Smart collagen in sea lilies

SIR — Sea lilies (Echinodermata; Crinoidea) are sedentary animals with a large crown of suspension-feeding arms and a jointed attachment stalk. The stalk can maintain an erect attitude or bend to permit changes in the orientation of the crown[1,2]. Despite this adaptability, the stalk lacks any form of muscle[3]. It has therefore been suspected[4,5] that the ligaments holding together its skeletal elements are 'smart' connective tissues. These tissues, also called mutable collagenous tissues, are unique to echinoderms. They can undergo drastic, nervously mediated changes in stiffness, switching between solid and semi-fluid states in less than a second[6,7]. We report here results of experiments which confirm that 'smart' connective tissues are indeed present in the sea-lily stalk.

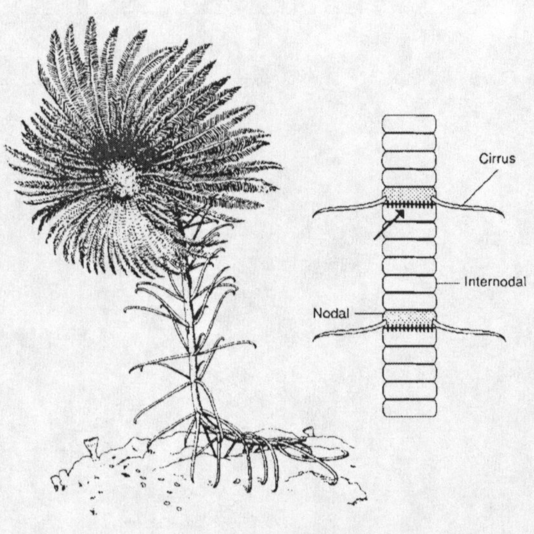

FIG. 1 *C. asterius* in a feeding attitude (after ref. 1, with permission), and on the right a diagrammatic representation of a short length of its stalk. The articulations between most of the ossicles are mobile. However, those between each nodal and the internodal below it are rigid junctions specialized for autotomy (arrow).

Specimens of the sea lily *Cenocrinus asterius* (L.) were collected at a depth of 600 m by the *Johnson-Sea-Link I* submersible at Egg Island and Chub Cay, Commonwealth of the Bahamas. The animals were kept in a darkened aquarium at 10 °C on board RV *Seward Johnson* and used within 4 days of capture.

The endoskeleton of the sea-lily stalk consists of a series of washer-shaped ossicles which in *C. asterius* are differentiated into nodals that carry jointed appendages known as cirri and internodals that lack cirri (Fig. 1). The flexibility of the stalk depends on the presence of mobile joints between most of the ossicles, the only exception being the junction between each nodal and the internodal below it which is a rigid joint specialized for autotomy. All these joints are connected by collagenous ligaments[3].

We performed tests on short lengths of stalk consisting of 7–9 internodals and including only mobile articulations. They were attached to a transducer as shown in Fig. 2*a* and subjected to a load of up to 100 g which tended to bend the stalk upwards. When a constant load was first applied, the preparations showed an immediate deflection which stabilized within a few seconds. When flooded subsequently with medium containing an elevated potassium ion concentration which would be expected to depolarize neural elements, such preparations exhibited a further deflection and then stabilized again (Fig. 2*b*).

Elevated K^+ concentrations had no effect on preparations which had been immersed in a sea water solution of the anaesthetic propylene phenoxetol, although they became responsive again after a wash in normal sea water. The preparations were also subjected to a stepwise increase in load before and after exposure to elevated K^+ concentrations. Excess K^+ increased the flexibility of the preparations, that is, the amount of deflection under a given load, an effect that could be reversed by returning them to normal sea water (Fig. 2*c*). Such potassium-induced alterations in mechanical behaviour can be due only to changes in the stiffness of the ligaments between the stalk ossicles: it is highly unlikely that other soft tissues such as epidermis or nerves[3] could contribute mechanically to the recorded responses. The reversible abolition of responsiveness to K^+ by anaesthesia suggests that these ions depolarize neural elements that influence the stiffness of the stalk ligaments. Similar neurally mediated responses have been demonstrated in mutable collagenous tissues in other echinoderms and are known to depend on changes in the cohesive properties of the molecular 'glue' that binds together the collagen fibrils in these tissues[6,7].

The sea-lily stalk acts primarily as a rigid strut keeping the main body of the animal well clear of the sea floor. However, the presence of mutable collagenous tissues enables its flexibility to be adjusted so that the body can be re-orientated in response to changes in current strength and direction and thus maximise the food-collecting potential of its arms[2,8,9]. The

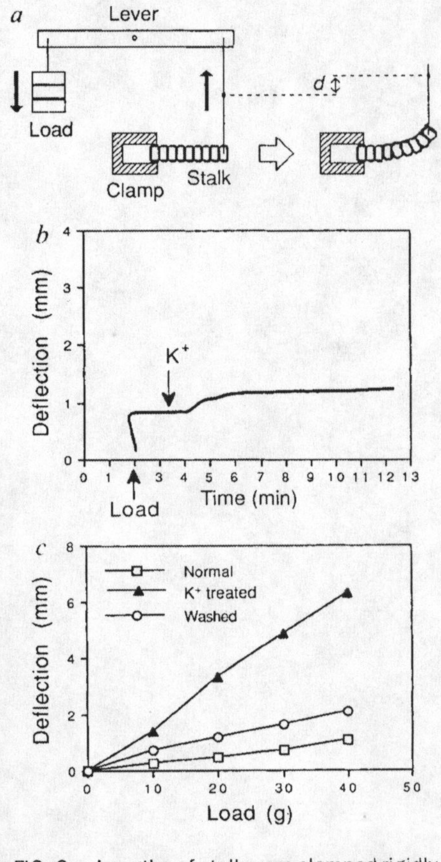

FIG. 2 *a*, Lengths of stalk were clamped rigidly at one end and the other end was attached to the lever of an isotonic transducer. Loads applied through the lever caused an immediate upwards deflection (*d*) of the stalk. *b*, Tracing of a curvilinear oscillograph recording of deflection against time for a typical preparation under constant load. The preparation was subjected to a load of 5 g which caused an immediate deflection, then flooded with 0.56 M potassium chloride (K^+) which caused a further deflection. *c*, Excess K^+ caused a reversible increase in the flexibility of internodal preparations. Typical results from a single preparation are given. Before treatment this was subjected to a load which increased by 10 g increments every 30 s. This procedure was repeated after the preparation had been immersed in 0.56 M KCl and then again after a prolonged sea water wash.

1. Messing, C. G. in *Proc. 5th Int. Echinoderm Conf.* (eds Keegan, B. F. & O'Connor, B. D. S.) 185–193 (Balkema, Rotterdam, 1985).
2. Baumiller, T. K., LaBarbera, M. & Woodley, J. D. *Bull. mar. Sci.* **48**, 731–748 (1991).
3. Grimmer, J. C., Holland, N. D. & Hayami, I. *Zoomorphology* **105**, 39–50 (1985).
4. Donovan, S. K. *Lethaia* **23**, 291–296 (1990).
5. Baumiller, T. K. & LaBarbera, M. *Comp. biochem. Physiol.* **106A**, 91–95 (1993).
6. Wilkie, I. C. *Mar. Behav. Physiol.* **11**, 1–34 (1984).
7. Wilkie, I. C. & Emson, R. H. in *Echinoderm Phylogeny and Evolutionary Biology* (eds Paul, C. R. C. & Smith, A. B.) 311–330 (Clarendon, Oxford, 1988).
8. Messing, C. G., RoseSmyth, M. C., Mailer, S. R. & Miller, J. E. *Bull. mar. Sci.* **42**, 480–487 (1988).
9. Baumiller, T. K. *J. Paleont.* **66**, 658–665 (1992).
10. Ausich, W. I. & Bottjer, D. J. in *Proc. 5th Int. Echinoderm Conf.* (eds Keegan, B. F. & O'Connor, B. D. S.) 3–11 (Balkema, Rotterdam, 1985).

sea lilies are the only survivors of a wide diversity of stalked echinoderms which thrived in Palaeozoic seas[10]. Although all of these were heavily calcified, there is extraordinarily little evidence for the occurrence of muscles in most of them, even in their feeding appendages (equivalent to the arms of sea lilies)[7]. It is, however, highly unlikely that their lives were spent in a state of perpetual unresponsive rigidity or flaccidity. The stalk of modern sea lilies illustrates how mutable collagenous tissues, in combination with external agents such as gravity and water movements[2,8,9], could have conferred mechanical adaptability on these animals.

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