

Ecole Doctorale COMPLEXITE DU VIVANT – Fiche Projet CONCOURS

Nom et prénom du directeur de thèse (et si besoin du co-directeur) : J. Mark Cock
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Nom et prénom du co-encadrant (*non HdR*) : Erwan Corre
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Y-a-t-il un candidat déjà identifié pour le projet: OUI

Nom et prénom du responsable de l'équipe : J. Mark Cock

Intitulé de l'équipe : Algal Genetics

Nombre de chercheurs et enseignants-chercheurs statutaires de l'équipe titulaires d'une HDR (ou équivalent) : 1

Nom et prénom du responsable d'UMR ou de département: Stéphane Egée

Intitulé et N° d'UMR ou de département : Integrative Biology of Marine Models, UMR 8227

Signature du directeur d'UMR ou de département (vaut avis favorable pour le dépôt du projet) :



UMR8227 CNRS/SU
Laboratoire de Biologie Intégrative
des Modèles Marins / LBI2M
Stéphane EGÉE
Directeur

Titre du projet de thèse :

Endogenous viral elements and the evolution of brown algal genomes

Spécialité : Biologie du développement, Génomique

Résumé du projet de thèse

The brown algae (Phaeophyceae) are key components of coastal ecosystems with important roles as primary producers and as habitats for a broad range of other species. These seaweeds are attracting considerable interest as aquaculture crops as a consequence of their capacity to rapidly produce large quantities of biomass under sustainable culture conditions that do not require the use of arable terrestrial land nor freshwater resources. Brown algae are also of fundamental interest as they represent the third most complex lineage of multicellular organisms after animals and land plants, to which there are only very distantly related, being members of the Stramenopile supergroup. Despite these highly interesting features, the basic biology of these organisms is still quite poorly understood. The Phaeoexplorer project (<https://phaeoexplorer.sb-roscoff.fr/home/>), funded by the France Génomique large-scale sequencing program and coordinated by the host laboratory in Roscoff, aims to address this knowledge gap using a genomics approach. Phaeoexplorer has recently completed the sequencing and annotation of 66 complete genomes, corresponding to 46 species of brown algae (Phaeophyceae) and closely-related sister species. The specific objective of this PhD project is to use this newly-available resource to analyse the role that integrating viral genomes have played in the evolution of brown genomes.

Genome sequencing has detected the presence of integrated viral DNA in the genomes of diverse eukaryotes and this integrated DNA is thought to play an important role in genome evolution^{1,2}. In most cases, integration of viral sequences is thought to involve non-specific processes but a small number of eukaryotic viruses are lysogenic, so that integration into the genome of their host is actually part of the viral life cycle. This is the case for the phaeoviruses that infect brown algae^{3,4}. The phaeoviruses are members of the phylum Nucleocytoplasmic Large DNA Viruses (NCLDVs), are remarkable for the large sizes of their genomes, often extending to several hundred kilobases and containing large numbers of genes. The large size of NCLDV genomes, and the diversity of genes they contain, means that they have a strong potential

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to influence the evolution of their host's genomes, particularly in the case of phaeoviruses, which spend a significant part of their life cycle as integrated sequences.

A pipeline has been developed to detect viral genes in the Phaeoexplorer genomes and application of this pipeline has identified a large number of diverse inserted viral sequences (referred to as endogenous viral elements or EVEs) in the algal genomes. Analysis of the EVEs indicates that they include both complete, inserted viral genomes (proviruses) and fragments of viral genomes that probably correspond to ancient insertions that have partially degenerated. There are also indications that some viral genes have been or are being assimilated into the alga host gene repertoire (for example, viral sequences that would normally be monoexonic and silent in the host genome acquiring introns and becoming transcriptionally active). The aim of this PhD project is to analyse the EVEs in the Phaeoexplorer genomes to further our understanding of the interaction between the viruses and their algal host and to understand how the integrated viral sequences impact the evolution of the host genomes. For the former, analysis of the EVEs will provide an overview of the diversity of phaeoviruses and the diversity of the overall viral geneset. The dataset will also be used to investigate phylogenetic associations between viral and algal taxa (i.e. general host specificity). The EVEs will also be analysed to understand the fates of inserted sequences, in particular the relative roles of degeneration and assimilation of genes by the algal host. Characteristics associated with the former include provirus fragmentation, transposon insertion and gene inactivation (e.g. frame shift mutations), whereas characteristics of the latter include intron acquisition and activation of transcription. Genomes corresponding to 15 different species from the genus *Ectocarpus* will be particularly useful to precisely map EVEs and to identify newly assimilated viral genes using genome synteny.

The analyses proposed for this PhD project will address several important outstanding questions including How diverse are the phaeoviruses? How do phaeoviruses insert into their algal hosts genomes? What is the long-term fate of proviruses after they have inserted into a genome? Are inserted viral genomes a source of important new genes via horizontal gene transfer (HGT) and, if so, are these genomes an important source of HGTs?

References

1. Moniruzzaman, M., Weinheimer, A. R., Martinez-Gutierrez, C. A. & Aylward, F. O. (2020). Widespread endogenization of giant viruses shapes genomes of green algae. **Nature** 588, 141–145
2. Feschotte, C. & Gilbert, C. (2012). Endogenous viruses: insights into viral evolution and impact on host biology. **Nat Rev Genet** 13, 283–296
3. Delaroque, N., Maier, I., Knippers, R. & Müller, D. (1999). Persistent virus integration into the genome of its algal host, *Ectocarpus siliculosus* (Phaeophyceae). **J Gen Virol** 80 (Pt 6), 1367–70
4. Cock, J. M. et al. (2010). The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. **Nature** 465, 617–621

Faisabilité du projet de thèse

The co-supervision proposed for this project will ensure that the student has access to all of the data and facilities necessary to carry out the project. Mark Cock of the UMR 8227 is coordinating the Phaeoexplorer project, which is being carried out in collaboration with Genoscope and involves a large, international consortium for the analysis of the Phaeoexplorer genome data (38 institutes in 14 countries on four continents). Erwan Corre leads the Analysis and Bioinformatics for Marine Science (ABiMS; <http://abims.sb-roscoff.fr/>) platform within the FR2424, which is part of the French Bioinformatics Institute (IFB) and has extensive experience with providing bioinformatic support to diverse scientific projects both within and outside Roscoff Biological Station and with providing the calculation and storage environment for large-scale bioinformatics projects.

The student will have full, pre-publication access to the Phaeoexplorer genome dataset and will carry out his analyses using the extensive server facilities available in Roscoff (<http://abims.sb-roscoff.fr>). The PhD project will build on work carried out by a postdoctoral fellow (co-supervised by the Algal Genetics group, UMR 8227 and ABiMS), Dean McKeown, which involved identification and manual validation of the large number of EVEs in the Phaeoexplorer genomes. The PhD project will therefore be based on solid preliminary work and we therefore estimate that the risk attached to the project is minimal. The student will benefit from interactions with the extensive international consortium that has been formed around the Phaeoexplorer project, in particular from a collaboration with Declan Schroeder at the University of Minnesota

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(<https://www.virology.umn.edu/bio/virology/declan-schroeder>) who is providing extensive expertise in virology, including for phaeoviruses. Dean McKeown is currently in Declan Schroeder's laboratory and will continue to work on the Phaeoexplorer dataset and provide support for the PhD student's analyses. The project will involve bioinformatic analysis of an existing dataset and no wet laboratory experiments are planned.

Both Mark Cock and Erwan Corre will participate in all aspects of the PhD project, including regular, joint meetings with the student and concerted help with addressing both scientific and technical aspects of the project. In terms of complementarity, Mark Cock will provide input regarding brown algal biology and genomics, whereas Erwan Corre will provide high-level guidance for the implementation of bioinformatic approaches and coding.

Thèses actuellement en cours dans l'équipe

Tous les encadrements doivent être indiqués (y compris les co-directions avec un autre HDR pour des doctorants d'une autre ED, et les encadrements dans le cadre de programmes doctoraux tels qu'IPV, FDV...)

Nom et Prénom du doctorant	Directeur(s) de thèse	Année de 1ère inscription	ED	Financement
Pélagie Ratchinski	J. Mark Cock	2021	CdV	Bourse ENS Lyon

Trois publications récentes du directeur de thèse (du co-directeur ou du co-encadrant s'il y a lieu). Mettre en gras le nom du directeur de thèse.

Bourdareau, S., Tirichine, L., Lombard, B., Loew, D., Wu, Y., Coelho, S.M. and **Cock, J.M.** (2021). Histone modifications during the life cycle of the brown alga *Ectocarpus*. **Genome Biology**, 22, 12.

Badis, Y., Scornet, D., Harada, M., Caillard, C., Raphalen, M., Gachon, C.M.M., Coelho, S.M., Motomura, T., Nagasato, C. and **Cock, J.M.** (2021). Targeted CRISPR-Cas9-based gene knockouts in the model brown alga *Ectocarpus*. **New Phytologist**, 231, 2077-2091.

Arun, A., Coelho, S.M., Peters, A.F., Bourdareau, S., Pérès, L., Scornet, D., Strittmatter, M., Lipinska, A.P., Yao, H., Godfroy, O., Montecinos, G.J., Avia, K., Macaisne, N., Troadec, C., Bendahmane, A. and **Cock J.M.** (2019). Convergent recruitment of TALE homeodomain life cycle regulators to direct sporophyte development in land plants and brown algae. **eLife**, 8, e43101.

Docteurs encadrés par le directeur de thèse ayant soutenu entre la date de dépôt de ce dossier et il y a 5 ans et publications relatives à leur sujet de thèse. Mettre en gras le nom du directeur de thèse et celui du docteur.

Nom Prénom : Josselin Gueno	Date de soutenance : 11/12/2019
	Durée de thèse (en mois): 38
Publications :	
Gueno, J. , Cossard, G., Bordareau, S., Godfroy, O., Lipinska, A.P., Tirichine, L., Cock J.M. and Coelho, S.M. (2022). Chromatin landscape associated with sexual differentiation in a UV sex determination system. Nucleic Acids Research , in press.	
Müller, D. , Gaschet, E., Godfroy, O., Gueno, J. , Cossard, G., Kunert, M., Peters, A.F., Westermeier, R., Boland, W., Cock, J.M. , Lipinska, A.P. and Coelho, S.M. (2021). A partially sex-reversed giant kelp sheds light into the mechanisms of sexual differentiation in the brown algae. New Phytologist , 232, 252–263.	
Coelho, S.M. , Gueno J. , Lipinska A.P., Cock J.M. and Umen J.G. (2018). UV chromosomes and haploid sexual systems. Trends in Plant Sciences , 23, 794-807.	

Nom Prénom : Haiqin Yao	Date de soutenance : 09/12/2019
	Durée de thèse (en mois): 38

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Publications :

Godfroy, O., **Yao, H.**, Peters, A.F., Scornet, D., Colin, S., Kinoshita, N., Nagasato, C., Motomura, T., **Cock J.M.** and **Coelho, S.M.** (2022). Mutations in the *BASELESS* gene affect initial cell fate determination in *Ectocarpus* sp. In preparation.

Yao, H., Scornet, D., Jam, M., Hervé, C., Potin, P., Oliveira Correia, L., **Coelho, S.M.** and **Cock, J.M.** (2021). Biochemical characteristics of a diffusible factor that induces gametophyte to sporophyte switching in the brown alga *Ectocarpus*. **Journal of Phycology**, 57, 742-753.

Yao, H., Scornet, D., Peters, A.F., Jam, M., Hervé, C., Potin, P., **Coelho, S.M.** and **Cock, J.M.** (2020). Production and bioassay of a diffusible factor that induces gametophyte-to-sporophyte developmental reprogramming in the brown alga *Ectocarpus*. **Bio-protocol**, 10: e3753.

Arun, A., **Coelho, S.M.**, Peters, A.F., Bourdareau, S., Pérès, L., Scornet, D., Strittmatter, M., Lipinska, A.P., **Yao, H.**, Godfroy, O., Montecinos, G.J., Avia, K., Macaisne, N., Troadec, C., Bendahmane, A. and **Cock J.M.** (2019). Convergent recruitment of TALE homeodomain life cycle regulators to direct sporophyte development in land plants and brown algae. **eLife**, 8, e43101.

Nom Prénom : **Laure Mignerot**

Date de soutenance : **14/12/2018**

Durée de thèse (en mois): **38**

Publications :

Mignerot, L., Nagasato, C., Peters, A.F., Perrineau, M.-M., Scornet, D., Pontheaux, F., Djema, W., Badis, Y., Motomura, T., **Coelho, S.M.** and **Cock, J.M.** (2019). Unusual patterns of mitochondrial inheritance in the brown alga *Ectocarpus*. **Molecular Biology and Evolution**, 36, 2778-2789.

Coelho, S.M., **Mignerot, L.** and **Cock J.M.** (2019). Origin and evolution of sex-determination systems in the brown algae. **Tansley Insight for New Phytologist**, 222, 1751-1756.

Mignerot, L., Avia, K., Luthringer, R., Lipinska, A., Peters, A.F., **Cock, J.M.** and **Coelho, S.M.** (2019). A key role for UV sex chromosomes in the regulation of parthenogenesis in *Ectocarpus*. **Public Library of Science Genetics**, 15, e1008211.

Avia, K., Lipinska, A., **Mignerot, L.**, Montecinos, A.E., Jamy, M., Valero, M., Peters, A.F., **Cock, J.M.**, Roze, D. and **Coelho, S.M.** (2018). Genetic diversity in the UV sex chromosomes of the brown alga *Ectocarpus*. **Genes**, 9, 286.

Bourdareau, S., **Mignerot, L.**, Heesch, S., Peters, A.F., **Coelho, S.M.** and **Cock, J.M.** (2017). Alternation of generations in plants and algae. In: **Evolutionary Developmental Biology - A reference guide**. Nuno de la Rosa, L. and Müller, G. (eds) Springer, Dordrecht, pp. 1-14.

Mignerot, L., **Coelho, S.M.** (2016). The origin and evolution of the sexes: novel insights from a distant eukaryotic lineage. **Comptes Rendus Academie des Sciences**, 339, 252-257.

Nom Prénom : **Simon Bourdareau**

Date de soutenance : **27/03/2018**

Durée de thèse (en mois): **41**

Publications :

Gueno, J., Cossard, G., Bordareau, S., Godfroy, O., Lipinska, A.P., Tirichine, L., **Cock J.M.** and **Coelho, S.M.** (2022). Chromatin landscape associated with sexual differentiation in a UV sex determination system. **Nucleic Acids Research**, in press.

Bourdareau, S., Tirichine, L., Lombard, B., Loew, D., Wu, Y., **Coelho, S.M.** and **Cock, J.M.** (2021). Histone modifications during the life cycle of the brown alga *Ectocarpus*. **Genome Biology**, 22, 12.

Arun, A., **Coelho, S.M.**, Peters, A.F., **Bourdareau, S.**, Pérès, L., Scornet, D., Strittmatter, M., Lipinska, A.P., Yao, H., Godfroy, O., Montecinos, G.J., Avia, K., Macaisne, N., Troadec, C., Bendahmane, A. and **Cock J.M.** (2019). Convergent

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recruitment of TALE homeodomain life cycle regulators to direct sporophyte development in land plants and brown algae. *eLife*, 8, e43101.

Bourdareau, S., Mignerot, L., Heesch, S., Peters, A.F., **Coelho, S.M.** and **Cock, J.M.** (2017). Alternation of generations in plants and algae. In: **Evolutionary Developmental Biology - A reference guide**. Nuno de la Rosa, L. and Müller, G. (eds) Springer, Dordrecht, pp. 1-14.

Cock, J.M., Liu, F., Delin, D., **Bourdareau, S.**, Lipinska, A., **Coelho, S.M.** and Tarver, J.E. (2017). Rapid evolution of microRNA loci in the brown algae. *Genome Biology and Evolution*, 9, 740-749.

Nom Prénom : Alexandre Cormier

Date de soutenance : 16/11/2015

Durée de thèse (en mois): 36

Publications :

Cormier, A., Avia, K., Sterck, L., Derrien, T., Wucher, V., Andres, G., Monsoor, M., Godfroy, O., Lipinska, A., Perrineau, M.-M., Van De Peer, Y., Hitte, C., **Corre, E.**, **Coelho, S.M.** and **Cock, J.M.** (2017). Re-annotation, improved large-scale assembly and establishment of a catalogue of non-coding loci for the genome of the model brown alga *Ectocarpus*. *New Phytologist*, 214, 219-232.

Avia, K., **Coelho, S.M.**, Montecinos, G.J., **Cormier, A.**, Lerck, F., Mauger, S., Faugeron, S., Valero, M., **Cock, J.M.** and Boudry, P. (2017). High-density genetic map and identification of QTLs for responses to high temperature and low salinity stresses in the model alga *Ectocarpus* sp. *Scientific Reports*, 7, 43241.

Luthringer, R., Lipinska, A., **Cormier, A.**, Peters, A.F., Roze, D., **Cock, J. M.** and **Coelho, S.M.** (2015). The pseudoautosomal region of the *Ectocarpus* UV sex chromosome. *Molecular Biology and Evolution*, 32: 2973-2985.

Tarver, J., **Cormier, A.**, Pinzon, N., Taylor, R., Carré, W., Strittmatter, M., Seitz, H., **Coelho, S.M.**, **Cock, J.M.** (2015). microRNAs and the evolution of complex multicellularity: identification of a large, diverse complement of microRNAs in the brown alga *Ectocarpus*. *Nucleic Acids Research*, 43, 6384-6398.

Lipinska, A.*., **Cormier, A.*.**, Luthringer, R., Peters, A.F., Corre, E., Gachon, C.M.M., **Cock, J.M.** and **Coelho, S.M.** (2015). Sexual dimorphism and the evolution of sex-biased gene expression in the brown alga *Ectocarpus*. *Molecular Biology and Evolution*, 32, 1581-1597. *joint first authors.

Ahmed, S., **Cock, J.M.**, Pessia, E., Luthringer, R., **Cormier, A.**, Robuchon, M. Sterck, L., Peters, A.F., Dittami, S.M., Corre, E., Valero, M., Aury, J.-M., Roze, D., Van de Peer, Y., Bothwell, J., Marais, G.A.B., **Coelho, S.M.** (2014). A haploid system of sex determination in the brown alga *Ectocarpus* sp. *Current Biology*, 24, 1-13.

Luthringer, R., **Cormier, A.**, Ahmed, S., Peters, A.F., **Cock, J.M.** and **Coelho, S.M.** (2014). Sexual dimorphism in the brown algae. *Perspectives in Phycology*, 1, 11-25.

Nom Prénom : Rémy Luthringer

Date de soutenance : 10/2012

Durée de thèse (en mois): 36

Publications :

Heesch S., Serrano-Serrano M., **Luthringer R.**, Peters A.F., Destombe C., **Cock J.M.**, Valero M., Roze D., Salamin N., **Coelho S.M.** (2019). Evolution of life cycles and reproductive traits: insights from the brown algae. *bioRxiv* 530477.

Mignerot, L., Avia, K., **Luthringer, R.**, Lipinska, A., Peters, A.F., **Cock, J.M.** and **Coelho, S.M.** (2019). A key role for UV sex chromosomes in the regulation of parthenogenesis in *Ectocarpus*. *Public Library of Science Genetics*, 15, e1008211.

Luthringer, R.*, Lipinska, A.*., Cormier, A., Peters, A.F., Roze, D., **Cock, J. M.** and **Coelho, S.M.** (2015). The pseudoautosomal region of the *Ectocarpus* UV sex chromosome. *Molecular Biology and Evolution*, 32: 2973-2985. *joint first authors.

Ahmed, S., **Cock, J.M.**, Pessia, E., **Luthringer, R.**, Cormier, A., Robuchon, M. Sterck, L., Peters, A.F., Dittami, S.M., Corre, E., Valero, M., Aury, J.-M., Roze, D., Van de Peer, Y., Bothwell, J., Marais, G.A.B., **Coelho, S.M.** (2014). A haploid system of sex determination in the brown alga *Ectocarpus* sp. *Current Biology*, 24, 1-13.

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Luthringer, R., Cormier, A., Ahmed, S., Peters, A.F., **Cock, J.M.** and **Coelho, S.M.** (2014). Sexual dimorphism in the brown algae. **Perspectives in Phycology**, 1, 11-25.

Lipinska, A., Cormier, A., **Luthringer, R.**, Peters, A.F., Corre, E., Gachon, C.M.M., **Cock, J.M.** and **Coelho, S.M.** (2015). Sexual dimorphism and the evolution of sex-biased gene expression in the brown alga *Ectocarpus*. **Molecular Biology and Evolution**, 32, 1581-1597.

Cock, J.M., Sterck, L., Ahmed, S., Allen, A.E., Amoutzias, G., Anthouard, V., Artiguenave, F., Arun, A., Aury, J.-M., Badger, J.H., Beszteri, B., Billiau, K., Bonnet, E., Bothwell, J.H., Bowler, C., Boyen, C., Brownlee, C., Carrano, C.J., Charrier, B., Cho, G.Y., **Coelho, S.M.**, Collén, J., Le Corguillé, G., Corre, E., Darteville, L., Da Silva, C., Delage, L., Delaroche, N., Dittami, S.M., Doulbeau, S., Elias, M., Farnham, G., Gachon, C.M.M., Godfroy, O., Gschloessl, B., Heesch, S., Jabbari, K., Jubin, C., Kawai, H., Kimura, K., Kloareg, B., Küpper, F.C., Lang, D., Le Bail, A., **Luthringer, R.**, Leblanc, C., Lerouge, P., Lohr, M., Lopez, P.J., Macaisne, N., Martens, C., Maumus, F., Michel, G., Miranda-Saavedra, D., Morales, J., Moreau, H., Motomura, T., Nagasato, C., Napoli, C.A., Nelson, D.R., Nyvall-Collén, P., Peters, A.F., Pommier, C., Potin, P., Poulain, J., Quesneville, H., Read, B., Rensing, S.A., Ritter, A., Rousvoal, S., Samanta, M., Samson, G., Schroeder, D.C., Scornet, D., Ségurens, B., Strittmatter, M., Tonon, T., Tregear, J.W., Valentin, K., von Dassow, P., Yamagishi, T., Rouzé, P., Van de Peer, Y., Wincker, P. (2012) The *Ectocarpus* genome and brown algal genomics. In: Genomic insights into the biology of algae. Piganeau, G. (ed) **Advances in Botanical Research** (special issue), 64, 141-184.

Nom Prénom : **Alok Arun**

Date de soutenance : **10/2012**

Durée de thèse (en mois): **36**

Publications :

Arun, A., Coelho, S.M., Peters, A.F., Bourdareau, S., Pérès, L., Scornet, D., Strittmatter, M., Lipinska, A.P., Yao, H., Godfroy, O., Montecinos, G.J., Avia, K., Macaisne, N., Troadec, C., Bendahmane, A. and **Cock J.M.** (2019). Convergent recruitment of TALE homeodomain life cycle regulators to direct sporophyte development in land plants and brown algae. **eLife**, 8, e43101.

Arun, A., Peters, N., Scornet, D., Peters, A.F., **Cock, J.M.** and **Coelho, S.M.** (2013). Non-cell autonomous regulation of the switch between the gametophyte and sporophyte generations of the brown alga *Ectocarpus*. **New Phytologist**, 197, 503-510.

Bogaert, K.A., **Arun, A., Coelho, S.M.** and De Clerck O. (2013). Brown algae as a model for plant organogenesis. In: **Plant Methods in Molecular Biology - Plant Organogenesis**. De Smet I. (ed.) Springer Verlag. 959, 97-125.

Collén, J., Porcel, B., Carré, W., Ball, S., Chaparro, C., Tonon, T., Barbeyron, T., Michel, G., Noel, B., Valentin, K., Elias, M., Artiguenave, F., **Arun, A.**, Aury, J.-M., Barbosa-Neto, J.F., Bothwell, J.H., Bouget, F.-Y., Brillet, L., Cabello-Hurtado, F., Capella-Gutierrez, S., Charrier, B., Cladière, L., **Cock, J.M.**, **Coelho, S.M.**, Colleoni, C., Czjzek, M., Da Silva, C., Delage, L., Denoecd, F., Deschamps, P., Dittami, S.M., Gabaldón, T., Gachon, C.M.M., Groisillier, A., Hervé, C., Jabbari, K., Katinka, M., Kloareg, B., Kowalczyk, N., Labadie, K., Leblanc, C., Lopez, P.J., McLachlan, D., Meslet-Cladiere, L., Moustafa, A., Nehr, Z., Nyvall Collén, P., Panaud, O., Partensky, F., Poulain, J., A. Rensing, S.A., Rousvoal, S., Samson, G., Symeonidi, A., Weissenbach, J., Zambounis, A., Wincker, P. and Boyen C. (2013). Genome structure and metabolic features in the red seaweed *Chondrus crispus* shed light on evolution of the Archaeplastida. **Proc. Natl. Acad. Sci. USA**, 110, 5247-5252.

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