Marine Environmental Research 93 (2014) 123–132

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Comparing dynamic connective tissue in echinoderms and sponges: Morphological and mechanical aspects and environmental sensitivity

Michela Sugni [a], Dario Fassini [a], Alice Barbaglio [a,*], Anna Biressi [a], Cristiano Di Benedetto [a], Serena Tricarico [a], Francesco Bonasoro [a], Iain C. Wilkie [b], Maria Daniela Candia Carnevali [a]

[a] Department of Biosciences, University of Milan, Via Celoria 26, 20133 Milan, Italy
[b] Department of Life Sciences, Glasgow Caledonian University, Cowcaddens Rd, Glasgow G4 0BA, UK

A R T I C L E I N F O

Article history:
Received 9 July 2013
Accepted 31 July 2013

Keywords:
Echinoderms
Sponges
Collagen
Mutable collagenous tissues
Temperature
Ionic strength

A B S T R A C T

Echinoderms and sponges share a unique feature that helps them face predators and other environmental pressures. They both possess collagenous tissues with adaptable viscoelastic properties. In terms of morphology these structures are typical connective tissues containing collagen fibrils, fibroblast- and fibroclast-like cells, as well as unusual components such as, in echinoderms, neurosecretory-like cells that receive motor innervation. The mechanisms underpinning the adaptability of these tissues are not completely understood. Biomechanical changes can lead to an abrupt increase in stiffness (increasing protection against predation) or to the detachment of body parts (in response to a predator or to adverse environmental conditions) that are regenerated. Apart from these advantages, the responsiveness of echinoderm and sponge collagenous tissues to ionic composition and temperature makes them potentially vulnerable to global environmental changes.

1. Introduction

Marine invertebrates often display morphofunctional adaptations that contribute markedly to their ecological success. Echinoderms and sponges are among the most representative groups in the marine environment; despite their phylogenetic distance, they share the presence of very peculiar connective tissues, regarded as “dynamic” or “mutable”, due to their unusual ability to reversibly change their mechanical properties (Wilkie, 2005; Wilkie et al., 2006). The so-called mutable collagenous tissues (MCT) of echinoderms are the best-known and characterized examples of dynamic connective tissues and their microstructure, physiology, biomechanics and biochemistry have recently undergone intensive investigation (Barbaglio et al., 2012; Ribeiro et al., 2011, 2012a, 2012b; Tamori et al., 2010; Wilkie, 2005; Yamada et al., 2010). Since in echinoderms the phenomenon of connective tissue mutability is under direct nervous control, this allows the animal to control the mechanical state of the tissue according to specific functional needs (Wilkie, 2005). MCTs play a key role in echinoderm biology and ecology, being involved in many important physiological phenomena such as autotomy, asexual reproduction and energy-sparing postural control (often in cooperation with muscle activity) (Wilkie, 2005).

In sponges comparable dynamic phenomena, particularly involving changes in the mechanical properties of the collagenous mesohyl, have been reported in *Pseudocorticium jarrei* (Boury-Esnault et al., 1995), *Oscarella lobularis* (Sarà and Vacelet, 1973), *Chondrilla nucula* (Gaino and Pronzato, 1983; Sidri et al., 2005), *Plakina weinbergi* (Muricy et al., 1998) and *Clathrina clathrus* (Gaino et al., 1991). These phenomena can be easily observed in the field, in both natural and experimental conditions, and are expressed as the marked loss of body stiffness (with production of long propagules) or by increased body stiffness after repeated mechanical stimulation. In this phylum the species demonstrating the presence of dynamic tissue most convincingly is the marine demosponge *Chondrosia reniformis*. This sponge shows unexpected mesohyl properties, being able to become stiff or pliant in response to specific stimuli, which is reminiscent of some mechanical aspects of echinoderm MCT. This intriguing similarity led us to investigate in depth sponge mutability in terms of microstructure (Bonasoro et al., 2001), physiology and biomechanics (Fassini et al., 2012; Parma et al., 2007; Wilkie et al., 2006). When compared with MCT behaviour, these phenomena, which are clearly cell-mediated

* Corresponding author. Tel.: +39 02 50314796.
E-mail addresses: michela.sugni@unimi.it (M. Sugni), dario.fassini@unimi.it (D. Fassini), alice.barbaglio@unimi.it (A. Barbaglio), anna.biressi@gmail.com (A. Biressi), cristiano.dibenedetto@unimi.it (C. Di Benedetto), francesco.bonasoro@unimi.it (F. Bonasoro), i.wilkie@gcu.ac.uk (I.C. Wilkie), daniela.candia@unimi.it (M.D. Candia Carnevali).

0141-1136/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.marenvres.2013.07.010

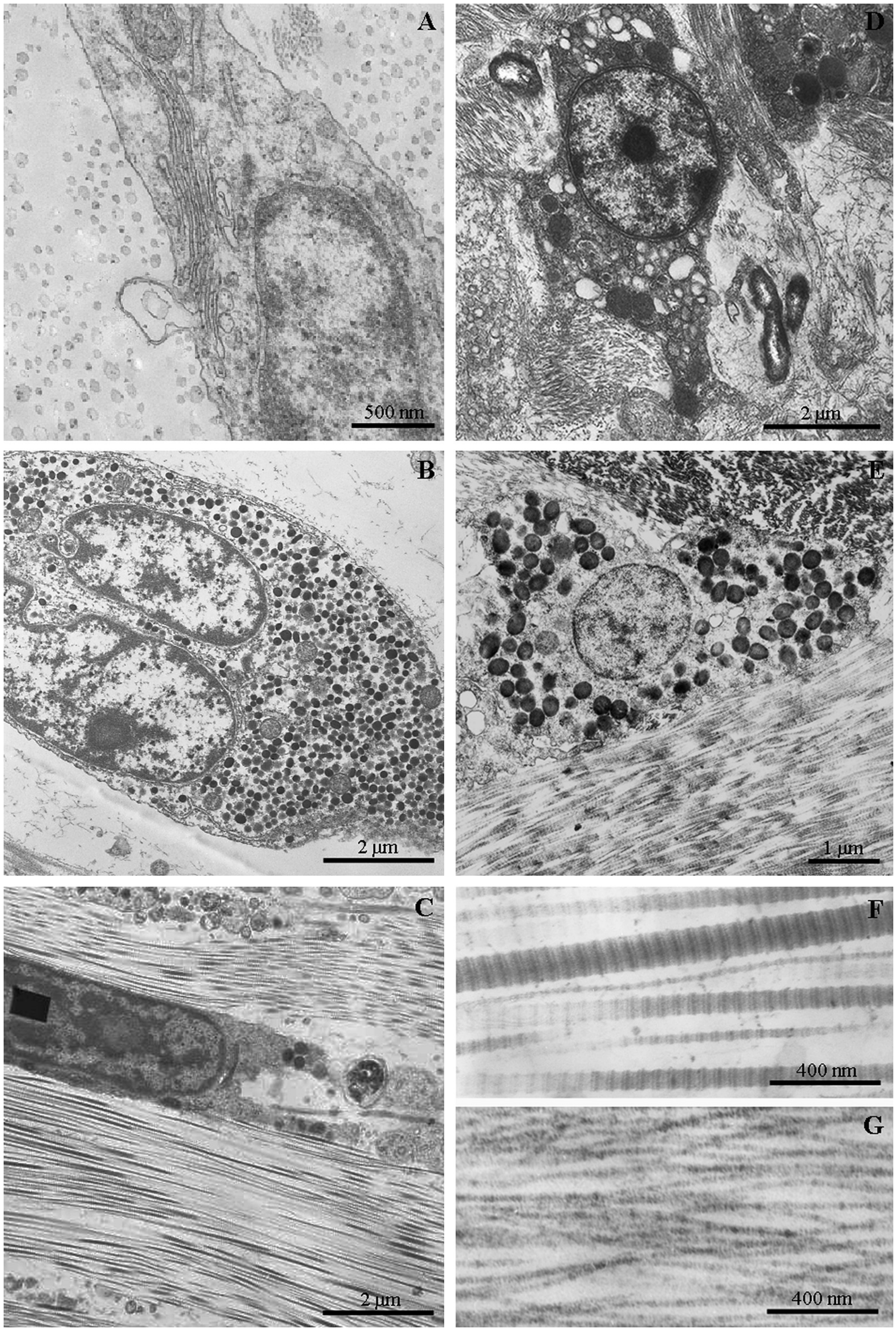

Fig. 1. Comparison of echinoderm and sponge collagenous tissue ultrastructure. TEM. A, D) Fibroblast-like cells in a *P. lividus* mutable ligament (A) and in *C. reniformis* mesohyl (D). B, E) Putative effector cells: *P. lividus* juxtaligamental cells (B) and *C. reniformis* gray cell (E). C) *P. lividus* phagocyte encircling a collagen fibril. Note the distinctive iron crystal present in the nucleus. F, G) Collagen fibrils: *P. lividus* (F) collagen fibrils show a wider diameter than those of *C. reniformis* (G).

(Wilkie et al., 2006), appear to depend closely on environmental factors (*e.g.* temperature and substratum instability: Fassini et al., 2012; Parma et al., 2007). In particular, the ability to lose tensility (creeping phenomenon) and produce terminal propagules when part of the substratum becomes detached is regarded as a passive form of asexual reproduction that can both preserve the viability of the parent sponge and allow the formation of a new individual by cloning (Bavestrello et al., 1998; Connes, 1967; Di Camillo et al., 2012; Fassini et al., 2012; Gaino and Pronzato, 1983; Sarà and Vacelet, 1973; Zilberberg et al., 2006). The capacity to modulate such a process could represent added value for the success of this asexual reproductive strategy, allowing the sponge to modulate the speed of creeping, or completely stop the phenomenon and the release of the terminal propagules when environmental conditions