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Regeneration, predatory–prey interaction, and evolutionary history of articulate crinoids

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Abstract

Regeneration and predatory–prey interaction of crinoids are reviewed. Crinoids have strong powers of regeneration, and arm regeneration is common in fossil and Recent crinoids. Regenerated arms commonly start from the ligamentary articulation called syzygy or cryptosyzygy, where crinoids can autotomize their arms. Therefore, regenerated arms can be formed after loss of arms by autotomy of arms, and such autotomy is commonly the response to predatory attacks. Thus, regenerated arms can be used as the clue to estimate the predatory frequencies. Regeneration of "correct" skeletal morphology as in the original depends on the existence of adoral nerve center. A stalk without the adoral nerve center cannot regenerate the "correct" morphology of the original skeleton, but forms of "callus" as skeletal overgrowth. The strong ability of regeneration is a key factor of the success of articulate crinoids in the geologic history since the Triassic onward.

Keywords: Crinoidea; Isocrinine; Regeneration; Predation; Ontogeny

1. Introduction

Echinoderms have a strong ability to regenerate body parts after injury or autotomy, and crinoids are no exception (Wilkie, 2001). Generally, crinoids have many regenerated arms, and many have lost the visceral mass, whose regeneration is known in comatulid crinoids. This paper reviews previous studies on autotomy and regeneration of crinoids, and discusses ecologic relationship of crinoids to their predators. An excellent review on the crinoid regeneration was done by Gahn and Baumiller (2010), and therefore, this paper focuses on the strong ability of autotomy and regeneration in articulate crinoids, the only survivors after the end-Permian mass extinction, and also on the existence of programmed autotomy in comatulid crinoids, which was not well documented in the ontogeny.

2. Regeneration in articulate crinoids

Regenerated skeletal parts are common in crinoids. They are most commonly found in the arms (Oji, 2001), but also other body parts such as the visceral mass which can regenerate after autotomy (Reichensperger, 1912; Meyer, 1985, 1988). During the growth of regenerated arms, there is a clear boundary between the original and the regenerated parts with an abrupt diameter change, or color difference (for extant crinoids) (Fig. 1). Examples of regenerated arms in fossil crinoids are summarized in Oji (2001). The position where regenerated arms begin tends to be random, but for articulate crinoids, they are commonly at the ligamentary articulation called syzygy (or cryptosyzygy) where crinoids can autotomize their distal arms. Syzygy consists of a tightly connected pair of brachials (arm plates) called epizygal and hypozagal, the epizygal being the distal and the hypozygal being the proximal brachials among the pair. If mechanical or chemical stimuli are applied to the distal arms, or a predatory attack such as a bite occurs in the distal arms of comatulid criniods, the break occurs at the proximal syzygy that is closest to the location of stimuli, attacks or bites.

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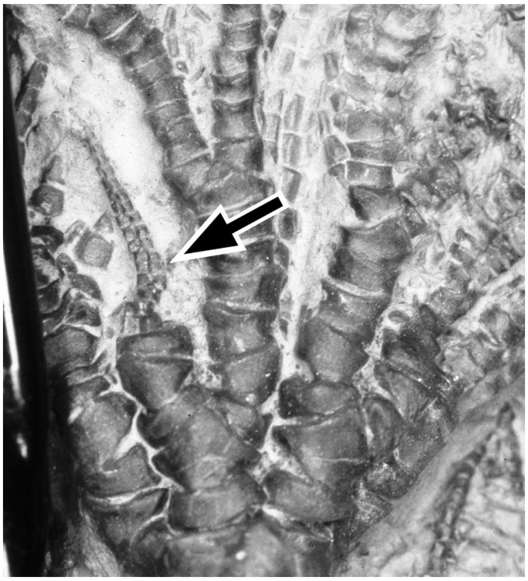

Fig. 1. Regenerated arm of *Isocrinus oregonensis* (Moore and Vokes, 1953). Note that a small regenerated arm (arrow) extends from the upper surface of hypozygal (lower pair of brachials with a syzygial articulation), where autotomy preferentially occurs. Photo by J. Schneider.

The correspondence of the start of regenerations at syzygies in most museum specimens suggests that most of the regenerated arms in articulates were the result of autotomy (and probably non-lethal predatory attacks) to crinoid arms. Articulate crinoids generally possess numerous syzygies or cryptosyzygies in the arms, and thus they probably have more ability in autotomizing and regenerating arms than most of the Paleozoic crinoids. Gahn and Baumiller (2010) noted that crinoids have always had the ability to regenerate lost arms, and such ability has been maintained through the history of crinoids. Regeneration of lost arms is a common phenomenon through the crinoid history; but since the evolution of articulate crinoids, chances of autotomy and regeneration should be increased.

The most basal place for autotomy in the crown (arms plus theca) is between the basal and radial plates in isocrinines. In *Metacrinus*, this facet is flat and cryptosyzygial. Even if *Metacrinus* loses its entire body above the basals, including the visceral mass, it can regenerate its entire arms (and radials) and its visceral mass within several months in aquarium (Amemiya and Oji, 1992). Thus, crinoids are thought to possess very strong ability of regeneration.

3. Correct and incorrect regenerations after autotomy

Crinoids tend to regenerate the lost body parts exactly the same as or similar to the original one. However, sometimes they regenerate a very different morphology, such as callus. Whether crinoids regenerate their lost body parts correctly (i.e., morphology similar to the previous one) or not seems to depend on the existence of the adoral nerve center (or the entoneural nerve center (chambered organ), Gahn and Baumiller, 2010) located in the basal part of theca.

After "decapitation" below the basal circlet, stalks cannot regenerate the original morphology, but tend to produce an irregular "callus" above the non-damaged stalk. These examples were reported from both extant (Donovan and Pawson, 1997) and fossil (Ausich and Baumiller, 1993; Donovan and Schmidt, 2007) crinoids.

Experiments with extant crinoids in a tank (Nakano et al., 2004) demonstrated that *Metacrinus rotundus*, after the most of the stalk was cut below the basals but retained the aboral nerve center, could regenerate the entire crown, but the stalk cut below the basals cannot regenerate the lost part of stalk (but continues to live at least for a year, and probably more years). Therefore, the adoral nerve center housed in the basal part of theca (near the basal circlet) is necessary for the "correct" regeneration of lost body parts. Instead, if the adoral nerve center is missing, the crinoid either cannot regenerate the lost body parts, or they reproduce skeletal parts with different morphology from the original ("incorrect regeneration", or "overgrowth" in the sense of Oji and Amemiya, 1998b).

The adoral nerve center located in the basal part of theca is thought to be crucial for the correct regeneration of the body parts. However, even with the existence of the adoral nerve center, the number of brachials, when regenerated, tends to change from the original number (Oji, 1986 for *Metacrinus* and *Saracrinus*), thus leading to incorrect regeneration. In *Metacrinus* the number of primibrachials tends to be reduced from the original seven, whereas in *Saracrinus* the number tends to increase from the original four. Also aberrant arm branching can be formed in the regenerated part of the arms (Gahn and Baumiller, 2010).

4. Autotomy of stalk

Autotomy also occurs in isocrinine stalks. Autotomy occurs only at an articulation called cryptosymplexy, which is located at the distal articulation of the nodal. After autotomy of the distal stalk, crinoids can temporally move and change the locations (Baumiller and Messing, 2007). The discarded stalk can continue to stand for a while on the sea floor (Fujita et al., 1987). In a tank experiment, stalk fragments of *Metacrinus rotundus* left on the bottom of the tank can live more than a year after they were detached, but there was no regeneration or overgrowth afterwards from the detached stalk (Oji and Amemiya, 1998a).

If this stalk autotomy is caused by the response of crinoids to escaping from predators such as sea urchins (Baumiller et al., 2008), the growth rate of stalk and the frequency of stalk autotomy should depend on the rate of encounter of predators: high growth speed in the environment with frequent predation, and vice versa.

In some isocrinines such as *Endoxocrinus parrae* or *Annacrinus wyvillethomsoni*, calcification occurs on the distal facet of stalk, sealing the axial canal (Roux, 1977).

5. Regenerated arms as a response to nonlethal predatory attack

Except for the juvenile stage during which crinoids tend to increase the number of arms, they do not autotomize their arms.