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

Jean Vacelet[1] & Michelle Kelly[2]

[1]*Centre d'Océanologie de Marseille, Aix-Marseille Université, CNRS UMR 6540 DIMAR, Station Marine d'Endoume, rue Batterie des Lions, 13007 Marseille, France (jean.vacelet@univmed.fr)*

[2]*National Centre for Aquatic Biodiversity and Biosecurity, National Institute of Water & Atmospheric Research Ltd, P. O. Box 109-695, Newmarket, Auckland, New Zealand (m.kelly@niwa.co.nz)*

Some deep-sea poecilosclerid sponges (Porifera) have developed a carnivorous feeding habit that is very surprising in sponges[1]. 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 plans[2]. 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 surprising[1]. 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 tract[3]. 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 paraphyletic[4-6]. 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 understood[7]. 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 carnivory[8].

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 Alps[14] (Fig. 2). Similar spicules have also been recorded from strata of deep-sea sediments dating back to the Miocene from the NE Atlantic near Iceland[15]. These fossil spicules were termed 'microcricorhabds'[14], deriving from 'cricorhabd', a general term coined[16] 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 upon[17]. 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 Triassic[19]. The evolution to carnivory apparently preceded their greatest diversification in the Cretaceous, which led to the modern poecilosclerid fauna, already represented in Eocene strata[20].

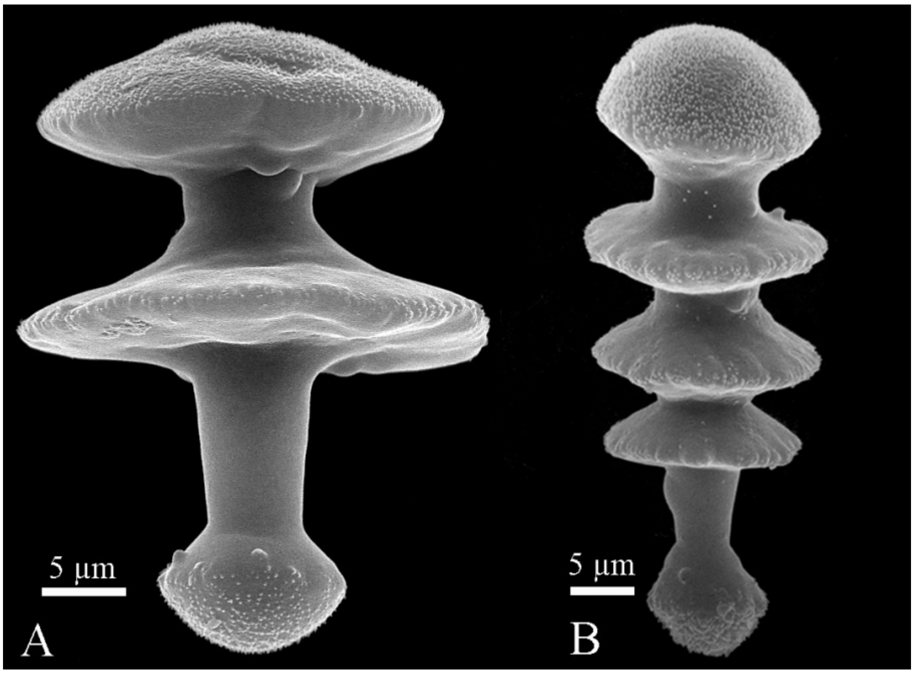

Fig. 1

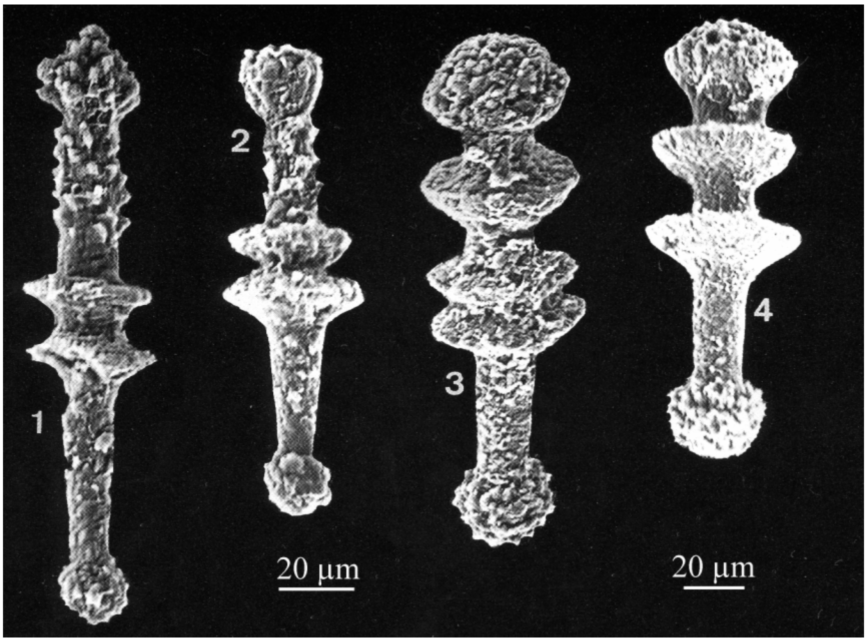

Fig. 2

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)

References

1.Vacelet, J. & Boury-Esnault, N. Carnivorous sponges. *Nature* **373**(6512), 333-335 (1995).

2.Dewel, R. A. Colonial origin for Eumetazoa: major morphological transitions and the origin of bilaterian complexity. *J. Morphol.* **243**, 35-74 (2000).

3.Vacelet, J. & Duport, É. Prey capture and digestion in the carnivorous sponge *Asbestopluma hypogea* (Porifera: Demospongiae). *Zoomorphology* **123**, 179-190 (2004).

4.Borchiellini, C. *et al.* Sponge paraphyly and the origin of Metazoa. *J. Evol.Biol.* **14**(1), 171-179 (2001).

5.Peterson, K. J. & Butterfield, N. J. Origin of the Eumetazoa: Testing ecological predictions of molecular clocks against the Proterozoic fossil record. *Proc. natl. Acad. Sci., USA* **102**, 9547-9552 (2005).

6.Sperling, E. A., Pisani, D. & Peterson, K. J. Poriferan Paraphyly and its Implications for Precambrian Paleobiology, in *The Rise and Fall of the Ediacaran Biota* (eds Vickers-Rich, P. & Komarower, P.) 355-368 (Geological Society, London, Special Publication 286, London, 2007).

7.Vacelet, J. Diversity and evolution of deep-sea carnivorous sponges, in *Porifera Research: biodiversity, innovation and sustainability, Vol. Serie Livros 28* (eds Custódio, M. R. *et al.*) 107-115 (Museu Nacional, Rio de Janeiro, 2007).

8.Hooper, J. N. A. & Lévi, C. *Esperiopsis desmophora* n. sp. (Porifera: Demospongiae): a desma-bearing Poecilosclerida. *Mem. Queensl. Mus.* **27**, 437-441 (1989).

9.Vacelet, J. New carnivorous sponges (Porifera, Poecilosclerida) collected from manned submersibles in the deep Pacific. *Zool. J. Linn. Soc.* **148**, 553-584 (2006).

10.Vacelet, J. A new genus of carnivorous sponges (Porifera: Poecilosclerida, Cladorhizidae) from the deep N-E Pacific, and remarks on the genus *Neocladia*. *Zootaxa* **1752**, 57-65 (2008).

11. Cristobo, F. J., Urgorri, V. & Rios, P. Three new species of carnivorous deep-sea sponges from the DIVA-1 expedition in the Angola Basin (South Atlantic). *Organisms Diversity & Evolution* **5**(suppl. 1), 203-213 (2005).
12. Lehnert, H., Watling, L. & Stone, R. *Cladorhiza corona* sp. nov. (Porifera: Demospongiae: Cladorhizidae) from the Aleutian Islands (Alaska). *J. mar. biol. Assoc. U.K.* **85**(6), 1359-1366 (2005).
13. Reiswig, H. M. & Lee, W. L. A new species of *Cladorhiza* (Porifera: Cladorhizidae) from S. California (USA), in *Porifera Research: biodiversity, innovation and sustainability, Vol. Serie Livros 28* (eds Custódio, M. R. *et al.*) 517-523 (Museu Nacional, Rio de Janeiro, 2007).
14. Mostler, H. Mikroscleren von Demospongien (Porifera) aus dem basalen Jura der Nördlichen Kalkalpen. *Geol. Paläont. Mitt. Innsbruck* **17**, 119-142 (1990).
15. Bukry, D. 18. Coccolith and silicoflagellate stratigraphy, northern Mid-Atlantic Ridge and Reykjanes Ridge, Deep Sea Drilling Project leg 49, in *Initial Reports of the Deep Sea Drilling Project, Vol. 49* (eds Luyendyck, B. P. *et al.*) 551-581 (U.S. Governement printing Office, Washington, 1979).
16. Rauff, H. Palaeospongiologie. Parts I (1893) and II/1 (1894). *Palaeontographica* **40**, 1-232 (1893).
17. Kübler, B. & Barthel, D. A carnivorous sponge, *Chondrocladia gigantea* (Porifera: Demospongiae: Cladorhizidae), the giant deep-sea clubsponge from the Norwegian trench. *Mem. Queensl. Mus.* **44**, 289-298 (1999).

18. Lehnert, H., Stone, R. & Heimler, W. New species of Poecilosclerida (Demospongiae, Porifera) from the Aleutian Islands, Alaska, USA. *Zootaxa* **1155**, 1-23 (2006).

19. Reitner, J. & Wörheide, G. Non-Lithistid Fossil Demospongiae - Origins of their Palaeobiodiversity and highlights in history of preservation, in *Systema Porifera: A Guide to the Classification of Sponges, Vol. 1* (eds Hooper, J. N. A. & Soest, R. W. M. van) 52-68 (Kluwer Academic/Plenum Publishers, New York, 2002).

20. Hinde, G. J. & Holmes, W. M. On the sponge-remains in the lower tertiary strata near Oamaru, Otago, New Zealand. *J. Linnean Soc. London, Zool.* **24**, 177-263 (1892).

Acknowledgements.

The authors thank Dr Monika Schlacher-Hoenlinger for providing specimens of a new species of *Chondrocladia* with trochirhabds, from Tasmanian seamounts off southern Australia. Fieldwork leading to the discovery of New Zealand material of the same genus was supported by the Foundation for Research Science & Technology (Contract C01X0219) to the National Institute of Water & Atmospheric Research (NIWA), and is gratefully acknowledged.