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Catch connective tissue: The connective tissue with adjustable mechanical properties

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ABSTRACT: The catch connective tissue is defined as the collagenous connective tissue whose mechanical properties can be changed rapidly (in seconds to minutes) under nervous control. This tissue is found in all the supportive systems of echinoderms. When the tissue is in a catch state, the supportive systems become hard and immovable so that they maintain the animal posture and serve as protective "shells". When it relaxes, the supportive systems become flexible so as to allow deformation and locomotion of the animal. Further softening allows for autotumy (defence) and for fission (reproduction). The echinoderms' success has very likely depended on the development of catch connective tissues.

1 DEFINITION OF CATCH CONNECTIVE TISSUE

Echinoderms have developed a connective tissue whose mechanical properties can be changed rapidly. I have studied 6 kinds of such connective tissues from 12 species out of 4 classes of the phylum Echinodermata. Some common features of these connective tisses have been revealed:

1. They are collagenous connective tissues with or without muscles in them.
2. They change their mechanical properties spontaneously and in response to stimulation of various modalities.
3. The change is reversible except at autotomy and fission.
4. The change is rapid: it completes in the order of seconds or minutes.
5. The change in mechanical properties occurs mainly in viscosity; the change in elasticity is small.
6. The viscosity is controlled by nerves.
7. Neurosecretory-like cell processes with electron-dense granules are always found in the tissue.
8. The viscosity seems to be controlled through the ionic environment in the tissue.
9. The tissues are found in the supportive systems of echinoderms. They are used in control of the body tone, in defence including autotomy, and in fission.

I propose to call this connective tissue with adjustable mechanical properties "the catch connective tissue": I define it as the collagenous connective tissue whose mechanical properties can be changed rapidly (in seconds to minutes) under nervous control. I will briefly review how these tissues are used in the supportive systems of echinoderms, and discuss the possible contribution of catch connective tissues in echinoderms' success.

2 THE ROLE OF CATCH CONNECTIVE TISSUES IN SUPPORTIVE SYSTEMS

The main role of animal connective tissues is in support. Supportive systems must be rigid enough to bear the body weight and to withstand the forces imposed by the environment. The supportive system must be flexible; however, efficient movements are impossible if the body is so rigid as to be nondeformable. These requisites for a supportive system seem incompatible. In echinoderms, however, the supportive systems meet these requirements by being able to change the mechanical properties of the catch connective tissues. Echinoderms have three kinds of supportive systems: hydrostatic, articulated, and imbricate skeleton. Catch connective tissues are found in all these supportive systems; they function in the maintaining the tone of the body.

2.1 Animals with hydrostatic skeleton: sea cucumbers

Aspidochirotid holothurians have a large coelom which is surrounded by a thick body wall (Fig. 1a). The body wall is mainly composed of a connective tissue dermis, which is a catch connective tissue. The isolated dermis changes its mechanical properties in response to various kinds of stimuli: photic, chemical, electrical, and mechanical stimulations are effective (Serra-von Buddenbrock, 1963; Stott et al., 1974; Motokawa, 1981, 1982a,b, 1984a,b). When an animal is mechanically irritated, it stiffens the body wall. When it pushes itself through a narrow crevice, the body wall softens and becomes deformable. Although there is no in vivo measurements, the dermis is most possibly responsible for these changes.

Another instance of a hydrostatic skeleton in echinoderms is found in tube feet. The connective tissue layer in the wall of echinoid tube feet has been suggested to be a catch connective tissue (Florey & Cahill, 1977).

2.2 Animals with articulated skeleton: sea lilies, brittlestars, and sea urchins

The arms of crinoids and ophiuroids consist of series of ossicles which are articulated and bound with ligaments and muscles (Fig. 1b). These ligaments are catch connective tissues (Wilkie, 1978a,b, 1983; Motokawa, 1984c). When they are stiff or in catch , the joints are immobilized so that the posture of the animal is maintained. When the ligaments are soft or relaxed, the joints are free to move so that the animal can flex and move the body.

Sea urchins have spines which articulate on the tubercles of their tests (Fig. 1c). There are two kinds of ligaments at a spine joint; both are catch connective tissues (Takahashi, 1967; Motokawa, 1983). One ligament, the catch apparatus, controls the movability of the joint and thus maintains the posture of the spine. The other ligament, the central ligament, limits the excursion of spines and thus prevents disarticulation.

Some sea stars and brittlestars have articulated spines. Their joint ligaments change the mechanical properties (starfish ligament: Motokawa, 1982b; brittlestar ligament: unpublished observation).

In summary, the catch connective tissues control the movability of the joints and thus control the posture of animals.

2.3 Animals with imbricate skeleton: starfish

The body wall of some starfish consists of imbricate ossicles, which are bound together with muscles and dermis. The merit of this arrangement is that although the body is covered with rigid plates it remains flexible: the animal can deform the body by sliding the adjacent plates past one another. Starfish have remarkable abilities to change body shape and to make the body stiff. These abilities can be explained if we assume that the connective tissues between the plates are catch connective tissues (Wainwright, 1982): when the connective tissues are soft the plates can slide and thus the body is flexible; when the connective tissues become stiff the plates are frozen at that position and thus the posture of the animal is maintained. This mechanism is very probable because of the wide occurrence of catch connective tissues in echinoderms, although the stiffness change of the connective tissue between the starfish ossicles has not yet been shown by mechanical tests.

Imbricate skeletons are found not only in modern asteroids but also in some extinct echinoderms such as helicoplacoids and edrioasteroids (see U133 and U238 of Moore, 1966). The catch connective tissues have quite possibly controlled the flexibility of the bodies of these animals.

3 AUTOTOMY AND FISSION

Autotomy is found in every class of echinoderms (Emson & Wilkie, 1980). Crinoids, ophiuroids, and sometimes asteroids autotomize their arms when they are grasped by the arms. The connective tissue ligaments, which bind the ossicles, become soft enough to lose tensile strength at autotomy (Wilkie, 1978a; Holland & Grimmer 1981). These responses have defensive roles. The most active defensive reaction is the attack autotomy of echinoid pedicellariae. The globiferous pedicellaria detaches from the test after it has bitten the enemy; it keeps on biting after autotomy. The connective tissue ligament which connects the pedicellaria to the test softens to break at autotomy (Hilgers & Splechtna, 1982). In sea cucumbers evisceration is an autotomy phenomemon. When an animal is strongly poked or when aquarium conditions are poor, a part of the body wall softens to break, and through the rupture the viscera are

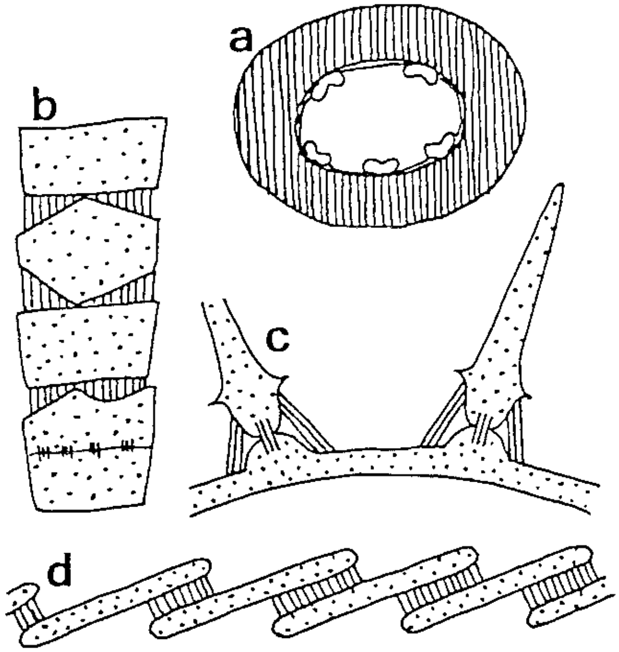

Figure 1. Disposition of catch connective tissues in the supportive systems of echinoderms. Stripes indicate catch connective tissue; stipples indicate the ossicle. a) hydrostatic skeleton: cross section of a sea cucumber. b) articulated skeleton: crinoid arm joints. c) articulated skeleton: longitudinal section of echinoid spine joints. The catch connective tissue which surrounds the joint is the catch apparatus, the tissue disposed at the centre is the central ligament.
d) imbricate skeleton: cross section of starfish integument.

extruded.

The stiffness change of holothurian dermis depends on the intensity of mechanical stimulation: when the stimulation is weak the response is stiffening; at a strong stimulation the response is softening and it is often followed by evisceration. The intervertebral ligament of a brittlestar has been shown to reversibly change its stiffness (Motokawa, 1984c). Therefore it is a simpler and thus a more probable interpretation to consider that the softening at autotomy as an extreme case of softening in the connective tissue catch pheomenon rather than to postulate two separate mechanisms, connective tissue catch and autotomy.

The catch connective tissues become extremely soft to allow a part of the body to break off in the event of an emergency. This ability to divide the body into parts may have led the echinoderms to employ fission: asexual reproduction by fission is observed in a number of echinoderms (Emson & Wilkie, 1980). In some coral reef asteroids, fission is suggested to be the main reproductive method (Rideout, 1978).

4 THE SECRET OF ECHINODERMS' SUCCESS

The Echinodermata is one of the most successful animal phyla: echinoderms are conspicuous large animals in the sea; they are dominant among the fauna of the deep sea floor. Although their distribution is restricted to the sea, there is no doubt that they constitute a significant part of the total standing crop of the earth, because the most of the surface of the earth is covered with sea water. Why are echinoderms so successful? A contributory reason may be that they have developed the catch connective tissues.

The success of an animal group depends on how well protected it is from predation. There are two trends in avoiding predation: one is to develop a protective shell around the body, and the other is to develop a high locomotory ability with which the animal can escape from predators. Let me call the animals with the former strategy the "defense-oriented animals", and those with the latter the "locomotion-oriented animals". Because the defense-oriented animals are covered with rigid, thick, and thus heavy shells, their locomotory activities are quite limited; they sometimes lead sedentary lives. The examples are shelled molluscs and corals. The locomotion-oriented animals must develop not only powerful muscles but also light and flexible supportive systems. Their integuments are therefore soft and pliant, and thus they have little defensive function. These two groups have different supportive systems: the defense-oriented animals have rigid and inflexible supportive systems whereas the locomotion-oriented animals have flexible ones. These animals fulfil only one of the two requisites for supportive systems (i.e. rigid and flexible, see Section 2).

In contrast to these animals there are certain animals which have supportive systems with both rigid and flexible characteristics. With these supportive systems, they can undertake extensive locomotory activities without sacrificing the defensive function of integuments. Examples are found among the arthropods and echinoderms, the two major successful animal groups.

The arthropods developed a chitinous

cuticle. The cuticular exoskeleton is strong and rigid, and thus it provides an effective defensive shell. In addition, it is light so that locomotion is not hindered. The cuticle is flexible at joints where appendages for locomotion are connected. In some instances the active change in mechanical properties of cuticle can be observed (Reynolds, 1975; Tychsen & Vincent, 1976). It is widely accepted that the arthropod cuticle is the key to their present success (Currey, 1970).

Echinoderms have developed a dermal system in which ossicles are bound together by catch connective tissues. Because the catch connective tissue rapidly changes its viscosity by 100-1000 fold (Motokawa, 1984d), the rigidity of the dermal system can be adjusted in order to meet the mechanical environment and the needs of the animal: the system can become stiff to be a defensive "shell" against predators and environmental mechanical stress; it can be stiffened to maintain the posture of the animal; it can become soft to allow the animal to change the body shape so as to hide into a narrow crevice; it can become soft to allow the animal to flex the body for locomotion; it can become very soft to enable the animal to divide the body at autotomy and fission.

The catch connective tissues soften to make the body flexible to improve locomotion efficiency: sea cucumbers make the dermis soft and generate peristaltic waves; sea urchins make the catch apparatus soft and move the spines for walking; brittlestars make the intervertebral ligaments soft and generate propagating waves on the arms when they move; featherstars make the brachial ligaments soft and swim by flapping movement of the arms. Many echinoderms walk with tube feet. The rigidity and flexiblity of tube feet may be controlled by the catch activity of the connective-tissue wall.

This remarkable connective tissue has enabled echinoderms to live exposed on the sea floor. Other locomotion-oriented animals with locomotory ability similar to echinoderms (such as annelids), however, are usually found hidden in the substrate, because they have no stiff integuments to protect them against more active predators. Echinoderms have integuments which can make defensive barriers when necessary: the imbricate skeleton of asteroid body wall can become an excellent armour; the arrays of echinoid spines which are held rigid and straight by catch connective tissues makes a barrier against attack; body walls with catch connective tissues and ossicles (which are large in ophiuroids and crinoids while very small in holothuroids, probably compensated for by the thickness of the body wall) become rigid protective integuments. Moreover when these stiff integuments are inadequate to resist the attacks of powerful enemies, the echinoderm makes the integument very soft to autotomize a part of the body so that they can sacrifice that part to the enemy as food. The animal can escape while the enemy is eating the autotomized part (Aldrich, 1976). This ability to live safely exposed enables the echinoderms to feed freely irrespective of their feeding habits: rheophilic suspension feeders can stand exposed in the currents; starfish can attack clams in an exposed position; sea urchins can graze algae on the open sea floor.

The catch connective tissues are used in maintenance of posture in echinoderms. This is unusual: in other animals the posture is maintained by muscles. The catch connective tissues probably consume less energy than muscles, because crinoids and ophiuroids engaged in suspension feeding (and thus with ligaments in catch state) have lower metabolic rate than those of other animals (LaBarbera, 1982). The economical echinoderm body plan may also have contributed to their success.

The success of echinoderms in the sea is very likely dependent on the catch connective tissues. This very dependence has been suggested to be the reason echinoderms have failed to invade fresh water (Eylers, 1982). The catch connective tissue is quite sensitive to the ionic environment in the tissue. This dependence has led to the proposal of an "ionic environment hypothesis" for the viscosity change mechanism of the catch connective tissues (see review by Motokawa, 1984c). In fresh water, echinoderms may have difficulties in maintaining the ionic environment of the catch connective tissues, and thus they may lose the ability to control the mechanical properties of their supportive systems.

Because this unique connective tissue is so deeply involved in the life of echinoderms, I believe that the study of this tissue provides answers to why echinoderms have such unique and different features from other animal phyla (Nichols, 1975).

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