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Inferring the developmental basis of the sea star abnormality "double ambulacral groove" (Echinodermata: Asteroidea)

Inferencia sobre la base de desarrollo en estrellas de mar de la anormalidad "doble surco ambulacral" (Echinodermata: Asteroidea)

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ABSTRACT

Very rarely a ray of a sea star is unusually wide and has two parallel ambulacral grooves that extend to a single tip. Such a ray has two terminal plates that are coalesced laterally. This abnormality is inferred to develop as a rare result of regeneration because it is recorded from a species with obligate asexual reproduction (fission and regeneration of halves; no gametes). This conclusion is supported also by an example where the abnormality affects only the distal third of a ray.

Key words: Echinodermata, Asteroidea, regeneration, teratology, symmetry.

RESUMEN

Muy raramente un rayo de estrella de mar es desproporcionadamente ancho y tiene dos surcos ambulacrales paralelos que se extienden hasta su único extremo. Dicho rayo tiene dos placas terminales que coalecen lateralmente. Se ha inferido que esta anormalidad se desarrolla como un resultado raro de regeneración, porque se describe de una especie con reproducción asexual obligada (fisión y regeneración de mitades; no gametos). Además, esta conclusión se sostiene por un ejemplo de anormalidad que afecta sólo el tercio distal de un rayo.

Palabras clave: Echinodermata, Asteroidea, regeneración, teratología, simetría.

INTRODUCTION

The rays of sea stars possess on their underside an ambulacral groove or furrow that is bordered by adambulacral plates. The groove is the underside expression of an A-frame arch formed by ambulacral plates that sit upon the adambulacral plates. Within the groove are the tube feet, the radial nerve and the radial water vessel. Movable spines on the adambulacral plates cover or uncover the groove (furrow spines).

Very rarely a sea star is found that has two ambulacral grooves that run parallel to each other in a single ray (Fig. 1). The number of instances of this abnormality that have been reported is so few that they can be recited. Fisher (1945:296) commented that "Although I have examined sea stars in almost galactic numbers, I have never before encountered these deviations from the normal." Three new reports are mentioned here. The question asked in this paper is whether this abnormality is 'congenital' and arises at the time of metamorphosis, or whether it arises later as the result of injury and regeneration. Ordinarily this question is very difficult to answer, but in this instance there is unexpected collateral information that allows a strong inference that it is the result of regeneration.

CASE HISTORIES

Lutken (1873:329): "Of *Asterias problema* (Steenstrup, 1855) [=*Stephanasterias albula* (Stimpson 1853)] I have examined several hundred specimens obtained from Greenland by Prof. Steenstrup, and noted the characters of about half of them. It is extremely rare to meet with five-armed specimens of this species. ...The appearance of five arms arises sometimes from the union of two arms; the double ambulacrum explains this apparent reduction of the arms. ...The great majority are furnished with six arms, three of which, on one side, are shorter and in all respects less developed than the others..."

Ganong (1890:54): "Monstrosities which are the result of fusion of parts. We have seen but one instance of this, a specimen of *Asterias vulgaris* Verrill, 1866, in the collection of Mr. Van Vleck in which two arms are distinctly united throughout their length, showing two separate ambulacral furrows with a line of adambulacral plates and spines between."

Fortin (1901:121): "Among a large quantity of *Asterias rubens* Linnaeus, 1758, on the beach of Sainte-Adresse, 27 October 1900, I collected a specimen which has only four apparent rays, of which one is bifurcated. But the ray that is bifurcated is double, meaning that it is formed of two rays coupled laterally and intimately soldered throughout their length, a fact that is easy to see

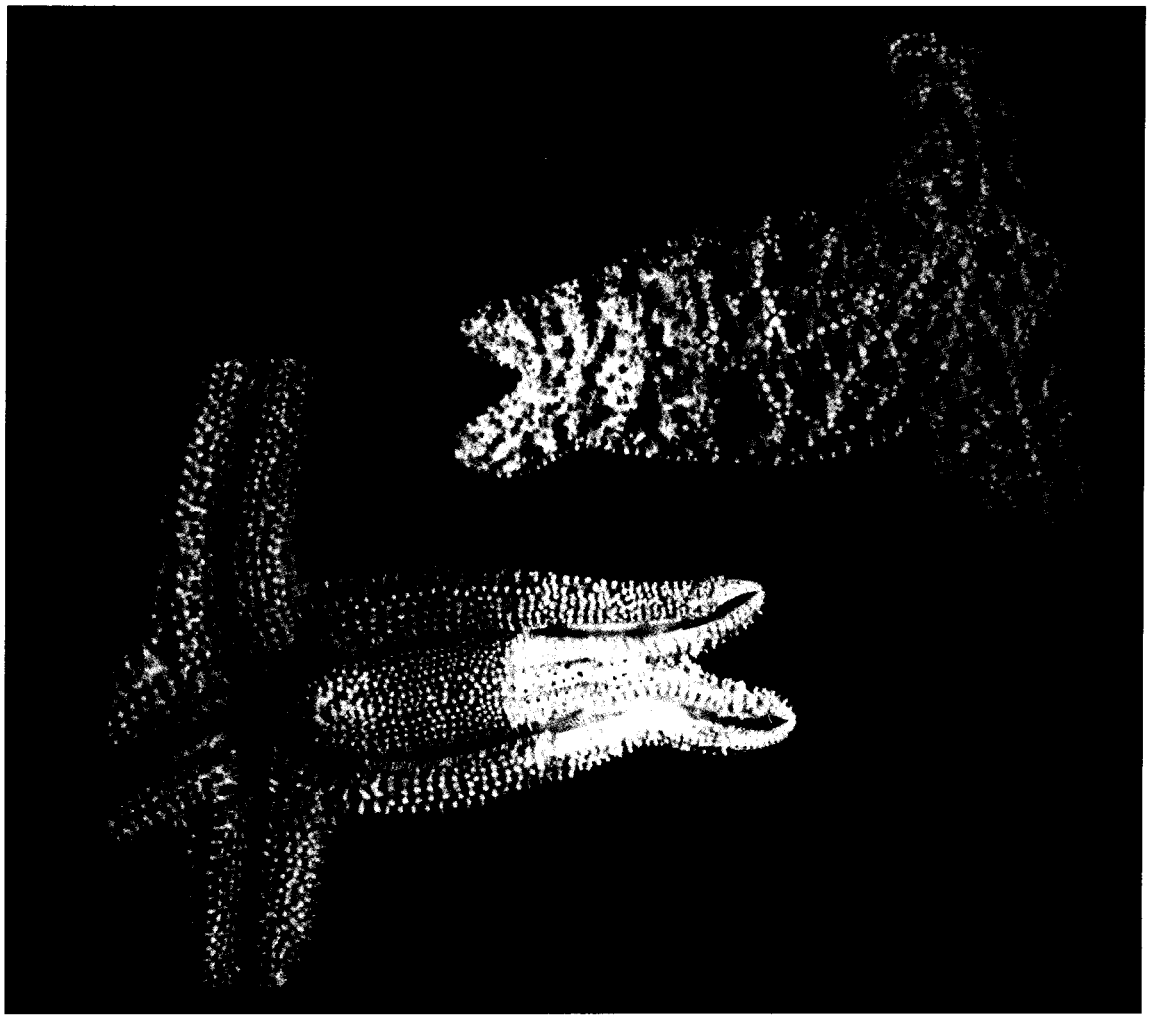

Fig. 1. Pisaster ochraceous segnis Fisher 1926. Photograph of the specimen described by Fisher (1945). The parallel ambulacral grooves indicate that the terminal plates were coalesced for most of the growth of the ray. The two tips on this ray most likely indicate a subsequent injury to the tip of the ray. Following the injury, regeneration of a separate terminal plate for each groove would initiate the growth of two ray tips as seen here. The major radius of the double ray, measured from the center of the mouth to the tip of the longer of the two ambulacral grooves, is R = 74mm. [U.S. National Museum No. E 6607, southern coast of California, probably near San Pedro, Compton Junior College/A.E. Blagg]

Pisaster ochraceous segnis Fisher 1926. Fotografía de el espécimen descrito por Fisher (1945). Los surcos ambulacrales paralelos indican que las placas terminales coalecieron durante la mayor parte del crecimiento del rayo. Las dos puntas sobre este rayo probablemente indican una herida subsecuente a la punta del rayo. Luego de la herida, la regeneración de una placa terminal para cada surco iniciaría el crecimiento de dos puntas de rayo tal como se observa aquí. El radio mayor del rayo doble, medido desde el centro de la boca hasta la punta más larga de los surcos ambulacrales, es de R = 74mm. [U.S. National Museum No. E 6607, costa sur de California, probablemente cerca de San Pedro, Compton Junior College/ A.E. Blagg]

by noticing on ventral surface the two ambulacral furrows of this double ray. In fact, the bifurcation in our example is composed of three rays, one free and two fused laterally. In addition, in the angle of two of the normal rays one can see also another very small ray which is commencing to grow, from which it follows that the total number of rays in this specimen, which appeared at first sight to possess only four rays, is in reality seven rays.

Mortensen (1910:268 and pl. 13 fig. 1): "In a specimen of *Stichaster albulus* (Stimpson, 1853) (=*Stephenasterias albula*) from Station 58, Danmarks Havn, 10 August 1907, 0-10m depth, two of the larger arms are coalesced nearly in their inner half length, the ambulacral furrows remaining separate (pl. 13 fig. 1); another specimen from the same station shows a similar concrescence, but to a smaller extent." (These may not be true examples of 'double ambulacral groove' because we cannot be sure from the description that the two ambulacral grooves run parallel in the coalesced region. If the grooves diverge throughout the coalesced region, then these are 'ray pair' abnormalities (Hotchkiss 1979)).

Clark (1920:77), *Eremicaster vicinus* (Ludwig 1907): "One specimen has the terminal third of a ray curiously doubled; seen from above, the abnormal width with the two terminal plates, coalesced along their inner margins, are striking; on the lower surface there are two distinct ambulacral furrows, each with six or seven pairs of tube feet."

Davenport & Davenport (1921:251-252): "Abnormalities are frequently found among starfishes, — partly on account of their capacity for regeneration, even from the disk and a single arm. Thus one may find a starfish with three or four rays, or with a small ray between normal-sized ones. Not all abnormalities seem to be the result of mutilation, however; for example, sometimes two arms seem to be fused (Fig. 241)." Fig. 241 caption: "Abnormal starfish (*Asterias*), apparently produced by fusion of two rays" *A.*(*forbesi* (Desor 1848)). The specimen has four rays of equal length; one ray is much wider than the three other rays; the wide ray seems to have two terminal plates.

Guibé (1940:510-512 and fig. 1.III): "*Asterias rubens* L. (Le Quilhot , a rock ledge exposed only at extreme low tides, August 1939). This sea star, of small size (diameter 65mm), possesses only four rays. One among them is remarkable for its size. It is clearly wider than the others; its width, measured at its base, is 15.5mm, while that of the other rays is only 11mm. The dorsal surface of this specimen offers nothing of note; it is not the same for the ventral surface where one finds the existence of two independent ambulacral furrows in the abnormal ray. These furrows are separated one from the other by a zone of spines of which the width is clearly double that of the analogous zones that border the furrows exteriorly. One notes as well the presence of two ocelli at the extremity of the ray. On dissection I established that the arrangement of the internal organs corresponds to that which is found in a normal ray. There are only two gastric caeca; however, at the base of the canal of one of the caeca, on its internal border, there is a small unpaired caecal bud. Therefore it is difficult to decide if the disposition of these organs represents the state of a normal ray or if it is due to an anomaly of development. Whatever the case, it probably is true that this malformation is the result of the fusion of two primordia during development; the abnormal ray should be interpreted as a double-ray."

Fisher (1945:296-298 and Fig. 3), *Pisaster ochraceous segnis* Fisher, 1926: "In the specimen shown (see Fig. 1 herein) (U.S. National Museum No. E 6607) the rays have fused nearly to the tip along the lateral part of the abactinal surface. The dorsal surface of the fused rays has two series of carinal spines, the space between which is equal to about half width of the two other dorsolateral areas. The superomarginal plates of the fused halves as well as the inferomarginal, are on the ventral surface and are in somewhat less regular alignment than normally. While on the outer halves of the fused rays there are three series of actinal plates, on the inner halves there are but two. Along the middle of the ventral surface between the two series of superomarginals is a narrow area of irregular plates, carrying spines very similar to the superomarginal spines, which must be reckoned as part of the abactinal system. The coelomic cavity of the two rays is in perfect continuity, and there is only one pair of hepatic caeca".

In December 1974 Sergeant Reg. Berger informed me of an abnormal specimen of South African sea star (not identified) with five rays, "one arm splitting about two-thirds of the way into two points ... the split arm has two ambulacral grooves running parallel until the arm splits where they also split, one for each point". In November 1978 a student at Lehigh University received a specimen of *Asterias forbesi* for dissection that was found to have a double ambulacral groove. The specimen had five rays, one of which was wider than the others, and had two ambulacral grooves; thus this individual had six ambulacral grooves; the terminal plates were fused. In January 1979 James F. Clark collected

an *Asterias vulgaris* in the harbour of Marblehead, Massachusetts, that had four rays, one ray being wider and having two ambulacral grooves; the terminal plates were fused.

ANALYSIS

From the descriptions it can be deduced that as long as the two terminal plates remain coalesced along their inner margin, the ambulacral grooves are kept parallel and there is just one tip to the 'double ray' (the specimens of Lutken 1873, Ganong 1890, Clark 1920, Davenport & Davenport 1921, Guibé 1940, J.F. Clark and Lehigh University). If the two terminal plates cease to be coalesced there will develop two tips to the ray (the specimens of Mortensen 1910, Fisher 1945 and Sgt. Berger) (see Fig. 1). If one of the grooves bifurcates forming a branch that has its own terminal plate there will also be two tips (the Fortin 1901 specimen). Except for *Eremicaster vicinus* (Porcellanasteridae) and the unidentified South African specimen, all of the examples belong to the family Asteriidae. Six of the eleven cases are Atlantic species of *Asterias*, perhaps only reflecting the abundance of these species around the marine laboratories of Europe and New England.

Stephanasterias albula is a species that undergoes fission through the disk and subsequent regeneration of the halves. A minority of specimens are 5-rayed and may not show evidence of fission and regeneration, but the vast majority of the specimens ever collected do indeed show evidence of fission and regeneration and a variable number of rays. This information suggests that perhaps fission and regeneration is linked to the appearance of the abnormality "double ambulacral groove" in *S. albula*. The suggestion is confirmed (strong inference) by the reports that *S. albula* is strictly asexually reproducing and does not produce gametes for sexual reproduction (Thorson 1936, Mladenov et al. 1986, Clark & Downey 1992:454). It follows that *S. albula* does not pass through larval development and metamorphosis. Accordingly, this excludes the possibility that the abnormality 'double ambulacral groove' in *S. albula* developed at the time of metamorphosis. Likewise, the 'double ambulacral groove' in the distal third of the ray of *Eremicaster vicinus* did not develop at metamorphosis. It is plausible to generalize from this finding to infer the developmental basis of the sea star abnormality 'double ambulacral groove.'

DISCUSSION

This research relates to theories on the number of ambulacra/rays in sea stars (Hotchkiss 1998a,b, in press). Specimens that have five ambulacral grooves but only four evident rays do not conflict with the idea that the number of rays/ambulacra in sea stars is limited to five (no more than five). Here we are speaking of the five primary hydrocoel lobes that arise at metamorphosis. However, specimens that have six ambulacral grooves and only five evident rays conflict with the proposition that the number of rays/ambulacra is strictly limited to five primary hydrocoel lobes at metamorphosis. The conflict is resolved when it is understood that the abnormality 'double ambulacral groove' does not arise during metamorphosis. The strong inference is that this abnormality arises as the result of injury and regeneration.

Referring now to other classes of echinoderms, a 'doubled ambulacra' abnormality has been noted in blastoids (Macurda 1980, Horowitz et al. 1986). Such specimens have five radials (apparent pentameral symmetry) or four radials (apparent tetrameral symmetry) and have two ambulacra in one of the radial sinuses. The ambulacra may be completely doubled with two entire sets of food grooves and four sets of side plates, or they may exhibit aborted features of one side, such as shortened side food grooves. The structure of echinoids can be described as one in which five 'rays' are coalesced but without the ocular plates being fused. Although the columns of plates of the echinoid test are called ambulacra and interambulacra, they are homologous with the ambulacral and adambulacral ossicles of sea stars (Mooi & David 1997). As a rare abnormality two ambulacral areas may occur side by side, not separated by an interambulacral area. At the head of such double ambulacra in some specimens there is a 'twin ocular' without indication of suture; in other specimens there are two oculars that are in contact (Jackson 1927:515, 517, 550). I conjecture that the developmental basis of the double ambulacra in blastoids and echinoids is likely to be the same as in asteroids.

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