Available online at www.sciencedirect.com
ScienceDirect
micron
Micron 39 (2008) 209–228
www.elsevier.com/locate/micron

Review

Structure and composition of calcareous sponge spicules: A review and comparison to structurally related biominerals

Ingo Sethmann [a,*], Gert Wörheide [b]

[a] *Institut für Mineralogie, Universität Münster, Corrensstr. 24, D-48149 Münster, Germany*
[b] *Geowissenschaftliches Zentrum Göttingen, Abteilung Geobiologie, Universität Göttingen, Goldschmidtstr. 3, D-37077 Göttingen, Germany*

Received 9 November 2006; received in revised form 18 January 2007; accepted 18 January 2007

Abstract

Since the early 19th century, the skeletons of calcareous sponges (Porifera: Calcarea) with their mineralized spicules have been investigated for their morphologies, structures, and mineralogical and organic compositions. These biomineral spicules, up to about 10 mm in size, with one to four rays called actines, have various specific shapes and consist mainly of magnesium-calcite: in only one case has an additional phase of stabilized amorphous $CaCO_3$ (ACC) been discovered. The spicules are invariably covered by a thin organic sheath and display a number of intriguing properties. Despite their complex morphologies and rounded surfaces without flat crystal faces they behave largely as single crystal individuals of calcite, and to some degree crystallographic orientation is related to morphology. Despite their single-crystalline nature, most spicules show nearly isotropic fracture behaviour, not typical for calcite crystals, indicating enhanced fracture resistance. These unusual morphological and mechanical properties are the result of their mechanism of growth. Each spicule is formed by specialized cells (sclerocytes) that supply mineral ions or particles associated by organic macromolecules to extracellular cavities, where assembly and crystallization in alignment with an initial seed crystal (nucleus) takes place. As a result of discontinuous mineral deposition, cross-sections of larger spicules display concentric layering that mantles a central calcitic rod. On a smaller scale, the entire spicule displays a 'nano-cluster' structure with crystallographically aligned and putatively semicoherent crystal domains as well as a dispersed organic matrix intercalated between domain boundaries. This ultrastructure dissipates mechanical stress and deflects propagating fractures. Additionally, this nano-cluster construction, probably induced by intercalated organic substances, enables the formation of complex crystal morphologies independent of crystal faces. In this review, the current knowledge about the structure, composition, and formation of calcareous sponge spicules is summarised and discussed. Comparisons of calcareous sponge spicules with the amorphous silica spicules of sponges of the classes Hexactinellida and Demospongiae, as well as with calcitic skeletal elements of echinoderms are drawn. Despite the variety of poriferan spicule mineralogy and the distant phylogenetic relationship between sponges and echinoderms, all of these biominerals share similarities regarding their nano-scale construction. Furthermore, echinoderm skeletal elements resemble calcareous sponge spicules in that they represent magnesium-bearing calcite single-crystals with extremely complex morphologies.

Keywords: Biomineralization; Calcarea; Calcite; Echinodermata; Porifera; Single-crystals; Silica; Skeletons; Sponges; Ultrastructure

Contents

* Corresponding author. Fax: +49 251 1449635.
E-mail address: isethma@uni-muenster.de (I. Sethmann).

0968-4328/$ – see front matter
doi:10.1016/j.micron.2007.01.006

1. Introduction

Sponges (Porifera Grant, 1836) possess the most primitive morphology of all animals (Metazoa), lacking distinct tissues and organs as they occur in all more complex animals that possess those traits (Eumetazoa) (Hooper and Van Soest, 2002). Adult sponges are sessile, predominantly marine, and feed on suspended organic particles and micro-organisms by actively filtering ambient water through an aquiferous system. In the simplest case, the so-called asconid body plan, the sponge body is tube- or bottle-shaped with an apical opening (osculum), and numerous small pores (ostia) and unbranched canals that perforate the body wall (Fig. 1). Flagellated cells (choanocytes) line the canals and the inner body wall (choanoderm) and produce a water current that flows from the exterior through the ostia and canals into the inner cavity (atrium), and leaves the sponge body through the osculum. In the so-called syconid and leuconid grade of aquiferous system-construction, the choanoderm is folded to increase its surface, resulting in a more complex system of branched canals and distinct choanocyte chambers. A general description of sponge anatomy is given by Boury-Esnault and Rützler (1997). In order to maintain morphological rigidity of the body wall and aquiferous system, most sponges produce mineralized spicular skeletons (see Fig. 1) that consist either of silica (skeletal opal, in the Hexactinellida and Demospongiae) (reviews: Simpson, 1984; Uriz et al., 2003a,b; Müller et al., 2006; Uriz, 2006) or of calcium carbonate (almost exclusively calcite, in the Calcarea) (reviews: Jones, 1970; Simpson, 1984; see also Uriz, 2006). However, some demosponges, for example the ‘Keratosa’ (a polyphyletic group, not defined by common ancestry), only produce collagenous spongin-fibres and completely lack mineralized spicules (e.g., Hooper and Van Soest, 2002). Another polyphyletic group of sponges formerly known as ‘Sclerospongiae’ produce a secondary calcareous skeleton of aragonite or Mg-calcite, in addition to their primary spicular skeleton (e.g., Reitner, 1992; Wörheide, 1998).

In the present review, we will focus on the calcareous primary spicules of the poriferan class Calcarea, comprising exclusively marine species. These spicules occur in various elaborate shapes and in a size range of several micrometres to centimetres. Apparently species-specific varieties of spicules, together with their spatial arrangement and mineralogy have been used as distinctive criteria for sponge taxonomy and systematics (e.g., Haeckel, 1872; Wörheide and Hooper, 1999, 2003; Manuel et al., 2002; Borojevic et al., 2002a,b,c; Vacelet et al., 2002a,b) although recent molecular-systematic studies have demonstrated that the existing systematic system of the Calcarea is probably highly artificial (Dohrmann et al., 2006). However, despite their low complexity of body organization and lack of specialized intercellular communication (nerve) system, the high degree of architectural complexity and diversity of forms and shapes of skeletal elements in different sponge groups makes it clear that controlled biomineralization *sensu* Mann (1983) occurs by the concerted action of specialized cells.

Early investigators of sponge biology and taxonomy have already described spicules and skeletal structures using light microscopic techniques. They have also addressed the process of formation of the elaborate spicules, their ultrastructure, and the composition of the spicule materials. These detailed analyses are the basis for refined contemporary studies on $CaCO_3$ biomineralization in sponges. Therefore, the following review comprises the recent developments in sponge spicule research, and also gives an account of early fundamental works (for reviews, see Haeckel (1872) and Minchin (1909)) as a basis for discussion.

2. Spicule types

The spicular skeletons of the Calcarea consist of calcareous spicules with a considerable morphological diversity, in the two subclasses Calcinea and Calcaronea with four basic spicule types, classified by their numbers of actines that grow outwards from a common point of origin. Monactines are spicules with a simple, needle-like, in some cases slightly curved geometry, with the tip growing out from one end (Fig. 2c). There are various different characteristic forms of monactine ‘heads’. Diactines have a similar appearance but with two opposite tips (Fig. 2b). In triactines the three actines may be oriented in various ways, the simplest being the regular star-shaped spicules, with the equiradiate actines oriented in one plane, enclosing angles of 120°, respectively (Fig. 2a). Additionally, there are several variations of this basic regular triactine geometry, usually with one straight basal actine, and the other two actines deformed as a morphologically inverse pair, as in ‘tuning fork’ triactines with two actines curved upwards, or in ‘sagittal’ triactines with two actines curved downwards, with two equal angles and one unequal angle between them. In other triactines the rays are not oriented in a plane but may show