini* (THURMANN), Lower Effingen beds, Schofgraben, Switzerland. Type IIc deviation (disc diameter = 6.2 mm)

The other three arms are obviously thinner and appear from the smaller half of the disc with a radius of 2.7 mm. It appears at first sight like an animal which is regenerating after fission, a phenomen which is discussed below.

4. Discussion

SWAN (1966) cites some instances of abnormal symmetry in recent regular echinoids, but does not speculate as to the cause, apart from a suggestion that a study of larval cultures might be a useful starting point for future studies. HYMAN (1955), on the other hand, discusses symmetry abnormality only in relation to fissiparous species. To our knowledge, little information exists concerning the regularity of occurrence of symmetry abnormalities in the living non-fissiparous Ophiuroidea as a whole. Similarly, the fossil record yields only very little information about abnormal symmetry in echinoderms. Tetramery is recorded from a Tertiary irregular echinoid of France (PHILLIPPE 1983). An unusual number of rays in fossil asteroids is very well documented (LEHMANN 1950, 1951, 1957). LEHMANN (1951, 1957) found three different ophiuroid species in the Palaeozoic Hunsrück slates (Lower Devonian, W. Germany) which deviated from patterns of five. *Ophiurina lymani* STUERTZ, *Loriolaster mirabilis* STUERTZ and *Taeniaster beneckei* STUERTZ show four and six-armed specimens with a corresponding number of jaw plates. The deviant symmetry is thought to be either a feature of fission or a genetic defect (LEHMANN 1950).

Symmetry deviation is common in fissiparous species, i.e. those which reproduce vegetatively by splitting their discs and regrowing the two halves to form new individuals. Only one member of the genus *Amphiura* is known to be fissiparous according to EMSON & WILKIE (1980), and that is *Amphiura sexradiata* KOEHLER. None of the tetramerous specimens (Type I, Fig. 1, 2) of *A. filiformis* or *O. gagnebini* showed any sign of recent regeneration around the disc region, which would indicate that either fission or accidental damage and consequent irregular regeneration might be the cause. It is possible, though by no means certain, that the observed Type I symmetry deviation results from genetic factors, affecting the early development stages of both species.

The deviation described as Type IIa (Fig. 3) above occurred only in *A. filiformis*, and the six arms and otherwise pentaradial configuration are not easy to explain. *A. filiformis* undergoes constant loss of arm parts due to sublethal predation (BOMWER & KEEGAN 1983). Perhaps if the arm is lost sufficiently close to the oral ring, i.e. right under the disc, an abnormal regrowth might occur. It should be borne in mind that *A. filiformis* can regenerate the entire disc cap, including the stomach and gonads. Type IIb (Fig. 4) most likely demonstrates an injury due to predators probably made by fish or lobsters. However it is difficult to tell whether its symmetry was tetramerous before or as a result of injury.

Type IIc probably occurs by much the same means as IIb above and raises a number of interesting considerations. Firstly, one could think this specimen to be an excellent example of fission in fossil ophiuroids, because six armed animals are very common in fissiparous species (LUETKEN 1872). The figured specimen could represent a freshly split and almost regrown brittlestar. However, at a population level fissiparity is not supported by either the normal size frequency distribution of the sample (see MEYER 1984, Fig. 7) or the low ratio of this deviation type (1:100). Indeed, it is doubtful whether most non-fissiparous species can survive once the oral nerve ring is severed (HYMAN 1955). However, the robust and heavily plated *O. gagnebini* (Type IIc) appears to have been able to carry out regenerative repair, to a similar extent as regrowth after fission, when half the disc was removed, perhaps by a predator. *A. filiformis*, on the other hand, while capable of regenerating arms and the entire disc cap containing stomach and gonads, does not survive once the oral ring is severed.

The authors argue that genetic or ontogenetic causes create(d) symmetry deviation at a low population rate in both of these living and fossil ophiuroids. The repair of predation or other tissue damage also causes some superficial symmetry abnormality. We consider that *Ophiomusium gagnebini* (THURMANN) is the first reported case of disc regenerating ability from a severed oral ring in fossil ophiuroids. It would be interesting to know if living, heavily plated ophiurids have the same regenerative capacity.

Acknowledgments

We would like to thank John Gage for his willing co-operation with examples of *Ophiomusium lymani* from the Rockall Trough; Stuart Burley, Bern, for the corrections of the English manuscript of one of us (C.M.); Andy Werthemann for the photographs of the fossil ophiuroids and the Atelier Imhof, Olten, for donating the fossil specimens to the Museum of Nature, Solothurn.

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Manuscript received and accepted 20 June 1987