New species from the deep Pacific suggest that carnivorous sponges date back to the Early Jurassic.

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Some deep-sea poecilosclerid sponges (Porifera) have developed a carnivorous feeding habit that is very surprising in sponges¹. As shown by the typical morphology of their spicules, they most probably evolved from "normal sponges" under the difficult conditions of a deep-sea environment. Such evolution, which implies the loss of the diagnostic character of the phylum Porifera, i.e. a filter feeding habit through a complex aquiferous system, should be of great interest in the understanding of the origin of metazoans. Some scenarios, based on the hypothesis of the paraphyly of Porifera, allege that metazoans could derive from a sponge filter-feeding body plan. A difficulty, however, is to imagine the transition from a sponge grade of organization to other organization plans². Carnivorous sponges demonstrate that a functional, non filter-feeding animal may derive from a conventional sponge body plan, albeit

nothing is known of the age of this evolution. Here we report that newly discovered species of *Chondrocladia* from the deep Pacific display special spicules that were previously recorded only as isolated spicules from sediment dating back to the Early Jurassic and Miocene periods. This suggests that the evolution of carnivorous sponges from filter-feeding poecilosclerid demosponges could date back at least from the Early Mesozoic.

Sponges (Porifera) are filter-feeding animals, with a body plan entirely devoted to filtering large amounts of water, devoid of specialized tissue and organs, and in which cells act individually. The discovery that such a body plan could have evolved in another organization scheme, enabling a macrophagic, carnivorous feeding habit, was highly surprising¹. This evolution implies the loss of the diagnostic feature of Porifera, i.e. an aquiferous system and choanocyte chambers, whereas they conserved the relative independency of cells and the absence of organs, including a digestive tract³. This evolution may have important consequences in the hypothesis that the last common ancestor of metazoans had a filter-feeder organization similar to that of sponges, a hypothesis that has been strengthened by recent results suggesting that sponges are paraphyletic⁴⁻⁶. The spicule complement suggests that carnivorous sponges, at present localized in deep-sea environments, derived from poecilosclerid demosponges. Their relationships with "normal" poecilosclerids, however, are poorly understood⁷. Furthermore, we have no idea of when this evolution occurred in the geological time. Carnivory in sponges is not at all easy to demonstrate in the deep sea, where it is for most species inferred from their morphology, and virtually impossible in the fossil record. The only, very faint indication is from an Ordovician sponge,

Saccospongia baccata, which displays a gross morphology rather similar to that of a deep Pacific sponge, *Esperiopsis desmophora*, which has a stipitate shape and an anatomy suggestive of carnivory⁸.

Recent results have shown that the carnivorous sponges, at present classified in three families of Poecilosclerida, are far more diversified in the deep sea than previously believed. Direct observation and collection techniques by submarines and remotely operated underwater vehicles (ROVs) have provided a number of new species^{7,9-13}, especially in the deep Pacific. Among these, we have found two new species of Chondrocladia (Cladorhizidae), which display a special spicule, a rhabd with a straight shaft ending in a rugose, unequal swelling at each end and bearing one to three rings (Fig. 1). Until now, such spicules have been unknown in the Recent, but are remarkably similar, although smaller, to peculiar fossil spicules found free in sediments of the Early Jurassic of the Northern Calcareous Alps¹⁴ (Fig. 2). Similar spicules have also been recorded from strata of deep-sea sediments dating back to the Miocene from the NE Atlantic near Iceland¹⁵. These fossil spicules were termed 'microcricorhabds'¹⁴, deriving from 'cricorhabd', a general term coined¹⁶ for monaxial spicules bearing a series of annuli. The Recent, and Northern Calcareous Alps fossil spicules, are more differentiated, and we propose for them the new term 'trochirhabd', derived from the Greek troch, disc, spinning top, and rhabd, straight rod, referring to their resemblance to some spinning tops. Their discovery in modern Chondrocladia indicates that this carnivorous sponge genus already existed in the Early Jurassic.

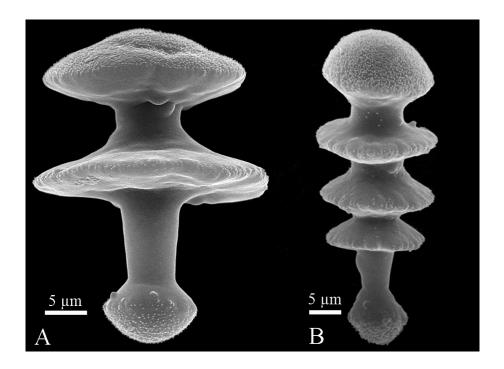
Among carnivorous sponges, *Chondrocladia* spp. are rather special. In contrast to other genera (*Asbestopluma, Abyssocladia, Cladorhiza, Esperiopsis (pars*),

Euchelipluma, and *Lollipocladia*) that have lost the aquiferous system and the choanocyte cells, *Chondrocladia* has conserved an aquiferous system including choanocytes, albeit considerably modified. The aquiferous system is not apparently used for water filtration, but for the inflation of turgescent spheres, the surface of which prey capture is performed upon¹⁷. Sponges of this genus are stipitate, consisting of a stalk frequently anchored in the deep-sea mud by a rhizoid system, and an ovoid body with or without lateral appendages ending in inflatable spheres.

The genus *Chondrocladia* numbers at present 33 species, not including a tenth new species that we have in the process of description. Among them, three species are distinguished by a stalk lined with a dense cover of trochirhabds. Two are undescribed species from New Zealand and South Australia, which we will describe elsewhere. The third, *Chondrocladia occulta*¹⁸, known by a single specimen from the deep North Pacific, has been incorrectly identified as a chimera sponge, a *Chondrocladia concrescens* bearing a diminished epizoic species of *Latrunculia* on the stalk, a misinterpretation due to a superficial resemblance of trochirhabds with the discorhabds characteristic of Latrunculiidae. The three species of *Chondrocladia* with trochirhabds have the same gross morphology, being stipitate with a globular body devoid of the lateral expansions ending in inflatable spheres found in many *Chondrocladia*. They may thus represent a new genus.

This discovery indicates that carnivorous sponges, bearing the same special spicules as their ancestor from the Early Jurassic, thrive today in the deep Pacific. Although the presence of a spicule type does not constitute absolute evidence of a carnivorous feeding habit, the similarity of the trochirhabds of the Recent species and

of the fossil strata strongly suggests that stipitate *Chondrocladia* representatives date back from the Early Jurassic. The identification of this genus in Jurassic strata was already suggested by Mostler (1990)¹⁴ on the basis of the presence of unguiferate isochelae microscleres. However, these isochelae, which are found in several Poecilosclerida, are not unique to *Chondrocladia*. The first poecilosclerid sponges are documented by isolated spicules from the Permian, and they were already common by Middle Triassic¹⁹. The evolution to carnivory apparently preceded their greatest diversification in the Cretaceous, which led to the modern poecilosclerid fauna, already represented in Eocene strata²⁰.





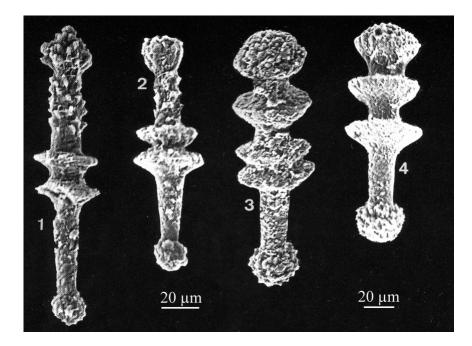




Figure legends

Fig. 1: Trochirhabds of Chondrocladia spp. A: sp. 1 (from Australia); B: sp.2 (from New Zealand)

Fig. 2: Trochirhabds from sediment of the Lower Liassic of the Northern Calcareous

Alps (from Mostler, 1990)

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