LETTERS

The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae

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Brown algae (Phaeophyceae) are complex photosynthetic organisms with a very different evolutionary history to green plants, to which they are only distantly related[1]. These seaweeds are the dominant species in rocky coastal ecosystems and they exhibit many interesting adaptations to these, often harsh, environments. Brown algae are also one of only a small number of eukaryotic lineages that have evolved complex multicellularity (Fig. 1). We report the 214 million base pair (Mbp) genome sequence of the filamentous seaweed *Ectocarpus siliculosus* (Dillwyn) Lyngbye, a model organism for brown algae[2–5], closely related to the kelps[6,7] (Fig. 1). Genome features such as the presence of an extended set of light-harvesting and pigment biosynthesis genes and new metabolic processes such as halide metabolism help explain the ability of this organism to cope with the highly variable tidal environment. The evolution of multicellularity in this lineage is correlated with the presence of a rich array of signal transduction genes. Of particular interest is the presence of a family of receptor kinases, as the independent evolution of related molecules has been linked with the emergence of multicellularity in both the animal and green plant lineages. The *Ectocarpus* genome sequence represents an important step towards developing this organism as a model species, providing the possibility to combine genomic and genetic[2] approaches to explore these and other[4,5] aspects of brown algal biology further.

The 16,256 protein coding genes present in the 214 Mbp haploid male genome of *E. siliculosus* are rich in introns (seven per gene on average), have long 3′ untranslated regions (average size: 845 bp) and are often located very close to each other on the chromosome (29% of the intergenic regions between divergently transcribed genes are less than 400 bp long; Table 1 and Supplementary Information 2.1).

Repeated sequences, including DNA transposons, retrotransposons and helitrons, make up 22.7% of the *Ectocarpus* genome. Small RNAs mapped preferentially to transposons, indicating that they have a role

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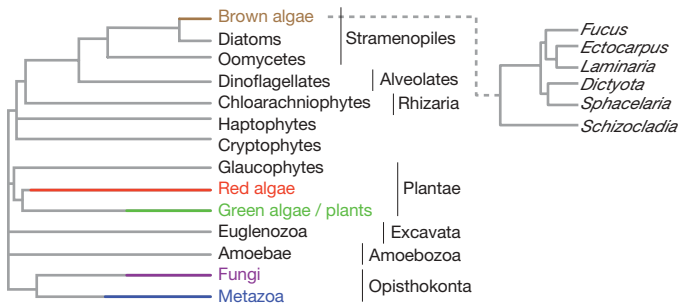
Figure 1 | Simplified representation of the evolutionary tree of the eukaryotes showing the five major groups that have evolved complex multicellularity (indicated in colour). Here we define groups showing complex multicellularity as those that include macroscopic organisms with defined, recognizable morphologies and composed of multiple cell types. Coloured bars indicate the approximate, relative times of emergence of complex multicellularity in each lineage. The inset tree to the right indicates the relationship of *Ectocarpus* to selected brown algal genera. Kelps are represented in the tree by the genus *Laminaria*.

in silencing these elements despite the absence of detectable levels of cytosine methylation in the genome (Supplementary Information 2.1). Sequencing also revealed the presence of an integrated copy of a large DNA virus, closely related to the *Ectocarpus* phaeovirus EsV-1 (ref. 8; Fig. 2a). Approximately 50% of individuals in natural *Ectocarpus* populations show symptoms of viral infection[9,10] but the sequenced *Ectocarpus* strain Ec 32 has never been observed to produce virus particles and expression analysis showed that almost all of the viral genes were silent (Fig. 2b and Supplementary Information 2.1.17).

The shallow waters of the intertidal region are an attractive habitat for marine, sedentary, photosynthetic organisms providing them with both a substratum and access to light. However, the shoreline is a also a hostile environment necessitating an ability to cope with tidal changes in light intensity, temperature, salinity and wave action, and with the biotic stresses characteristic of dense coastal ecosystems. Several features of the *Ectocarpus* genome indicate that this alga has evolved effective mechanisms for survival in this environment (Supplementary Information 2.2). For example, there is a large family of light harvesting complex (LHC) genes in *Ectocarpus* (53 loci, although some are probably pseudogenes), including a cluster of 11 genes with highest similarity to the LI818 family of light-stress related LHCs. The *Ectocarpus* genome is also predicted to encode a light-independent protochlorophyllide reductase (DPOR), allowing efficient synthesis of chlorophyll under dim light (Supplementary Information 2.2.2 and 2.2.3). Together these data indicate that *Ectocarpus* has a complex photosynthetic system that should enable

it to adapt to an environment with highly variable light conditions. The high levels of phenolic compounds in brown algae are thought to protect against ultraviolet radiation, in a manner analogous to flavonoids in terrestrial plants[11]. Homologues of most of the terrestrial plant flavonoid pathway genes were found in *Ectocarpus* but these are completely absent from diatom or green algal genomes (Supplementary Information 2.2.9). The diverse complement of enzymes involved in the metabolism of reactive oxygen species (Supplementary Information 2.2.11) is also likely to represent an important adaptation to osmotic and light stresses.

In the Laminariales, the high concentration of apoplastic iodide is thought to be used in a new anti-oxidant system that, through the emission of iodine, has an impact on atmospheric chemistry[12]. *Ectocarpus* also accumulates halides, although to a significantly lower level than in kelps (Supplementary Information 2.2.10). This difference was reflected in the genome; only one vanadium-dependent bromoperoxidase was found in contrast to the large families of haloperoxidases in *Laminaria digitata*[13]. The *Ectocarpus* genome does, however, encode 21 putative dehalogenases and two haloalkane dehalogenases. These enzymes may serve to protect *Ectocarpus*
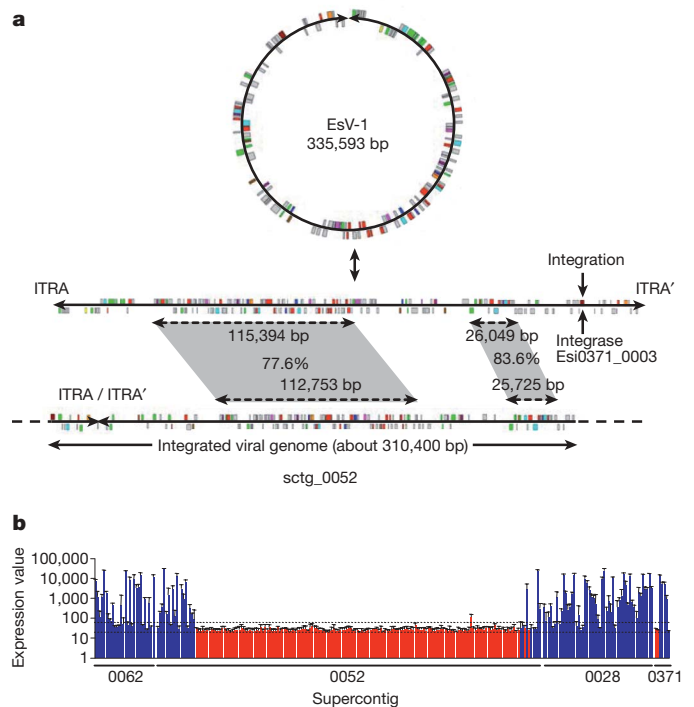
Figure 2 | An integrated viral sequence in the *Ectocarpus* genome. a, Representation of the linear and circular forms of the EsV-1 genome compared to the inserted viral genome. Genes on the upper and lower strands are above and below the line, respectively. A short region of the viral genome containing the putative integrase gene has been transposed to supercontig 0371. Gray parallelograms connect regions of high gene density that are also found in other phaeoviruses. These regions contain many of the genes that are thought to be important for the viral life cycle. Percent nucleotide identities between cognate regions in EsV-1 and in the integrated viral genome are indicated. Dashed line, algal DNA. ITRA and ITRA', inverted terminal repeats. **b**, Mean expression levels of the inserted viral genes: the graph shows the mean of the normalized expression values (4 replicates) ± s.d. of the genes that were included in the microarray experiments carried out in ref. 29. Expression data are shown for the control condition, but gene expression profiles were highly similar under stress conditions (not shown). Each bar represents the expression value for one coding sequence, the bars are in the same order as the corresponding genes along the supercontigs. Red bars correspond to virus genes, blue bars to host genes. Supercontigs 0062, 0052 and 0028 are adjacent on the genetic map, supercontig 0371 is part of another linkage group. The hybridization signals for 95% of the negative controls (median of four random probes on the same array) were between 19 and 59 (indicated by the two dotted lines).

Table 1 | *Ectocarpus* genome statistics

Size of the sequenced genome (Mbp)	195.8
Number of supercontigs (scaffolds) over 2 kbp	1,561
Supercontig (scaffold) N50 (bp)	504,428
Number of contigs	14,043
Contig N50 (bp)	32,862
Percentage of the 91,041 cDNA sequences that match the genome	97.4%
Genomic G+C content (%)	53.6%
Percentage of repeated sequences	22.7%
Number of genes	16,256
Average gene length (bp)	6,859
Average coding sequence length (bp)	1,563
Number of introns	113,619
Average intron length (bp)	703.8
Average number of introns per gene	6.98
Number of exons	129,875
Average exon length (bp)	242.2
Number of single exon genes	856
Number of genes with protein similarity support (Blast e-value cutoff $<e^{-10}$)	10,278 (63.2%)
Number of genes with expressed sequence tag support	9,601 (59%)
Number of genes with tiling array support	6,474 (40%)

against halogenated compounds produced by kelps as defence molecules[12], allowing it to grow epiphytically on these organisms[14,15].

The cell walls of brown algae contain unusual polysaccharides such as alginates and fucans[16], with properties that are important both in terms of resistance to mechanical stresses and as protection from predators. Analysis of the *Ectocarpus* genome failed to detect homologues of many of the enzymes that are known, from other organisms, to have roles in alginate biosynthesis and in the remodelling of alginates, fucans and cellulose, indicating that brown algae have independently evolved enzymes to carry out many of these processes. However, a number of polysaccharide modifying enzymes, such as mannuronan C5 epimerases, sulphotransferases and sulphatases, were identified. These enzymes are likely to modulate physicochemical properties of the cell wall, influencing rigidity, ion exchange[16] and resistance to abiotic stress.
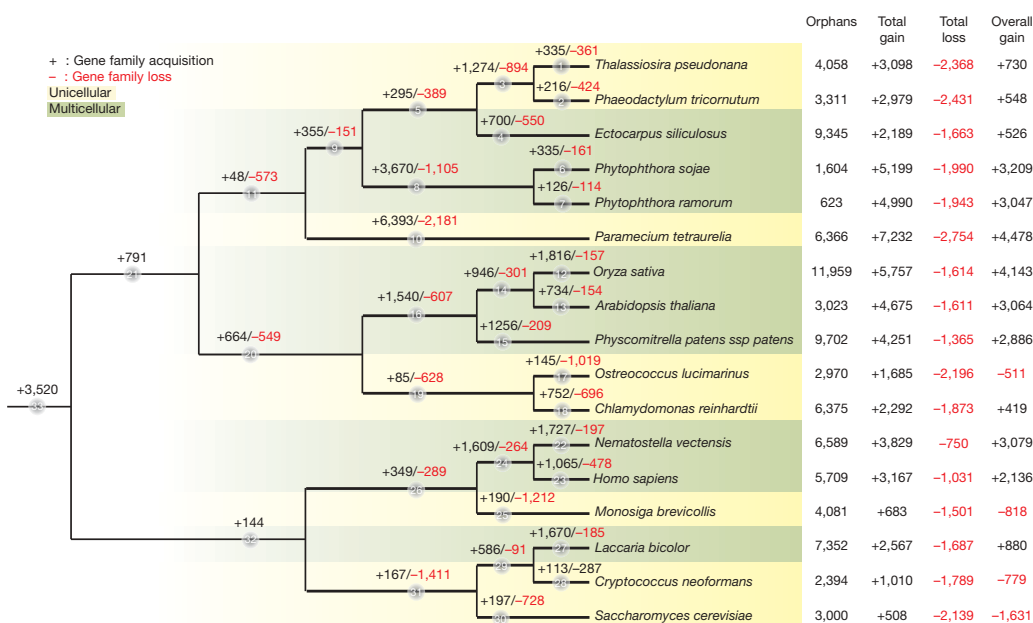
Comparison of genomes from a broad range of organisms (Fig. 3) indicated that the major eukaryotic groups have retained distinct but overlapping sets of genes since their evolution from a common ancestor, with new gene families evolving independently in each lineage. On average, lineages that have given rise to multicellular organisms have lost fewer gene families and evolved more new gene families than unicellular lineages. However, we were not able to detect any significant, common trends, such as a tendency for the multicellular lineages to gain families belonging to particular functional (gene ontology) groups.

Analysis of the gene families that are predicted to have been gained by the *Ectocarpus* genome since divergence from the unicellular diatoms indicated a significant gain in ontology terms associated with protein kinase activities, and these genes include a particularly interesting family of membrane-spanning receptor kinases. Receptor kinases have been shown to have key roles in developmental processes such as differentiation and cellular patterning in both the animal and green plant lineages[17]. Animal tyrosine and green plant serine/threonine receptor kinases form two separate monophyletic clades, indicating that these two families evolved independently, and in both lineages the emergence of receptor kinases is thought to have been a key event in the evolution of multicellularity[18,19]. The *Ectocarpus* receptor kinases also form a monophyletic clade, discrete from those of animal and green plant receptor kinases, indicating that the brown algal family also evolved

independently (Fig. 4). The evolution of membrane-spanning receptor kinases may, therefore, have been a key step in the evolution of complex multicellularity in at least three of the five groups that have attained this level of developmental sophistication. No orthologues of the *Ectocarpus* receptor kinase family were found in other stramenopile genomes, but a detailed analysis of two complete oomycete genome sequences identified a phylogenetically distinct family of receptor kinases (Fig. 4).

The *Ectocarpus* genome contains a number of other genes that could have potentially had important roles in the development of multicellularity (see Supplementary Information 2.3; although it should be noted that the functions of these proteins will need to be confirmed experimentally). For example there are several additional membrane-localized proteins of interest, including three integrin-related proteins. Integrins have an important role in cell adhesion in animals[20] but integrin genes are absent from all the previously sequenced stramenopile genomes. The *Ectocarpus* genome also encodes a large number of ion channels, compared to other stramenopile genomes. These include several channels that are likely to be involved in calcium signalling such as an inositol triphosphate/ryanodine type receptor (IP3R/RyR), four 4-domain voltage-gated calcium channels, and an expanded family of 18 transient receptor potential channels. Members of all these classes are found in animal genomes but are absent from the genomes of land plants[21,22]. No *IP3R* genes have been identified in the sequenced diatom and oomycete genomes, but the presence of an *IP3R* in *Ectocarpus* is consistent with the demonstration of 'animal-like' fast calcium waves and inositol-phosphate-induced calcium release in embryos of the brown alga *Fucus serratus*[23,24].

The ion channels in the *Ectocarpus* genome illustrate how the evolutionary fates of eukaryotic lineages have probably depended not only on the evolution of new gene functions but also on the retention of genes already present in ancestral genomes. Along similar lines, there is evidence that, compared to unicellular organisms, multicellular organisms have tended to retain a more complete Rad51 family, which encodes DNA repair proteins including members with important roles during meiosis[25]. This is also the case in the stramenopiles, where *Ectocarpus* has a markedly more complete Rad51 gene family than the other sequenced members of the group (Supplementary Information 2.3.12). *Ectocarpus* also possesses a more extensive set of GTPase genes

			Orphans	Total gain	Total loss	Overall gain
Thalassiosira pseudonana			4,058	+3,098	−2,368	+730
Phaeodactylum tricornutum			3,311	+2,979	−2,431	+548
Ectocarpus siliculosus			9,345	+2,189	−1,663	+526
Phytophthora sojae			1,604	+5,199	−1,990	+3,209
Phytophthora ramorum			623	+4,990	−1,943	+3,047
Paramecium tetraurelia			6,366	+7,232	−2,754	+4,478
Oryza sativa			11,959	+5,757	−1,614	+4,143
Arabidopsis thaliana			3,023	+4,675	−1,611	+3,064
Physcomitrella patens ssp patens			9,702	+4,251	−1,365	+2,886
Ostreococcus lucimarinus			2,970	+1,685	−2,196	−511
Chlamydomonas reinhardtii			6,375	+2,292	−1,873	+419
Nematostella vectensis			6,589	+3,829	−750	+3,079
Homo sapiens			5,709	+3,167	−1,031	+2,136
Monosiga brevicollis			4,081	+683	−1,501	−818
Laccaria bicolor			7,352	+2,567	−1,687	+880
Cryptococcus neoformans			2,394	+1,010	−1,789	−779
Saccharomyces cerevisiae			3,000	+508	−2,139	−1,631

Figure 3 | Predicted pattern of loss and gain of gene families during the evolution of a broad range of eukaryotes. The number of gene families that were acquired (black) or lost (red) at each time point (grey circles) in the tree (Supplementary Information 1.15) was estimated using the Dollo

parsimony principle. For each species, the number of orphans (genes that lacked homologues in the eukaryotic data set), the total number of gene families gained or lost and the overall gain (that is, total gain minus total loss) is indicated.
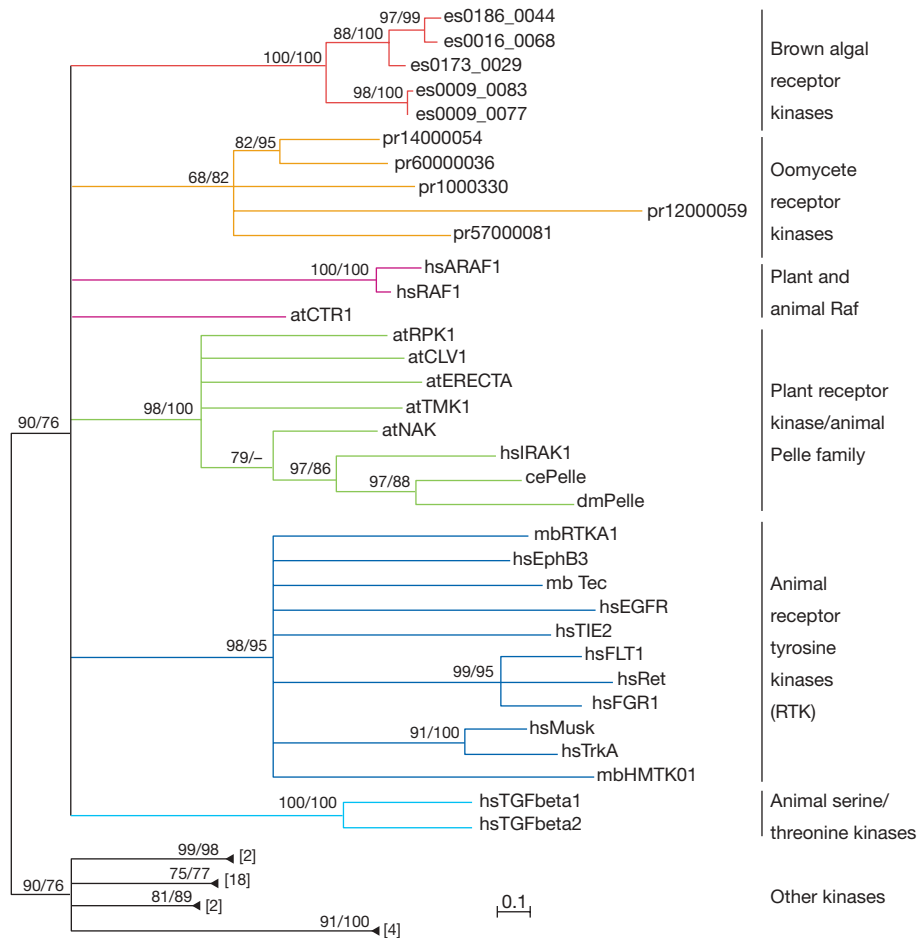
Figure 4 | Phylogenetic analysis showing the independent evolution of eukaryotic receptor kinases from the opisthokont, green plant and stramenopile lineages. Protein maximum-likelihood tree generated using a multiple alignment of kinase domains from eukaryotic receptor kinases and related cytosolic kinases. Bootstrap values, when above 65%, are provided at the nodes for maximum-likelihood (first value) and neighbour-joining (second value) analyses.

than other stramenopile genomes (Supplementary Information 2.3.7) and an analysis of transcription-associated proteins indicated that *Ectocarpus* and oomycete genomes have a broader range of transcription factor families than the unicellular diatoms (Supplementary Table 4).

Analysis of a large set of small RNA sequences allowed the identification of 26 microRNAs in *Ectocarpus* (Supplementary Table 17). This observation, together with the identification of microRNAs in three other eukaryotic groups, the archaeplastid, opisthokont and amoebozoan lineages[26], indicates that these regulatory molecules were present from an early stage of eukaryotic evolution. Sixty-seven candidate target sites were identified for 12 of the 26 microRNAs. Interestingly, 75% of these target sequences occur in genes with leucine-rich repeat (LRR) domains (Supplementary Information 2.3.14). The LRR genes include many members of the ROCO (Roc GTPase plus COR (C-terminal of Roc) domain) family[27] that are predicted to have evolved since the split from the diatoms. Taken together, these observations indicate that a significant proportion of the microRNAs identified may regulate recently evolved processes. This is interesting in the light of suggestions that microRNAs may have had a key role in the evolution of complex multicellularity in the animal lineage[28].

Analysis of the *Ectocarpus* genome has revealed traces both of its ancient evolutionary past and of more recent events associated with the emergence of the brown algal lineage. The former include the diverse origins of the genes that make up the genome, many of which were acquired via endosymbiotic events (Supplementary Information 2.3.15), whereas the latter include the recent emergence of new gene families and the evolution of an unusual genome architecture, in terms both of gene structure and organization (Supplementary

Information 2.1). It is likely that the evolution of complex multicellularity within brown algae depended on events spanning both timescales. The conservation of completeness and diversity within key gene families over the long term seems to have been as important as the more recent evolution of novel proteins, such as the brown algal receptor kinase family.

METHODS SUMMARY

Genome and cDNA sequencing were carried out using the *Ectocarpus siliculosus* strain Ec 32, which is a meiotic offspring of a field sporophyte collected in 1988 in San Juan de Marcona, Peru. The genome sequence was assembled using 2,233,253 and 903,939 paired, end-sequences from plasmid libraries with 3 and 10 kbp inserts respectively, plus 58,155 paired, end-sequence reads from a small-insert bacterial artificial chromosome library. Annotation was carried out using the EuGène program and optimized by manual correction of gene models and functional assignments. Sequencing of 91,041 cDNA reads, corresponding to six different cDNA libraries, and a whole genome tiling array analysis provided experimental confirmation of a large proportion of the transcribed part of the genome (Table 1). Small RNAs were characterized by generating 7,114,682 sequencing reads from two small RNA libraries on a Solexa Genome Analyser (Illumina). Analyses of the methylation state of genomic DNA and of specific transposon families were carried out using HPLC analysis of nucleotide methylation and McrBC digestion, respectively. Full information about the methodology used can be found in the Supplementary Information section.

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