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## Brown algae

J. Mark Cock<sup>1,2</sup>, Akira F. Peters<sup>2,3</sup> and Susana M. Coelho<sup>1,2</sup>

**What are brown algae?** Brown algae or brown seaweeds are the dominant organisms in many of the world's coastal regions, where they are responsible for the bulk of primary production, often forming extensive undersea forests that host a high level of biodiversity. From an evolutionary point of view, brown algae are members of the stramenopiles (or heterokonts), a group that has been evolving independently of the well-studied animal, fungal and green plant lineages for over a billion years. As a result of this unique evolutionary history, these organisms exhibit many novel features. For example, they represent one of a very limited number of eukaryotic groups that have independently evolved complex multicellularity. Brown algae also exhibit some remarkable characteristics in terms of their cell biology; cytokinesis for example having features typical of both animals (centrosomes) and green plants (centrifugal cell plate formation). Moreover, since their divergence from other eukaryotic groups, brown algae have evolved several innovative metabolic processes, making them highly interesting targets for the discovery of novel biomolecules for industrial use. There is also increasing interest in the use of brown algae as a source of biomass for fuel production due to their very rapid growth rates and the fact that cultivation does not compete with food crops for the use of arable land. The giant kelp, *Macrocystis pyrifera*, for example, is one of the largest and most rapidly growing organisms on the planet, reaching lengths of up to 60 metres.

**Has a model organism been developed to study all these interesting aspects of brown algal biology?** Yes, the small, filamentous brown alga *Ectocarpus* was proposed as a model organism for the brown algae about seven years ago and a number of genetic and molecular tools have been developed for this organism. Available tools include a considerable amount of cDNA and small RNA sequence data, various types of microarray, genetic methodologies and a genetic map. A transformation protocol, gene silencing techniques and a population adapted to the reverse genetic TILLING (Targeting Induced Local Lesions in Genomes) technique are under development.

**Why was *Ectocarpus* chosen as the model for this group of organisms?** The choice of *Ectocarpus* was based primarily on the fact that, in contrast to the much larger kelps, this small, filamentous alga is well adapted for genetic and genomic approaches. The life cycle of *Ectocarpus* is relatively short (3-4 months) and can be completed in the laboratory using simple culture conditions (Figure 1). Genetic techniques, such as crosses and mutant screens are possible. Strains can be grown axenically and can be maintained for long-term storage under low light condition, and many ecotypes are available. Importantly though, despite their relatively simple morphology, the Ectocarpales are one of the more recently evolved brown algal groups and are closely related to complex kelps of the group Laminariales. Information obtained using *Ectocarpus* as a model organism should therefore be relevant to the economically and ecologically important kelps.

**Do we have a genome sequence for *Ectocarpus*?** Yes, the complete genome sequence was published last year. As might have been expected, given the atypical evolutionary origin of this organism, the genome exhibits a number of remarkable features. For example, the genes are split into many short exons separated by long introns, and intergenic regions are often very short. One consequence of this is that intron sequence constitutes an unusually large proportion (40%!) of the genome.

**What biological processes can *Ectocarpus* be used to study?** Work on *Ectocarpus* dates back to the 19th century. Investigators initially concentrated on understanding its life cycle, which involves alternation between two independent, multicellular generations, the sporophyte and the gametophyte. Later work led to the characterisation of the pheromone that is produced by the female gamete to attract male gametes and to the characterisation of a giant DNA virus, EsV-1, which integrates into the alga's nuclear genome following infection.

Current research programs investigate several aspects of *Ectocarpus* biology. The life cycle continues to be an important area of study, with modern genetic methods now being employed to investigate the molecular mechanisms that underlie key life cycle transitions. For example, mutants have been obtained in which the alternation between the sporophyte and gametophyte generations is perturbed. Other active areas of study include sex determination, morphogenesis, gamete recognition, various aspects of metabolism including carbon storage and cell wall biosynthesis, and responses to both biotic and abiotic stress.

**You mentioned complex multicellularity, what is known about how this evolved in the brown algae?** Only five of the many phylogenetic groups of eukaryotic organisms are considered to have evolved complex multicellularity, which can be defined as the deployment of a developmental program that involves the creation of distinct organs made up of multiple different cell types. These five groups are the animals, green plants/algae, the fungi, the red algae and the brown algae. Multicellularity emerged independently in each of these groups, so that each can be considered to represent an individual evolutionary "experiment" and comparative analysis of the five lineages is expected to provide insights into the fundamental molecular processes underlying this key evolutionary transition. Unfortunately, very little is known about how developmental processes work in several of these groups, including the brown algae. The *Ectocarpus* genome sequence therefore presented an unparalleled opportunity to obtain some clues about how multicellularity might have emerged in this lineage. Analysis of the genome sequences identified several potentially important features, including the retention of key genes and gene families and the emergence of novel gene families. One particularly striking discovery was the identification of a family of membrane-localised receptor kinases, which is absent from unicellular members of the stramenopiles, such as the diatoms. Both animals and green plants possess families of membrane-localised receptor kinases. Importantly, not only do these molecules appear to have functions that are related to multicellular development, but they are encoded by gene families that evolved independently in the two lineages and their emergence may have been a key step along the path to multicellularity. Phylogenetic analysis of the *Ectocarpus* receptor kinase family indicated that it too evolved independently, substantially reinforcing the link between the invention of receptor kinases and the transition to multicellularity.

### **Where can I find out more?**

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- The *Ectocarpus* genome: <http://bioinformatics.psb.ugent.be/webtools/bogas/>

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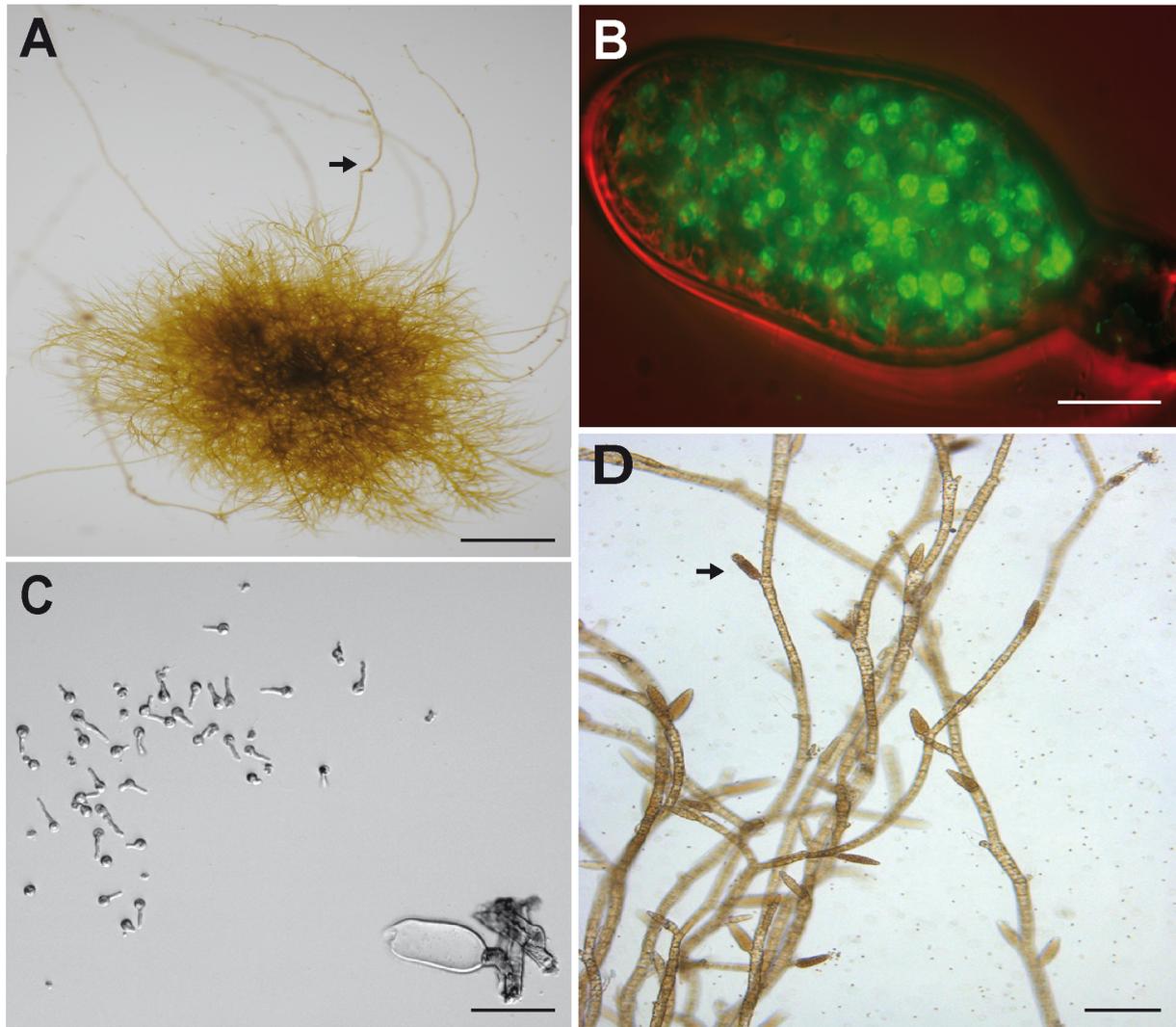


Figure 1. The *Ectocarpus* life cycle under laboratory conditions.

(A) *Ectocarpus* sporophyte showing the upright filaments (arrow) that bear the reproductive structures emerging from a densely branched, prostrate base. Size bar = 200  $\mu\text{m}$ . (B) DAPI-stained (green) meiospores within a unilocular sporangium borne by a sporophyte. Size bar = 20  $\mu\text{m}$ . (C) Germinating meiospores released from a single, isolated unilocular sporangium. The meiospores, which are all derived from a single meiotic event (followed by several mitoses), will develop to produce the gametophyte generation. Size bar = 100  $\mu\text{m}$ . (D) Mature gametophyte filaments releasing gametes (dark spots) into the medium from plurilocular gametangia (arrow). Size bar = 100  $\mu\text{m}$ .