On the Number of Rays in Starfish

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SYNOPSIS. Multiradiate starfish evolved independently in fourteen living families. Twenty living families are strictly 5-rayed. The FIVE-PLUS hypothesis is that supernumerary rays develop separately from the five primary rays. The ontogeny of the primary rays is proposed to be highly integrated ("en bloc" hypothesis), closely timed (synchronic hypothesis) and a developmental constraint ("tamper-proof" hypothesis). The "en bloc" hypothesis postulates that the five primary rays develop as a unit. The deep structure of this unit is believed to be a 2-1-2, BA-AB, organization. The synchronic hypothesis postulates that there is only a brief time at metamorphosis during which the "en bloc" pathway operates. There is a pause before the development of supernumerary rays. The "tamper-proof" hypothesis postulates that the "en bloc" pathway has no heritable variation and cannot be co-opted for the production of supernumerary rays. There is diversity of timing and pattern in the development of supernumerary rays. Postgeneration of rays in the rudiment and intercalary regeneration of rays in the imago are independent ray-producing pathways that may have been co-opted variously and recurrently in the multiple origins of multiradiate starfish.

INTRODUCTION

Aspects of echinoderm construction that are highly unique include the water vascular system, the calcite skeleton and catch connective tissue (Nichols, 1975; Emson, 1985; Motokawa, 1988; Welsch, 1998). Echinoderm rays form in association with the nervous system and the water vascular system. New investigations of the body plan of echinoderms are being made through studies of molecular genetics, comparative morphology, paleontology, development and metamorphosis (Davidson et al., 1995; David and Mooi, 1996; Lowe and Wray, 1997; Mooi and David, 1997, 1999; Popodi et al., 1998). Two current hypotheses are that echinoderm rays may be related to the "main body axis organization" of other phyla (Hotchkiss, 1998, pp. 421–423) or to appendages of other phyla (Raff, 1996a, b; Morris, 1999). The present study, however, does not depend on either of these hypotheses.

Pentamerism, or "five" as the predominant number of rays/ambulacra, appears to be a fixed attribute of echinoids and holothurians, but is not so definitely "fixed" in asteroids and ophiuroids. Variation in the number of rays in starfish has been the basis for two points of view concerning pentamerism. One viewpoint is that the number of rays intrinsically varies above and below five, and therefore restriction of the number of rays to five is a narrowing of the phenotype that needs explanation (such as by natural selection) wherever it occurs (Stephensen, 1967; Raff and Kaufman, 1983, p. 166; Dawkins, 1996, pp. 236–238). The other viewpoint is that the number of rays is intrinsically fixed at five, and therefore it is the deviations from pentamerism that need explanation wherever they occur (Hotchkiss, 1998, pp. 421–423).

Several hypotheses on control of ray number in development have been proposed. Raff and Kaufman (1983) described 3-, 4- and 6-rayed blastoids and 4-, 6- and 9-rayed edrioasteroids as "symmetry mutants" and indicated that a counting process was involved. Lawrence (1987b, p. 7) expressed the possibility that the pentamerous condition of the water vascular system might be "rigidly programmed into the developmental process." On the other hand,
Lawrence (1988, p. 597) described the “multiarmed condition” as “an example of phenotypic plasticity in that a basic characteristic of the group is variable.” and Lawrence and Komatsu (1990) discussed the number of rays in asteroids as examples of quantized and modal variation as defined by Maynard Smith (1960). Hotchkiss (1998a) took Lawrence’s (1987b) point of view that pentamerism is “rigidly programmed into the developmental process” as a working hypothesis and presented three sub-hypotheses as support: that the ontogeny of the primary rays is highly integrated (“en bloc” hypothesis), closely timed (synchronous hypothesis) and “tamper proof.” The “tamper-proof” hypothesis postulates that the “en bloc” pathway has no heritable variation and cannot be co-opted for the production of supernumerary rays.

The problem

How can we account for deviations from pentamerism if starfish are strictly limited to producing five primary rays (none beyond five)?

Possible solution: The FIVE-PLUS hypothesis

It is proposed that supernumerary rays develop separately from the five primary rays, by pathways that operate after the five primary rays have initially formed.

Basis for the hypothesis

In this paper the morphology, development and variability of supernumerary rays are reviewed first and found to be diverse. The imago can become multiradiate at the time of metamorphosis, or it can be 5-rayed at metamorphosis and add the supernumerary rays during post larval growth stages. The sequence and pattern of development of supernumerary rays differs among multiradiate starfish (Hotchkiss and Seegers, 1976, Lawrence and Komatsu, 1990). Second, the constancy of “five” in 5-rayed species and the etiology of aberrant ray number is reviewed. Lawrence and Komatsu (1990) showed that the control of ray number is very precise in 5-rayed species. Selective breeding for aberrant ray number is unsuccessful, producing only 5-rayed offspring (J. S. Pearse, personal communication). The findings are analyzed in the context of the FIVE-PLUS hypothesis of development of primary and supernumerary rays. It is noted that fissiparous and comet-forming starfish have entrained the regeneration pathway into their life cycle. In like manner, multiradiate starfish may have entrained regeneration or postgeneration pathways to develop supernumerary rays (post-generation terminology from Hörstadius 1973, p. 121).

Notation and terminology

In this paper the hydrocoel lobes of early metamorphosis are numbered 1 through 5 clockwise in oral view. Lobe 1 is at the dorsal end of the hydrocoel crescent. Lobe 5 is the terminal lobe on the ventral horn of the hydrocoel crescent. The brachiolar notch is between the ends of the hydrocoel crescent, hence between lobes 1 and 5. The same numbering but with Roman numerals was used by Gemmill (1912, 1916, 1920) and is retained herein when quoting Gemmill.

The five primary rays of the imago and adult are labeled using Carpenter letters A, B, C, D, E. Carpenter letters are assigned based on ray homologies with edrioasteroids (Hotchkiss 1995, 1998b). The anterior-posterior axis in edrioasteroids is the A-CD axis and corresponds (by deduction from echinoids) to the larval anterior-posterior axis. Ray A is anterior, and hydrocoel closure is in posterior interradius CD. In Luidiidae the madreporite is in interradius CD. In non-luidiid asteroids the madreporite is in interradius DE. In Figure 1 the primary rays are designated by Carpenter letters and the supernumerary rays by letter X or by numerals.

Review

Twenty living families of starfish are exclusively 5-rayed. Alphabetically they are the Archasteridae, Asterodiscididae, Asteropseidae, Astropectinidae, Benthopectinidae, Caymanostellidae, Chaetasteridae, Gonasteridae, Goniopectinidae, Korethasteridae, Mithrodiidae, Neomorphasteridae, Odontasteridae, Oreasteridae, Poraniidae, Porcellanasteridae, Radiasteridae, Sphaerasteridae, Xyloplacidae, and Zoroasteridae.
Nine families have both 5-rayed and multiradiate species: Asteriidae, Asterinidae, Echinasteridae, Ganeriidae (6-rayed Aleutia schafferi), Luidiidae, Myxasteridae, Ophidiasteridae (in the comet-forming species a percentage of individuals exceed five rays), Pedicellasteridae and Pterasteridae. Some genera have both 5-rayed and multiradiate species. Five families are exclusively multiradiate: Acanthasteridae (contains only Acanthaster), Brisingidae, Freyellidae, Heliasteridae (contains only Heliaster) and Labidiasteridae. The functional consequences of the multirayed state have been discussed by Verrill (1909, 1914, pp. 12–17), Lawrence (1987a, b, p. 13, 1988), Blake and Guensburg (1989), Lawrence and Komatsu (1990), Lawrence and Moran (1992), Blake (1993), and Pearse (1993).

Paleozoic multiradiate starfish were discussed by Blake and Guensburg (1989). Most Paleozoic starfish are strictly 5-rayed with only rare instances of aberrant ray numbers (Willard, 1926; Lehmann, 1957, p. 18). The oldest known multiradiate species is the Lower Silurian Lepidaster grayi. Devonian multiradiate starfish include Michiganaster inexpectatus with from 17 to 25 rays, Arkonaster topororum with 28 rays and Medusaster rhenanus with from 11 to 16 rays. Mississippian multiradiate starfish include Lacertasterias elegans with 19 or 20 rays and 10-rayed Schondoria fungosa. Michiganaster and Medusaster show an increase in ray numbers with size (Lehmann, 1957, p. 94; Kesling, 1971, p. 256; Lawrence and Komatsu, 1990). Blake and Guensburg (1989: Table 1, character 4) list five rays as the primitive character state and multiradiate as the derived character state. It is evident that there has been recurrent independent evolution of the multiradiate condition.

Aberrant ray number in 5-rayed species have been obtained experimentally under salinity stress (Watts et al., 1983; Marsh et al., 1986; Clark, 1988). The significance of this variation was pointed out by Marsh et al. (1986, p. 231): “If these levels of ray-number aberrancies do represent true genetic variability in the population, then selective pressures may influence ray number in the field.” However, breeding experiments seem to rule out genetic control of aberrant ray number (J. S. Pearse, personal communication).

No species of starfish is characterized by four or fewer rays (Delage and Hérouard, 1903, p. 35). The supposedly 4-rayed species “Culcita tetragona” mentioned by MacBride (1906, p. 453) and MacGinitie and MacGinitie (1949, p. 221) is an unexplained nomen nudum.

There are major qualitative differences in the patterns of development of supernumerary rays among starfish (Fig. 1). Breaks in the timing and lack of a single pattern (template) seem to rule out continuity between the development of supernumerary rays and the development of the five primary rays. Acanthaster planci (family Acanthasteridae) metamorphoses into a 5-rayed starfish 0.3–0.5 mm diameter (Henderson and Lucas, 1971) and attains up to 21 rays (Madsen, 1955). Yamaguchi (1973) described the formation of supernumerary rays. Signs of a first supernumerary ray appeared in 3 weeks in the CD interradius. New arms appeared one by one at intervals of 9–10 days. In 12 of 14 cases the second developed to the right of the first (to the left in two cases). Subsequent supernumerary rays appeared between the two most recently formed rays. By 12 mm overall diameter the juveniles had 16 to 18 rays (at about 18 weeks). The scheme of formation of new rays is illustrated in Figure 1. A few juveniles developed one or two extra rays at irregular positions (no details). A. brevispinus and its hybrid reciprocal crosses with A. planci also are 5-rayed at metamorphosis (Lucas and Jones, 1976). The hybrids and the A. planci added arms in the order described by Yamaguchi (1973) [no observations on the A. brevispinus, which died].

Leptasterias polaris and L. hexactis
(family Asteriidae) are 6-rayed. In the metamorphosis of *L. polaris* Emerson (1977) observed that “Five rays, and later a sixth, developed around the lobes of the hydrocoel” and that the 6th ray appeared between the preoral lobe and ray 5. In the metamorphosis of *L. hexactis* Chia (1968) observed that five hydrocoel lobes develop nearly simultaneously (p. 332); the first pair of tube feet on all five rays appear when the larva is 30 days old (p. 334); the 6th ray appears on day 32 between the preoral lobe and ray 5 (p. 334); when three pairs of tube feet have developed on the primary rays, the first pair of tube feet appears on the sixth ray. The 6th ray is qualitatively different from the primary rays in that it develops from larval “anterior coelom” that separated from the anterior end of the hydrocoel (Chia, 1968, p. 343).
Stichaster australis (Asteriidae) metamorphoses with five rays and attains 9 to 12 rays before it is 10 mm overall size (Barker, 1978, 1979). Immediately after metamorphosis juveniles have a diameter of ~0.85 mm. The supernumerary rays form when the juvenile is ~1.2 mm diameter (6th ray), 2.5 mm diameter (7th ray), 3.5 mm diameter (8th ray) and 5 mm diameter (9th ray). The supernumerary rays are added in clockwise sequence when the animal is viewed aborally (Barker, 1979). The madreporite was not visible until the juveniles were about 10 mm diameter and all the arms were of similar size. Consequently, the place of formation of the supernumerary rays could not be stated in terms of Carpenter letters (Fig. 1).

Pycnopodia helianthoides (Asteriidae) metamorphoses into a 5-rayed starfish of 0.7 mm diameter (Greer 1962) and attains up to 24 rays. The young individuals display a striking bilateral symmetry which Ritter and Crocker (1900, p. 265) used to identify the five primary rays and the sixth ray. The sixth ray “occupies the exact position of the preoral lobe, or ‘larval organ’ of [starfish] embryos” and (p. 264) “the facts are all against its being regarded as an accessory ray belonging to the same category as those acquired later.” Here the 6th ray is labeled X and is located in the CD interradius (Fig. 1). The next rays come in as pairs in strictly bilateral order on each side of ray X and always adjacent to C and D (p. 252). The budding area continues to give origin to new rays until late adult life. “Sometimes odd new rays appear in other places” (Verrill 1914, pp. 198, 200–201). Kjerschow-Agersborg (1922) showed that the five primary rays are anterior in locomotion. There are qualitative differences between the supernumerary rays and the primary rays concerning connections with the cardiac stomach, connections of the apical muscle bands, and presence/absence of Tiedemann’s bodies (Ritter and Crocker, 1900, p. 253; Brown, 1963).

Byrne and Anderson (1994) studied the development of 5-rayed Patiriella exigua, 6-rayed P. gunni, and 8-rayed P. calcar (Asterinidae) and their crosses, but did not report the sequence of ray addition or distinguish primary rays from the supernumerary rays. The field sample of P. calcar was 3% 7-rayed, 91% 8-rayed and 6% 9-rayed (N = 100). P. calcar cultures yielded 6.5% 6-rayed, 35.5% 7-rayed, 55% 8-rayed, and 3% 9-rayed juveniles (N = 62). Formation of the mouth opening (completion of metamorphosis) often occurred before formation of the supernumerary arms. Six rays are well formed before the seventh and eighth arms appear in the region where the larval body is resorbed. The proportion of seven-armed juveniles in the P. calcar cultures is higher than in the field sample (35.5% > 3%), “suggesting that an eighth arm may be added later” (p. 571). The hybrid cultures of P. gunni ♀ × P. calcar ♂ yielded 8% 5-rayed, 67% 6-rayed and 25% 7-rayed juveniles (N = 24) similar to the maternal arm number. The hybrid cultures of P. calcar ♀ × P. gunni ♂ yielded 2% 5-rayed, 33% 6-rayed, 57% 7-rayed, 6% 8-rayed and 2% 9-rayed juveniles (N = 115) intermediate between the parents, but “the possibility that an eighth ray might be added later could not be eliminated” (p. 571).

Sars (1875), Perrier (1888a, as Brisinga mediterranea) and Lawrence and Komatsu (1990) regarded the number of rays of Brisingella coronata as fixed at metamorphosis. Fisher (1940, p. 207) reported the number of rays (11–14) of Odinella nutrix as “determined at the outset of development and is not increased by later additions,” but the earliest stages he observed were 2.5 mm total diameter and the rays had three or four pairs of tube feet (p. 211). The early stages of metamorphosis have not yet been observed for the families Brisingidae and Freyellidae, and therefore I withdraw my suggestion (Hotchkiss 1979, p. 151) that “the Brisingidae are probably never pentamorous.” A specimen of B. coronata ~1 mm size had 8 rays (Downey, 1986, p. 15) whereas a specimen 2.5 mm disk diameter had 10 rays (Sars 1875, pp. 55, 67), perhaps indicating ray addition in the imago and a pentamorous stage in its development.

Specimens of Helaster (family Helasteridae) show an increase in the number of rays with overall size to about 100 mm diameter (Clark 1907). Small rays are observed to intercalate between preexisting
The number of rays in starfish

The smallest specimen examined by Clark (1907, pp. 56, 59, H. kubinji, USNM 21950) is 20 mm diameter with 12 rays, “eight well developed, three much smaller and a twelfth barely started,” allowing Clark to deduce the normal condition in an 8-rayed young. Clark showed that the stomach in Heliaster “is provided with five pairs of conspicuous muscles attached to the ambulacral plates of five of the rays” which are deduced to be “the original five rays of the starfish on first assuming the adult form.” According to Clark (p. 64), probably the first supernumerary ray appears in interradius CD, the second in BC, the third in AB. Then apparently the fourth in CD, the fifth in BC and the sixth in AB, then another in CD (total of 12 rays in this specimen). Ray formation in interradius EA begins later, “and by the time 25 rays are formed, it is going on at about an equal rate in those four interradii.” No supernumerary rays develop in interradius DE containing the madreporite (rare exceptions). The process of formation of new rays is cartooned in Figure 1.

Specimens of Labidiaster radiosus (family Labidiasteridae) with 23 to 42 rays show an increase in the number of rays with overall size (Perrier, 1891, p. 67). Small rays are observed to intercalate between preexisting rays. The observations of Perrier (1888b, 1891) on Labidiaster radiosus were summarized by Ritter and Crocker (1900, p. 249): (1) “new rays are added until far into adult life, (2) as many as six of these may bud from the disk simultaneously, and (3) these may be distributed at rather regular intervals around the entire circumference of the disk.” In L. annulatus, ray number increases with size (J. H. Dearborn, personal communication) and may exceed 50, which is more than for any other known asteroid (Dearborn et al., 1991).

Hörstadius (1926) observed that the hydrocoel in 7-rayed Luidia ciliaris (family Luidiidae) first develops five primary radial pouches. The supernumerary sixth and seventh radial pouches develop after the primary rays but before completion of metamorphosis. One arises between primary lobes 1 and 2; the other arises between primary lobes 4 and 5. These locations are laterally symmetrical with respect to the A-CD axis of the adult (Fig. 1). The 7-rayed imago is approximately 1.5 mm diameter (Tattersall and Sheppard 1934). In 7-rayed L. savignyi Mortensen (1938, p. 32) did not witness the formation of the radial pouches and “in the preserved larvae all the 7 radial pouches are formed, and in an equally advanced stage.” In 9-rayed L. maculata Komatsu et al., (1994, p. 331, Fig. 1E, 2I) reported that 9 radial lobes are formed during metamorphosis. Nine-rayed Luidia senegalensis metamorphoses with 5 rays (Komatsu et al., 1991). The sequence of development of the supernumerary rays after metamorphosis has not yet been determined. Lawrence and Komatsu (1990, p. 273) mention that “The multiarmed species of Luidia with 6–11 arms are considered to have a constant number of arms, but no data are available to confirm this.” Nichols has seen many hundreds of L. ciliaris at the Isles of Scilly but never any without seven rays (D. Nichols, personal communication). Of 200 L. senegalensis recorded, 197 (98.5%) had nine rays, only 1 had eight rays and 2 had ten rays (S. Miller, personal communication). A single 8-rayed specimen (Naples, Fla., 1996, J.M. Lawrence coll.) has features that suggest the former presence of a ninth ray (Hotchkiss and Lawrence, personal observations).

Mortensen (1921, p. 223) observed that Gemmill’s (1915) Brachiolaria hibernica shows “besides the five young arms, a sixth prominence” in the aboral notch which he “can hardly doubt is really the beginning 6th arm.” Brachiolaria hibernica and Kohler and Vaney’s (1906a, b) Stellosphaera mirabilis may be the larva and imago of Hydrasterias sexradiatus (family Pedicellasteridae) (Mortensen, 1921, pp. 223–225 as Pedicellaster; Clark and Downey, 1992, p. 410).

Most of the family Solasteridae is multiradiate. An example 5-rayed species is Lophaster furcifer. Brachisolaster moretonis of Jurassic age had 33 rays (Blake 1993). In the metamorphosis of Solaster endeca Gemmill (1912, p. 20) observed that “four pouches appear practically simultaneously and are succeeded almost at once by a fifth.” After this “There is a short pause till..."
VI appears. VII follows after an interval of similar length. VIII is delayed relatively longer, and IX longer still.” “The short pause between the formation of the first five radial pouches and that of the sixth is an indication that the Solaster family was derived from a five-rayed ancestor” (p. 21). The pouches form prior to completion of the ring canal. Pouches VI, VII and VIII append to the ventral end of the hydrocoel crescent (clockwise to ray V in oral view), and pouch IX appends to the dorsal end of the hydrocoel crescent (counterclockwise to ray I) (Gemmill, 1916, p. 561). The primary and supernumerary rays are cartooned in Figure 1. In the metamorphosis of Solaster dawsoni, S. stimpsoni and S. endeca, Carson (1988) observed for all three species that “Five rays form initially, and the remaining rays are added in sequence between the first and the fifth ray. Metamorphosis is completed 40±50 days after fertilization. The juvenile is 1–1.5 mm in diameter, and has its full complement of rays with two pairs of tube feet and one terminal tentacle per ray.”

In the metamorphosis of Crossaster papposus (Solasteridae) Gemmill (1920, p. 164) observed that “Pouches I–V are formed at much the same time, I being perhaps a little delayed; VI comes immediately thereafter,” and succeeding pouches come more slowly. The pouches form prior to the completion of the ring canal. Pouches VI–IX append to the ventral end of the hydrocoel crescent (clockwise to ray V in oral view); pouches X–XII append to the dorsal end of the hydrocoel crescent (counterclockwise to ray I). The primary and supernumerary rays are cartooned in Figure 1.

The starting assumption underlying the FIVE-PLUS hypothesis is that the number of primary rays is intrinsically fixed at five and there is no heritable variation of ray number in 5-rayed species. Data on ray number listed by Lawrence and Komatsu (1990) include Luidia clathrata with 100% 5-rayed (N = 1143), Archaster typicus with 97% 5-rayed (N = 1707) and Pisaster ochraceus with 100% 5-rayed (N = 986). In Patiriella exigua studied by Byrne and Anderson (1994) a field sample was 99% 5-rayed and 1% 4-rayed (N = 100) and laboratory culture yielded 100% 5-rayed juveniles (N = 600). In Anseropoda placenta studied by Guillou and Diop (1988) cumulative observations recorded 4,333 (97.8%) with five rays, 4 with four rays, 91 with six rays and 2 with seven rays (M. Guillou, personal communication).

The logic of the FIVE-PLUS hypothesis does not state that 6-rayed species cannot have heritable phenotypic variability. Nevertheless, and convenient to the present arguments, the 6-rayed species seem to be strongly canalized to form only six rays. Examples listed by Lawrence and Komatsu (1990) include Leptasterias epichlora with 99% 6-rayed (N = 739) and Patiriella gunni with 95% 6-rayed (N = 173). In P. gunni studied by Byrne and Anderson (1994) a field sample was 1% 5-rayed, 97% 6-rayed and 2% 7-rayed (N = 100) and laboratory culture yielded 100% 6-rayed juveniles (N = 20). However, not all data are as straightforward. Fisher (1940, pp. 253–255) documented considerable complexity surrounding ray number and taxonomy in Diplasterias (family Asteriidae). Typical D. brucei are 5-rayed but “all the specimens from South Georgia have 6 rays and are therefore not typical brucei.” A 6-rayed typical D. meridionalis had 4 out of 50 young with only 5 rays. A 5-rayed typical D. brucei had 65 young about 6mm diameter and all 5-rayed. The Diplasterias observations are mentioned for fairness of presentation. My working hypothesis is that the Diplasterias story will not prove to be an exception to the FIVE-PLUS hypothesis.

The heritability of ray number in Asterina miniata (Asterinidae) has been studied by John Pearse and his students Steven Sadro and Katherine Clark. Sadro (unpublished) crossed 4-, 5-, 6- and 7-rayed individuals and reared over 5,300 of the resulting larvae through metamorphosis. “Over 99.8% were 5-rayed regardless of the number of rays in the parents. The other 0.2%—9 individuals—were 4-rayed, that being the frequency of 4-rayed parents. Many of the juveniles were kept for an additional 5 months and none added more rays. There does not seem to be any question that ray number in this species is not simply an expression of genes” (J. S. Pearse, personal
An abstract was published by Clark (1988) in which she states: “Ray number counts of 2,715 adults were taken in intertidal and subtidal locations in central California yielding 3.7% with six rays, 0.2% with seven rays, and 0.2% with four rays. Gametes from adults with four to seven rays were crossed. All crosses raised in normal salinity seawater (32±33‰) resulted in five rayed juveniles. Larvae raised in high salinity seawater (37‰ and 40‰) for one to 52 days resulted in a 1.5% frequency of juveniles with less than the normal five sets of tube feet. Thus, changes of salinity in the field may contribute to the observed 0.2% four rayed starfish. Salinity measurements during low tide sequences ranged from 32 to 38‰. In addition, preliminary data suggest that abnormal patterns of ray regeneration following mechanical damage may result in A. miniata with four, six, or more rays.” Six-rayed A. miniata dissected by Hotchkiss (1979 as Patiria) had internal anatomical abnormalities (N = 3).

Allain (1972) observed about a hundred 4-rayed and no 5-rayed specimens of Asterina gibbosa in a 60 m × 5 m intertidal area in August 1970, at Dinant, France. Neighboring patches had only normal 5-rayed specimens. The 4-rayed population was composed largely of 1967 year-class individuals, a few 1968 year-class, and no 1969 year-class individuals. The 1970 year-class escaped notice in August 1970 but was observed in January 1971 to be 5-rayed (rays 3 mm long) and to comprise nearly half the population. Neighboring 5-rayed populations were observed to spawn normally while the 4-rayed specimens were never observed to spawn. In October 1971 the quasi-totality was 5-rayed, and towards May 1972 the population had practically returned to normal, probably by mortality of the oldest year-classes (the 4-rayed individuals). Allain conjectured that this small plot somehow was polluted such that all the A. gibbosa developed only four rays in two successive years (i.e., teratology).

Marthy (1980) cultured Asterina gibbosa and A. phylactica. The great majority metamorphosed with 5 rays, but a few metamorphosed with 4, 6 and 9 rays. The 9-rayed individual had five larger rays and four smaller rays and eventually split into 5-rayed and 4-rayed unequal halves. The 6-rayed individual appeared to be symmetrical. The implication that more than five primary rays can develop is contrary to the working hypothesis and is mentioned for fairness of presentation. My working hypothesis is that the Marthy observations, if they could be repeated, would not prove to be an exception to the FIVE-PLUS hypothesis.

Watts et al. (1983) found that embryos of 5-rayed Echinaster graminicola (Echinasteridae) exposed to 39‰ salinity two days after fertilization metamorphosed with high frequencies of 3- and 4-rayed individuals. Marsh et al. (1986) transferred embryos of E. spinulosa to 39‰ salinity and kept them there for 13 days; fertilization was at 30‰ salinity. Mortality was 100% when transferred at 0 hr and 2 hr post fertilization, 8% at 12 hr, and 0% after 28 hr. The percentage of embryos that failed to develop recognizable ambulacra was ca 65%, 50%, 35%, and 25% when transferred at 12 hr, 28 hr, 48 hr and 60 hr post fertilization, respectively. Highest percentages of 3-rayed (9.7%) and 4-rayed (29%) occurred when transferred at 48 hr (pre-oral lobe stage). A second experiment was conducted: Embryos were transferred at the 48 hr stage to salinities of 33½, 36½ and 39½, or left at 30½. The percentages that failed to develop ambulacra (ND), that developed 4 rays, and that developed 3 rays increased with increasing salinity; at all salinities percentages ranked ND > 4-rayed > 3-rayed. All surviving 4-rayed and 3-rayed E. spinulosus from the second experiment were transferred to normal 30‰ sea water to monitor growth. Approximately 92% did not develop additional rays. Hotchkiss (1998a) proposed that the pathway of development of the primary rays operates for only a brief time at metamorphosis, after which it is switched off and does not recur (“synchronic hypothesis”). Approximately 8% developed additional rays resulting in 6- and 7-rayed individuals after one month (Marsh et al., 1986). Hotchkiss (1998a) proposed that the process by which a teratologically reduced number of rays is made up for (sometimes even exceeded) is by
"postgeneration" of non-primary rays (postgeneration terminology from Hörstadius 1973, p. 121).

Postgeneration of rays in the rudiment and intercalary regeneration of rays in the imago are independent ray-producing pathways that may have been co-opted variously and recurrently in the multiple origins of multiradiate starfish. A specimen of Stegaster inflatus of normal pentagonal shape had an intercalary ray X in the mouth frame (Hotchkiss 1979, p. 47). The ray X emerged on the aboral surface as a recumbent conical tube without an open ambulacral groove. Two specimens of A. forbesi had a single ray X intercalated at the mouth frame (6 mouth corners), disrupting the primary rays and emerging from beneath the edge of the disk just below the level of the superomarginals (Hotchkiss, 1979).

Regeneration has been entrained to complete an asexual life cycle in fissiparous and comet-forming starfish. Henricia sexradiata (family Echinasteridae) is fissiparous with six or seven rays (Clark and Downey, 1992). Representative fissiparous asterinid starfish are Asterina burtoni and Nepanthia belcheri. Seriaster regularis (family Scolasteridae) is fissiparous with six rays (Jangoux, 1984, p. 284). Representative fissiparous asteriid starfish are Coscinasterias tenuispina, Stephanasterias albula and Allostichaster polyplax. Reviews of fissiparity in starfish have been written by A. M. Clark (1967), Emson and Wilkie (1980) and Chia and Walker (1991). The typical number of rays in the fissiparous adults is six or more. The number of rays at metamorphosis is known only for Coscinasterias calamaria which metamorphoses with just five rays (Barker, 1977, Fig. 1; 1978). It is not yet known whether fission is initiated in the 5-rayed starfish (dividing it into unequal "halves") or whether supernumerary rays develop prior to fission. Bennett (1927, p. 149) stated that in C. calamaria "tiny arms arise in specimens showing no signs of injury or recent autotomy, rising from the edge of the mouth opposite the angle between the rays, and free from the disc except at the point of attachment." He did not know "whether these arms reach full size and if so, how they insert themselves in the disc between the other arms." Emson (1978) studied fission in Allostichaster polyplax. Eight is the usual ray number, and 4+4 is the usual formula of old plus new rays. Most of the individuals with 5 or 3 rays are regenerating 4 rays, indicating no special tendency to restore the arm number of eight. The number of regenerating rays in nature varied from 1 through 7 and appears to be "controlled by the amount of disc available for new arms." Experimental cuts showed that "the disc area exposed is fundamental to the determination of the number of arms regenerating."

A few Ophidiasteridae and one species of Echinasteridae reproduce asexually by autotomizing a part of the arm. The autotomized portion of the arm regenerates the missing disc and new rays. When the regenerating rays are small there is a fanciful resemblance to a comet. Comet-forming ophidiasterids are Linckia guildingi, L. multifora, L. columbiae, Ophidiaster cribraeaus, O. lorioli, and O. robillardi (Hotchkiss, 1979, p. 152; Emson and Wilkie, 1980, p. 190), and the echinasterid is Echinaster luzonicus (Clark, 1921; Soota and Sastry, 1977, 1979; Emson and Wilkie 1980, p. 190). In these species the modal arm number is five or six. Specimens with four rays, seven rays, etc., are accounted for by variation in the number of rays that regenerate in the comet. The number of rays at metamorphosis is not yet known for these species, but congeners are 5-rayed. A minute 5-rayed L. multifora collected during the International Indian Ocean Expedition is perfectly formed, has a single madreporite, and seems never to have autotomized (personal observation).

**Analysis**

The large number of strictly pentamericous families of starfish support the interpretation that there is "rigid control" of pentamerism. As noted by Lawrence and Komatsu (1990) the control of ray number is very precise in five-rayed species. The "en bloc" hypothesis is that the five primary rays develop as a unit.

The complete lack of any consistently 4-rayed species of starfish supports the hypothesis that the ontogeny is strictly con-
strained to produce five rays as a unit, and that four rays is “not permitted.” The proposal that four or three rays at metamorphosis is the result of teratological incomplete development is generally consistent with the observations of Allain (1972) on Asterina gibbosa, Marsh et al. (1986) on Echinaster spinulosus and Clark (1988) on Patiria miniata. The failure of the 4-rayed starfish to develop fifth rays after metamorphosis is consistent with the “synchronic hypothesis” that the pathway to form the rudiments of the five primary rays operates for only a short time, switches off and does not recur. Any primary rays that did not form during metamorphosis are not expected to form later.

The breeding experiments by Pearse and his students using Asterina miniata that had four to seven rays resulted only in 5-rayed juveniles (Clark, 1988; S. Sadro, unpublished; J. S. Pearse, personal communication). This supports the “tamper-proof” hypothesis that the ontogenetic pathway to form the rudiments of the five primary rays is devoid of heritable variation. Without heritable variation the pathway cannot be co-opted for the production of supernumerary rays.

If starfish ontogeny is limited to producing five primary rays (no more than five) and is “tamper proof,” then species having more than five rays require the entrainment of other developmental pathways to produce the supernumerary rays after the five primary rays have initially formed (FIVE-PLUS construction). The possibility that the FIVE-PLUS hypothesis may be generally correct is evident when it is seen that the five primary rays develop discernably ahead of (time separated from) the supernumerary rays in Solaster, Crossaster, Luidia ciliaris, Leptasterias polaris, L. hexactis, and Brachiolaria hibernica. This is the case also in the 6-rayed ophiuroid Ophionotus hexactis (Mortensen, 1921, p. 182; Clark, 1967, p. 154). The time separation is patently evident when the asteroid metamorphoses with five rays and the supernumerary rays develop by intercalation after metamorphosis, as in Acanthaster, Pycnopodia, Coscinasterias calamaria, Stichaster australis, and Luidia senegalensis. Descriptions of the development of Luidia maculata, Patiriella gunni and P. calcar do not mention the development of the five primary rays (assuming it was observed) as being distinctive from the supernumerary rays; this lack of mention fails to support the FIVE-PLUS hypothesis but does not negate it.

This review documents a considerable diversity of timing and pattern of development of supernumerary rays (Fig. 1). If the ontogenetic pathway to form the rudiments of the five primary rays is a template that can be entrained by selection to make extra rays (in violation of the tamper-proof hypothesis), and if such entrainment by selection occurred repeatedly, then there should be a tell-tale commonality of the pattern and sequence of ray addition in multiradiate starfish. The lack of a common pattern and sequence indicates that the pathway for the five primary rays cannot be co-opted for the production of supernumerary rays (tamper-proof hypothesis) and is not a template. By logical exclusion we can deduce the hypothesis that supernumerary rays develop by independent pathways that operate after the five primary rays have initially formed (FIVE-PLUS hypothesis).

Differences in the anatomy and development of the supernumerary rays versus the five primary rays also support the FIVE-PLUS hypothesis. Chia (1968, p. 343) reported that in Leptasterias hexactis the primary rays develop from the left lateral coelom whereas the sixth ray develops from the anterior coelom. Clark (1907) showed that in Heliaster only the five primary rays are connected to the five cardiac pouches by retractor ligaments (not so for the supernumerary rays). In Pycnopodia helianthoides most of the supernumerary rays lack Tiedemann’s bodies and have anatomically different relations to pyloric caeca and to aboral muscles than do the five primary rays (Ritter and Crocker, 1900). These data indicate that supernumerary rays are qualitatively different from primary rays.

**DISCUSSION**

Prior thinking has been that there is a morphological continuum between aberrant 4-rayed, normal 5-rayed, aberrant 6-rayed...
and the evolution of 6-rayed, 7-rayed, etc. multiradiate species. In his discussion of the evolution of multiradiate Acanthasteridae from 5-rayed Oreasteridae, Blake (1979, p. 309) stated: “Although species with more than five arms are rare in the Oreasteridae, individuals not obviously pathological do occur with seven, six, or four arms. Species and genera of sea stars with more than five arms are taxonomically widespread, occurring for example within the Luidiidae, Solasteridae, Asteriidae, and the Brisingidae. Multiplication of arm number does not appear to be a difficult evolutionary step.” The data reviewed here support the syllogism that the large numbers of unrelated multiradiate starfish imply that it is fairly “easy” for multiradiate starfish to evolve from strictly 5-rayed ancestors. In contrast, the data in this review speak against there being a morphological continuum between the rays of the normal 5-rayed species and the supernumerary rays of multiradiate species. The FIVE-PLUS hypothesis formalizes this suggestion that there is qualitative developmental difference between the five primary rays and the supernumerary rays.

The FIVE-PLUS hypothesis proposes that supernumerary rays develop by independent pathways that operate after the five primary rays have initially formed. What independent developmental pathways could be entrained to produce supernumerary rays? Two candidates are the regeneration pathway and the postgeneration pathway. The regeneration pathway is a fairly obvious candidate wherever we observe the postmetamorphic development of supernumerary rays between rays that are already formed. Selection for regulation of intercalary regeneration to produce multiradiate starfish can be imagined. The “genetic assimilation” model of selection for discontinuous morphological traits (Waddington, 1956) seems appropriate to the circumstances. Komatsu et al. (1994) reported as a correlation that the primitive condition among multiradiate starfish is to metamorphose with five rays and develop the supernumerary rays in the imago, whereas the derived condition is for the supernumerary rays to form during larval metamorphism. This shift in the time of development of the supernumerary rays from after metamorphosis to during larval metamorphosis would represent “adultation” of the larvae (terminology of Strathmann 1993). Assuming that the postgeneration pathway is distinct from the regeneration pathway, then similar scenarios involving postgeneration also can be imagined.

The ideas presented here are not proven. The report by Marthy (1980) of the metamorphosis of 6-rayed imagos of 5-rayed Asterina gibbosa is a direct challenge to the ideas presented here. It is possible that only five hydrocoel lobes developed and that one ray bifurcated almost immediately after formation. Challenges of this type emphasize the need for skeptical and critical studies on the metamorphosis of 5-rayed and multiradiate starfish.

The problems presented by the number of rays in starfish illustrate two main points made by Maynard Smith et al. (1985) on developmental constraints and evolution. The persistence of pentamery seems to illustrate the following point (pp. 276–277): “If there is no heritable variation in a trait, selection cannot alter that trait. . . . Features of the relevant phenotype are not maintained by selection, but are the products of constraint. If . . . variants breaking certain bilateral [or starfish pentameral] symmetries are not available, then constraint provides a sufficient explanation for the preservation of those symmetries.” The fact that there are multiradiate species of starfish seems to illustrate the next point (p. 282): “[E]volution is best viewed as a history of organisms finding devious routes for getting around constraints.”

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