

The sequence of origin of the postmetamorphic rays in *Heliaster* and *Labidiaster* (Echinodermata: Asteroidea)

Origen secuencial de los rayos postmetamorficos en *Heliaster* y *Labidiaster* (Echinodermata: Asteroidea)

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ABSTRACT

Postmetamorphic rays in *Heliaster* and *Labidiaster* originate in four 'quadrants' between the five primary rays, and not normally in the madreporic interradius. The rays originate in one of two very definite sequences depending on the species. *H. kubiniji* and *H. multiradiatus* share one sequence, whereas *H. canopus*, *H. helianthus* and *Labidiaster* share the other sequence. *Pycnopodia*, *Rathbunaster*, *Heliaster* and *Labidiaster* add rays at far greater sizes and in a manner that is distinctive from other multiradiate starfish, possibly indicating a new taxonomic unit.

Key words: Echinodermata, development, symmetry, *Heliaster*, *Labidiaster*.

RESUMEN

Los rayos post-metamórficos en *Heliaster* y *Labidiaster* se originan en cuatro "cuadrantes" entre los cinco rayos primarios, y no como ocurre normalmente en el interradio del madreporito. Los rayos se originan en una de dos secuencias definidas, dependiendo de la especie. *H. kubiniji* y *H. multiradiatus* comparten una secuencia, mientras que *H. canopus*, *H. helianthus* y *Labidiaster* comparten otra secuencia. *Pycnopodia*, *Rathbunaster*, *Heliaster* y *Labidiaster* adicional rayos de tamaños mucho mayores y de una manera que es distintiva de aquel de otras estrellas de mar multiradiadas, posiblemente indicando su pertenencia a una nueva unidad taxonómica.

Palabras clave: Echinodermata, desarrollo, simetría, *Heliaster*, *Labidiaster*.

Santiago, March 9, 1976

I did in fact investigate the origin of new, postmetamorphic rays in *Heliaster* during a residence at the MCZ [Museum of Comparative Zoology, Harvard University], back in 1958-59. I was led to this on finding a specimen of *H. helianthus*, in Chile, with several small rays regularly spaced every third large ray. Reviewing the literature, HL Clark's (1907) conclusion that rays originate with no definite order seemed untenable, in view of my specimen. Yet it took me a long time and the examination of very many specimens before I came to the answer, for the sequence is not simple. I reported my findings in seminars and lectures at several universities in the USA at that time (see: Emery Swan's comment on page 410 of Boolootian's Physiology of Echinodermata) (Swan 1966, Boolootian 1966) and I presented a formal account at the 1st. Chilean Zoological Congress in Santiago, September of

1960. As things are in this part of the world, the Proceedings of this Congress were never published completely and my report has remained unpublished so far. I myself became involved in other projects, which prevented me from preparing a text to be published elsewhere. Moreover, I was hopeful at that time to make a sizable collection of really young specimens in order to settle one final question which had remained unanswered, in spite of the collections I had examined in the USA - including one I left at the MCZ - which were mostly of large or medium size *Heliaster*. It turned out that very small specimens are difficult to find in large numbers and it is only after years of field work that I have of late come across a 'nursery ground' which has provided the material necessary for the purpose. So I am now back to this research and giving the final touches to my manuscript.

The sequence of origin of postmetamorphic rays is not simple in *Heliaster*, being 'obscured'

* Passed away on February 23, 1999. This paper was edited by Frederick H. C. Hotchkiss, 26 Sherry Road, Harvard, MA 01451 USA, from two letters.

by at least two factors: individual variability and regeneration of rays. Yet I will try to provide you with the core of the answer, in anticipation of the full story.

1. HL Clark (1907) was correct in assuming that new rays originate in four of the original interradial spaces (A-B, B-C, D-E, E-A) and not normally between the original rays C and D, the five original rays being those with gastric muscles (rays are lettered such that the madreporite is between rays C and D). He was also correct that certain territories or quadrants have different activity rates, in that new rays appear earlier and/or grow faster in some of the original interradial spaces, as illustrated in his plate no. 8. It is my conviction that Clark was mistaken in concluding that rays originate in no definite order in those four interradial spaces. Furthermore, it seems to me that the 'gradients' of new-ray-growth found by Clark in *H. kubiniji* (his plate 8) do not hold alike for all the species of the genus.

2. New postmetamorphic rays originate in very definite sequences in the original interradial

spaces A-B, B-C, D-E and E-A but, surprisingly enough, the sequence is not exactly the same in all *Heliaster* species. In *H. kubiniji* and *H. multiradiatus*, the sequence is the same as described by Ritter & Crocker (1900) for *Pycnopodia helianthoides*, but in these *Heliaster* species the process occurs in four regions, as mentioned. In all the other species (including *H. canopus*, which grows up to some 25 rays, as do *H. kubiniji* and *H. multiradiatus*), the sequence is another. I trust the difference can be easily grasped on examining the illustration from my manuscript which is enclosed (Fig. 1). As this illustration shows, the 'age' of the rays can be recognized by their differences in length (very small rays not shown there) and also by the alignment of the marginal aboral spines in the proximal portion of rays, even if of equal size. New rays are numbered 1, 2, 3 in this figure, implying the order of their appearance in each original interradial space (B-C in this figure); first one grows, then pairs, but this last statement requires qualification (see below).

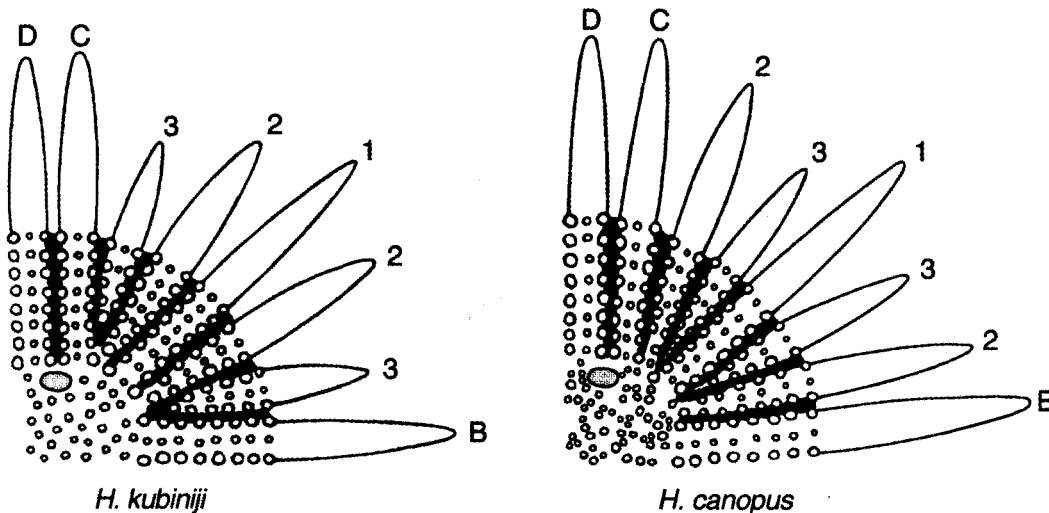


Fig. 1. The two sequences of origin of rays in *Heliaster* in aboral view. The C-D madreporitic interradius does not develop postmetamorphic rays. For simplicity the ray addition is shown for only the B-C 'quadrant'. New rays are numbered in the order of their appearance. First one ray grows, then pairs, so the numbering is 1, 2 (twice), 3 (twice). In *H. canopus* (right side of Fig. 1) new rays 3 arise between the two most recently formed rays 2 and 1. In *H. kubiniji* (left side of Fig. 1) new rays 3 arise between the most recently formed rays 2 and the adjacent primary rays B and C. The new rays can be recognized by the alignment of the marginal aboral spines in the proximal portion: toward the disk their full development is blocked by the preexisting rays.

Drawing by Prof. Sanchez, prepared for publication courtesy of Dr. Rich Mooi.

Las dos secuencias de origen de rayos en *Heliaster* en vista aboral. El interradio madreporítico C-D no desarrolla rayos postmetamórficos. Para efectos de simplicidad se muestra la adición de rayos sólo para el "cuadrante" B-C. Los rayos nuevos están numerados en orden de aparición. Primero crece un rayo, luego en pares. Así, la numeración es 1, 2 (doble), 3 (doble). En *H. canopus* (derecha de Fig. 1) el nuevo rayo 3 apareció entre los recientemente formados rayos 1 y 2. En *H. kubiniji* (izquierda de Fig. 1) el rayo nuevo 3 apareció entre el rayo 2 recientemente formado y el rayo primario adyacente B y C. Los rayos nuevos pueden ser reconocidos a través de la alineación de las espinas marginales aborales en la porción proximal: hacia el disco su desarrollo pleno es bloqueado por los rayos pre-existentes.

Dibujos por Prof. Sánchez, preparados para publicación por la cortesía de Dr. Rich Mooi

3. In *H. kubiniji*, *H. multirariatus* and *H. canopus*, three 'generations' of new rays growing in four of the quadrants bring the total number of rays to 25, which is the 'normal' for these species. Yet further rays can grow and they normally appear according to the pattern of each of the species; that is, in the angle between the youngest pre-existing rays and the originals (A,B,C..) in *H. kubiniji* and *H. multiradiatus*, whereas they appear between the two youngest rays of each quadrant in *H. canopus*. More than three 'generations' of new rays are needed to complete the process in all the other species, and they grow following the pattern described for *H. canopus*. A fourth generation of 8 new rays brings the total number of rays to 33; a fifth generation, to 41. Yet these 'final' numbers also require qualification.

4. Several qualifications are required in order to fully describe what occurs in each individual specimen. The most important is this: the schemes or patterns previously described indicate the relative position of subsequent 'generations' of new rays in each of the four interradial spaces A-B, B-C, D-E and E-A, for the two groups of species, but they do not imply that the members of each generation are strictly synchronous in their appearance, neither within nor between quadrants. In fact, there are cases where all rays of a given generation are of about equal size, smaller than the rest; these cases are rare but such was the specimen mentioned above which put me on this problem. In most cases, one member of a pair or generation is notably smaller, or even absent, in a quadrant and the smaller - or absent - member may be any of the pair. As recalled, Clark found that normally the process of ray multiplication is more advanced in some quadrants than in others and as mentioned, I have evidence indicating that these 'gradients' differ in both groups of *Heliaster* species. At any rate, what occurs in any one specimen is that one quadrant may, for example, be producing rays of 2nd. generation while another quadrant may have some of 3rd. or 4th. As a consequence of this variability, it is infrequent to find specimens, even with the same total number of rays, that are exactly alike in the position of their new rays and in the relative length of these. I have no indications as to differences in growth rates in different quadrants nor in different generations of new rays, which would certainly complicate things. Assuming no such difference is the simpler hypothesis but, even so, the variability observed in new ray appearance would seem to contradict my conviction of a definite sequence in specimens as a whole (beyond the sequence within each quadrant, illustrated in my figure). This conviction stems from my previous

observations, but could not be proven with the samples then available, large as they were. I trust that statistics of large samples of small specimens, as now available, will enable a solution to the question. This should also settle the question of differences in growth gradients in *Heliaster* species-groups.

5. Regeneration of rays is a frequent event in *Heliaster*. It can involve larger or smaller fragments of isolated rays, or of two or three adjacent rays, or it can involve the whole length - from their origin in the disc proper, on the aboral side - of a series of adjacent rays as shown in the photograph enclosed (Fig. 2). This last feature is in the literature but it is only recently known that it is due to autotomy in *Heliaster*. Dr. Carlos Antonio Viviani, a young colleague and former associate of us has found that *H. helianthus* reacts thus to the predation by the voracious Chilean sea star *Meyenaster gelatinosus*; a clever adaptation indeed! (see Viviani 1978). At any rate, with experience, regenerating rays can be distinguished from truly new ones, so this is no major confusing

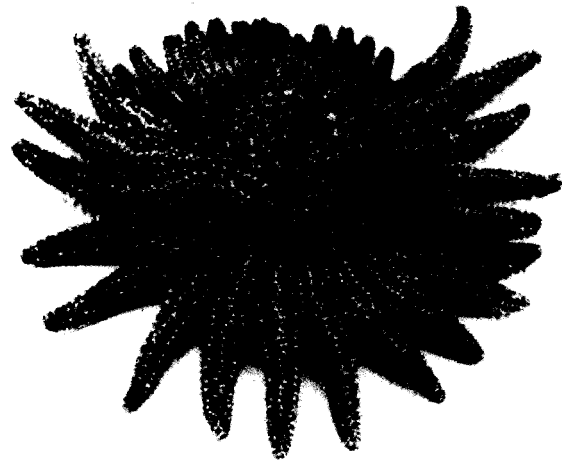


Fig. 2. Regeneration of 13 rays following autotomy from their origin in the disk proper. An inhibitory effect of regeneration could partly account for the intraspecific variation in the final number of rays in these species. *H. helianthus*, colección de la Sala de Sistemática No. 5446/1. R = ca. 45mm; 31 rays.

Photograph by Prof. Sánchez, prepared for publication courtesy of Mark Reilly.

Regeneración de 13 rayos a continuación de una autotomía desde el origen en el disco. Un efecto inhibitorio de regeneración podría dar parcialmente cuenta por la variación intraespecífica en el número final de rayos de estas especies. Colección de *H. helianthus* de la Sala de Sistemática N°. 5446/1. R= ca. 45mm: 31 rayos. Fotografía de Prof. Sánchez, preparada para publicación por cortesía de Mark Reilly.

factor in tracing back the history of origin of rays in a specimen with regeneration. But what can be important is that regeneration seems to inhibit the process of new ray appearance, at least in its vicinity. Yet this can only be proven by experiments, which I expect to do now that we have sea-water aquaria in our laboratory.

6. It is known that different species of *Heliaster* attain different numbers of rays, these being centered around ± 25 rays (*H. kubiniji*, *H. multiradiatus* and *H. canopus*) and ± 35 rays (all other species), yet with high intraspecific variability. It is also known that the origin of new rays diminishes in frequency with increasing size. There is a correlation between size and number of rays, which is different in the different species, and usually with very high dispersal (my data). The result is that beyond a given size, no further new rays arise, the individuals remaining with as many as could grow 'in time'. How much of this is due to genetic variability (for 'number of rays'), or to growth rates (genetically or environmentally controlled), I do not know. But it does seem possible to me that an inhibitory effect of regeneration, which is common in *Heliaster*, could partly account for the observed individual, intraspecific variation in the final number of rays in these species.

7. May I finally add that the resemblances between the patterns of new ray growth in *Pycnopodia helianthoides* and some *Heliaster* species seem to me of some significance, for I have good evidence that other multiradiate forcipulate sea stars (*Labidiaster*, *Rathbunaster*), also increase in number of rays by the same patterns as found in *Heliaster*. But that is another story.

Santiago, June 26, 1976

I have been in Uruguay, Brasil and Argentina for the last three months. I have returned recently to Santiago but only for a few days, on my way to Panama and México, from where I shall return in mid-August and remain here, to finish the *Heliaster* study. So I shall now comment only on some points.

My use of letters C and D for the rays between which occurs the madreporic plate follows Hyman's (1955) explanation of Carpenter's system. I was not aware of Moore & Fell's (1966) discussion and am grateful to learn about it. I have not checked on the position of the anus in *Heliaster*, and it seems, from my recollection,

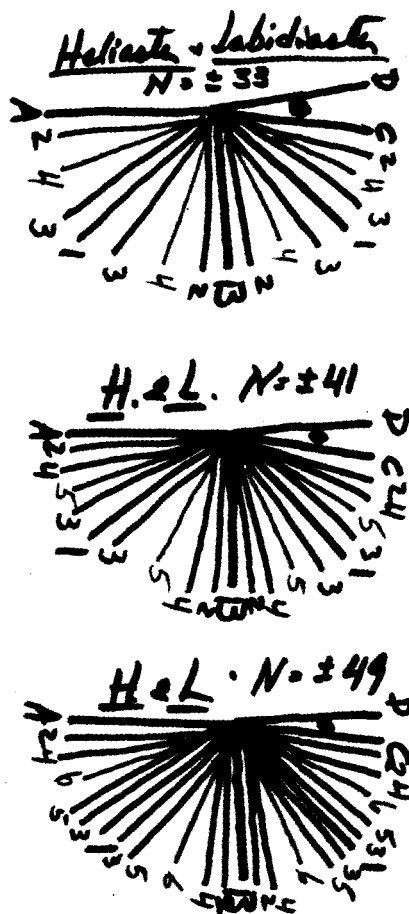


Fig. 3. Continuation of the sequence of origin of rays in *H. helianthus* and in *Labidiaster annulatus* in aboral view. Upper: 4th generation rays arise between 2nd and 3rd generation rays. Middle: 5th generation rays arise between 3rd and 4th generation rays. Lower: 6th generation rays arise between 4th and 5th generation rays. The total number of rays if all four quadrants are at the same 'generation' is $5 + 4\{1 + (N-1) \times 2\}$. Red = newest pairs of rays. Blue = previous pairs of rays. Black = primary rays and first (unpaired) supernumerary rays.

Original drawing from Prof. Sanchez, prepared for publication courtesy of Mark Reilly.

Continuación de la secuencia de origen de rayos en *H. helianthus* y en *Labidiaster* en vista aboral. Arriba: cuarta generación de rayos que se originan entre la segunda y tercera generación de rayos. Medio: quinta generación de rayos que se originan entre la tercera y cuarta generación de rayos. Abajo: sexta generación de rayos que se originan entre la cuarta y la quinta generación de rayos. El número total de rayos, si los cuatro cuadrantes son de la misma generación, es $5 + 4\{1 + (N - 1) \times 2\}$. Rojo = el par más nuevo de rayos formados. Azul = el par previo de rayos. Negro = rayos primarios y primer (no pareado) rayos supernumerarios.

Dibujos originales de Prof. Sánchez, preparados para publicación con la cortesía de Mark Reilly.

that it would be difficult to relate it to interradial spaces for it is small and central on the disk, but I shall try to determine this.

The news that *Acanthaster* also produces post-metamorphic rays is also new to me; I was unaware of Yamaguchi's (1973) research and my examination of figures of *Acanthaster* in the literature had convinced me that small rays in this genus were due to regeneration. The news is somewhat of a disappointment, for I was in the belief that only some isolated families of Forcipulata showed this feature (*Pycnopodia*, *Rathbunaster*, *Heliaster* and *Labidiaster*), which could have made a good case for a new taxonomic unit. *Acanthaster* lacks the first, unpaired ray which is present in *H. canopus* in each of the four quadrants that produce new rays (number 1 in Fig. 1). Furthermore, the next new rays in sequence, which are in pairs (2-2, 3-3, in Fig. 1), do not bear the same positional relations in *Acanthaster* and *H. canopus*.

The following diagram Figs. 3 & 4, continues the process beyond my drawing Fig. 1 of *H. canopus*. Such continuation occurs in *H. helianthus* and in other species with high numbers of rays but of the same pattern. It seems to me that

this *H. canopus* pattern does not occur in any of the genera that have been previously studied, but I am glad to be able to confirm now that *Labidiaster* also shares this same pattern. In fact, during my recent visit to Argentina I was able to examine a satisfactory collection of *L. annulatus* from Antarctica, which provided the evidence for the previous statement.

As to the evolution of the different patterns, I am unable to choose between alternative hypotheses. A switch from one to another pattern in species that are morphologically and ecologically so similar as the different *Heliaster* species seems to me as unlikely as their independent origin. We would have to know more about the genetic and developmental basis of these events. The conjecture that polymerism first developed in one interradius and then extended to others, makes sense it seems to me, but what excludes the possibility that the process could have been generalized to start with, and secondarily restricted to the anal interradius? Further knowledge on gradients between quadrants may contribute to the question. Also, of course, knowledge on the case in fossil multiradiate asteroids.

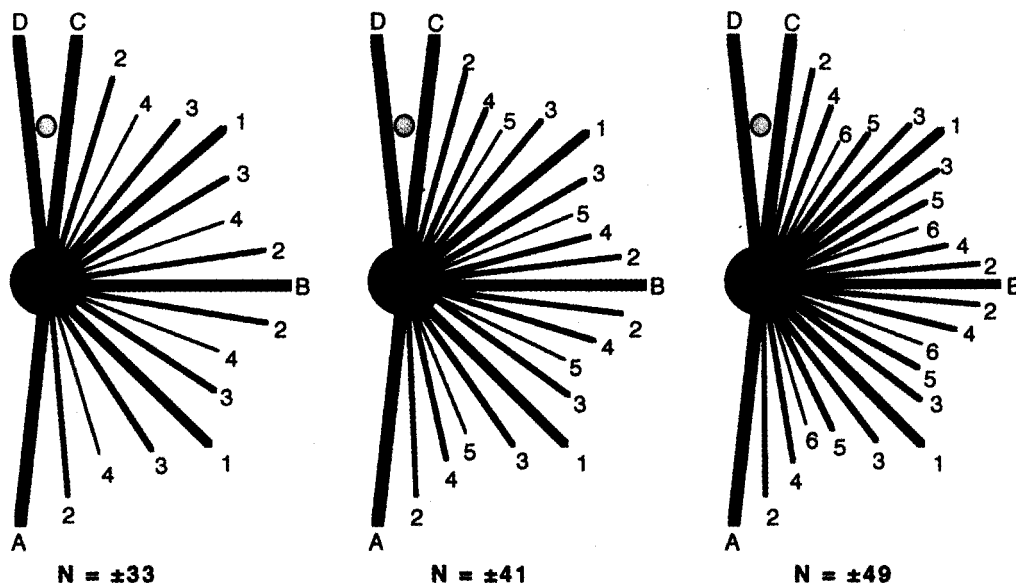


Fig. 4. Same information as Fig. 3. In this schematic drawing the lengths of the rays are varied to correspond to the 2nd, 3rd, 4th, 5th and 6th generation of the ray. In life the lengths of the rays are of essentially equal.

Drawing and artwork courtesy of Dr. Rich Mooi.

La misma información que en Fig. 3. En este dibujo esquemático la longitud de los rayos han sido variadas y corresponden a la segunda, tercera, cuarta, quinta y sexta generación de rayos. En la realidad la longitud de los rayos son esencialmente iguales.

Dibujos y trabajo artístico por cortesía de Dr. Rich Mooi.

Editor's explanation and postscript

The text of this posthumous paper was transcribed with minor editing from letters written by Prof. Sanchez to FHC Hotchkiss. Copies of the original correspondence are in the possession of JC Castilla and FHC Hotchkiss. The species mentioned are attributed to the following authors (see Madsen 1956, Maluf 1988): *Heliaster kubiniji* Xantus 1860, *H. multiradiatus* (Gray 1840), *H. canopus* Perrier 1875, *H. helianthus* (Lamarck 1816), *H. cumingii* (Gray 1840), *Pycnopodia helianthoides* (Brandt 1835), *Meyenaster gelatinosus* (Meyen 1834), *Labidiaster annulus* Sladen 1889. Prof. Sánchez was correct that undersized rays in *Acanthaster* are due to regeneration in specimens larger than approximately 20mm overall diameter. In *Acanthaster* the supernumerary rays form only while it is at a very small size, attaining 16 to 18 rays when only 12mm overall diameter. It was an insight of Prof. Sanchez to regard it significant that other multiradiate forcipulate starfish (*Labidiaster*, *Rathbunaster* and *Pycnopodia*) increase in number of rays by the same patterns as found in *Heliaster*. This argument for a new taxonomic unit is still intact today. The discovery by Prof. Sánchez that *Labidiaster* follows the same pattern as *Heliaster* and adds posmetamorphic rays in just four quadrants gives a probable explanation for the color pattern of *Labidiaster* that is seen in undersea photographs published by Dearborn et al. (1991). The color pattern has four distinctive dark quadrants that separate what must be deduced to be the five primary rays, with a primary ray on each side of the madreporite. AH Clark (1939) described an *H. cumingii* with new ray buds that tunnel from the oral to the aboral surface of the disk to take their places between preexisting rays. Although *Heliaster* is distributed at present only on parts of the eastern Pacific shoreline, fossils of *Heliaster* were found in the Pliocene of Florida (Jones & Portell 1988). The relationship between number of rays and body size diameter in *H. helianthus* based on a large sample was graphed by Tokeshi et al. (1989: Fig. 2). Hotchkiss (in press) undertakes a new analysis of the developmental basis that underlies the number of rays in starfish; that paper is dedicated to the memory of Prof. Sánchez. FHC Hotchkiss. Thanks Rich Mooi, Mark Reilly, JC Castilla, John Lawrence, John Dearborn, Cecelia McIsaac and Anita Hotchkiss for assistance, literature and data.

Invited Editor J.C. Castilla

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