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A brief history of speciation research at the *Station Biologique de Roscoff* (1872-2022)

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Abstract: The Station Biologique de Roscoff is celebrating its 150th anniversary. The occasion to take a break, to look back on the research done so far. Here we are interested in the origin of species. How does reproductive isolation evolve? How do barrier mechanisms appear and develop, and, accumulating, give rise to new species? These questions have been addressed in various ways at the *Station biologique de Roscoff*, in the framework of research projects that have as their most recent common ancestor the pioneering work of Georges Teissier in population genetics. Leaning on the soft or rocky substrates of the Roscoff coasts, with their feet in the water, Teissier and his colleagues and students gave a decisive impulse to French evolutionary biology. The mystery of the origin of species has since been the subject of various programs focused mainly on the evolution of marine algae and invertebrates. Some of these programs have been interested in describing the diversity and spatial distribution of species, focusing in particular on hybridization and gene flow at different spatial scales, across the foreshore, along the coasts, or between hydrothermal vents on an ocean scale. Another part of this work has sought to identify the mechanisms of reproductive isolation between species and their genetic basis. We retrace here the progress of these programs carried out at the station biologique de Roscoff since its foundation.

Résumé : *Une brève histoire de la recherche sur la spéciation à la Station Biologique de Roscoff (1872-2022).*La Station Biologique de Roscoff fête son cent cinquantième anniversaire. L'occasion de faire une pause, jeter un œil en arrière sur la recherche effectuée jusqu'ici. Nous nous intéressons ici à l'origine des espèces. Comment l'isolement reproducteur évolue-t-il ? Comment apparaissent et se développent des mécanismes barrière qui limitent la reproduction entre individus, et, s'accumulant, donnent naissance à de nouvelles espèces ? Ces questions ont été abordées de diverses manières à la Station Biologique de Roscoff, dans le cadre de projets de recherche qui ont pour plus récent ancêtre commun le travail pionnier de Georges Teissier en génétique des populations. Prenant appui sur les substrats meubles ou rocheux des côtes de Roscoff, les pieds dans l'eau, Teissier et ses collègues et élèves ont donné un élan décisif à la biologie évolutive française. Le mystère de l'origine des espèces a depuis été l'objet de programmes variés centrés essentiellement sur l'évolution des algues et invertébrés marins. Une partie de ces programmes s'est intéressée à décrire la diversité et la répartition spatiale des espèces en s'intéressant en particulier à l'hybridation et aux flux de gènes à différentes échelles spatiales, du haut en bas de la zone de balancement des marées, le long des côtes, ou encore entre sources hydrothermales à l'échelle d'un océan. Une autre partie de ces travaux a cherché à identifier les mécanismes d'isolement reproducteur entre espèce et leurs bases génétiques. Nous retraçons ici le cheminement de ces programmes réalisés à la Station Biologique de Roscoff depuis sa fondation.

Keywords: Origin of species ● Marine station ● Anniversary ● History of science ● Brittany

A browsing expedition to the evolution shelves of one's local university library should be required of all new students of evolutionary biology.
Stewart H. Berlocher (1998)

Exploring one's local scientific library is advisable, because the historical roots and ramifications of scientific thought, with its successes and failures, can nourish for a long time the thinking of successive researchers. We propose here the account of a (modest) browsing expedition to trace the history of research on the problem of species formation as it has been approached at the *Station Biologique de Roscoff* during its 150 years of existence.

Here, the formation of species is considered from the perspective of the evolutionary biologist. That is to say, he or she who wonders how reproductive isolation evolves between populations. We will try to recount how research at Roscoff has explored this question, sometimes digressing a bit to highlight some historical roots, context, or anecdotal connections. Although we have tried to be comprehensive, it is inevitable that we have been influenced by our respective research angles. We apologise in advance for the relevant information that we have missed or ignored.

Our story of speciation research begins in Roscoff at the beginning of the 20th century, when Yves Delage (the second director of the station, directly after its founder Henri de Lacaze-Duthiers) and Maria Goldsmith (a Russian-born biologist also well-known for her activism in the anarcho-syndicalism movement) published a book entitled *Les théories de l'évolution* (Delage & Goldsmith, 1909). This book proposed a state of the art of evolutionary biology and a discussion of the theories put forward until then to explain the evolutionary process. It included a chapter dedicated to the origin of species where the authors discussed the potential roles of what would be called today allopatry and reproductive barriers (then respectively called geographic and physiological segregation). In another chapter entitled «Résumé», Y. Delage & M. Goldsmith stress the absence of a synthetic theory that would be able to unite adaptation and speciation in a single conceptual framework, although, remarkably, their discussion had already put side by side several key ingredients such as Darwin's selective processes and a clear presentation of Mendel's results on heredity, which had just resurfaced a few years earlier. Such a synthesis was not to be due to emerge before several decades, notably through the development of population genetics.

Beyond Delage & Goldsmith's review, research on the origin of species at the *Station Biologique de Roscoff* has its roots directly in the development of evolutionary systematics and population genetics, two fields that were launched primarily by Georges Teissier. In addition to his achievements in zoology, developmental biology and biometry, G. Teissier was a pioneer and promoter of the study of evolution through population genetics. He spent his entire career at the University of Paris and in a CNRS laboratory at Gif-sur-Yvette, where he assumed important responsibilities (most notably, director of the CNRS from 1946 to 1950, and director of the laboratory of Evolutionary Genetics & Biometry at Gif-sur-Yvette from 1951 to 1964). However, an important part of G. Teissier's work was done at the Roscoff marine station, which he first visited in the summer of 1920 as a student, then countless times during the spring and summer university breaks, and of which he became the director from 1945 until his retirement in 1971 in parallel with his other duties (Toulmond, 2014 & 2016).

G. Teissier was a contemporary of André Lwoff, Edouard Chatton, and Boris Ephrussi, who were at the origin of the first French research programmes in genetics, partly based on work done during the summer in Roscoff. G. Teissier was one of the few proponents of Darwinism and the modern synthesis, against the tide of the dominant thinking at that time in France (unfortunately a thinking that died hard: as Loison (2013) reports, French biology was described by Boesiger (1980) as «a kind of living fossil in the rejection of modern evolutionary theories» as late as 1974!). G. Teissier instead contributed to the development of the modern synthesis, notably through his collaboration with Philippe l'Héritier between 1932 & 1938. P. L'Héritier spent a year in the United States in 1931-1932, discovering both the foundations of theoretical population genetics and Drosophila fruit flies by reading and meeting pioneers such as R.A. Fisher, S.G. Wright, T. Dobzhansky, & H.J. Muller, before writing the first French PhD thesis in genetics in 1937 (Ozier-Kalogeropoulos & Cabet-Busson, 2020). At that time, the roofs of the Roscoff station were even used to carry out selection experiments on populations of Drosophila exposed to the wind (L'Héritier et al., 1937), a piece of work that had a noticeable impact on the acceptance of Darwinism in France (Gayon, 2014).

The French school of evolutionary genetics thus has one of its roots in the *Station Biologique de Roscoff*, which naturally became a favourable environment for the emergence of projects on the study of speciation in the marine realm. This was to happen only after the end of the Second World War, during which G. Teissier took an early and active part in the Resistance against German occupation - among other scientists who frequented the Roscoff Biology Station, such as for example Yvette Neefs, who was an associate professor of natural sciences (L'Héritier et al., 1937; Toulmond, 2016). The first person to specifically address the origin of species was Charles Bocquet, who met G. Teissier in 1945 and then worked at Roscoff for nine years. C. Bocquet sought to quantify and understand the origins of polymorphism in a population genetics framework (reviewed in Carton, 2014), building on an absolutely mind-boggling number of meticulous descriptions of marine isopods and copepods obtained from field samples and experimental rearing. The four main groups of organisms studied by C. Bocquet led him along what we would call today the continuum between populations and species. Indeed, he worked on the evolution of intraspecific polymorphism (in the copepod *Tisbe reticulata* Bocquet,1951, year and the isopod *Sphaeroma serratus* (J.C. Fabricius, 1787), interspecific polymorphism (between parasitic copepods), and, just in the grey area between these two scales, polymorphism of the *Jaera albifrons* Leach, 1814 species complex

C. Bocquet's interest in the evolution of parasitic copepods was directly related to speciation. He described many parasitic species, with a particular attention to the origin of sibling species associated with different hosts or different parts of a common host, such as the ventral area versus the crown of tentacles of spiral tube-worms (Carton, 2014). In a biographical note, his former students and colleagues wrote that «the possibility of sympatric speciation fascinated him, but always an obvious, allopatric, explanation was found for the phenomena observed» (Solignac et al., 1978). Yet, among the taxa studied by C. Bocquet, the *Jaera albifrons* complex (Fig. 1) was to become the best model for the study of speciation. Initially interested in the colour polymorphism of these intertidal isopods, C. Bocquet realised that what was then called *Jaera marina* (Fabricius, 1780), year actually contained several reproductively isolated species. Building upon careful phenotypic observations (75,000 measures just to highlight the allometric differences between species, Carton, 2014) he described six species differing essentially in male secondary sexual traits (Bocquet, 1953) and drew several conclusions about their origin. Based on the complexity of the genetic determinism deduced from his phenotype observations, he ruled out the hypothesis of parallel repeated evolution, concluding instead to a single process of micro-evolution that gave birth to the six species described. He also proposed some conclusions regarding the timing of speciation events on the basis of large-scale

Figure 1. Female *Jaera albifrons* (isopod crustacean, about 4 mm long). The green colored eggs incubated by this individual are visible. The Jaera albifrons complex is an interesting model for studying speciation because it is composed by five species imperfectly isolated by ecological, sexual, and post-zygotic barriers. copyright : Wilfried Thomas@Station Biologique de Roscoff

geographic distribution patterns. Finally, he offered alternative hypotheses for the role of ecological isolation, which could have had either a subsidiary role upon secondary contact after sexual isolation had evolved in allopatry (involving secondary sexual traits and chemical signalling), or, alternatively, an earlier role in a form of ecological speciation. This work, published in 1953, is impressively modern, especially considering the context that was largely opposed to the synthetic theory of evolution in France at the time. E Mayr would later say that «Bocquet was the first zoologist to apply modern concepts of evolution to the study of marine organisms» (Solignac et al., 1978).

The work undertaken by C. Bocquet on the *Jaera albifrons* complex was then extended in different directions, first at the University of Caen (Normandy), where C. Bocquet became a professor in 1954, then at Gif-sur-Yvette ten years later. In Caen, he launched the reconstruction of the marine station at Luc-sur-Mer (on the coast 15 Km north of Caen). As we have no record of this, we can only guess that he observed the isopods under the stones of the nearest beach just across the street (Second World War D-Day Sword beach), and that he was particularly excited when he discovered that some males carried intermediate phenotypes between two of the species he had so carefully described at Roscoff. Whatever way it actually started, the Luc-sur-Mer populations of *Jaera albifrons* later became the subject of study for the «Diplôme d'études supérieures» (today's equivalent of a Master thesis) of one of his student, Michel Solignac, in 1965-1966, who then concentrated on the mechanisms of reproductive isolation and introgressive hybridization for his PhD thesis (Solignac, 1978). Five other PhD theses were produced at this period, focusing on evolutionary systematics (Prunus, 1968), evolution of chromosomes (Lécher, 1968), genetic determinism of polychromatism (Cléret, 1970), enzyme polymorphism (Cariou, 1977), and finally the evolution of reproductive systems and reproductive isolation (Veuille, 1982). By that time, all this work had produced a remarkable body of knowledge about the *Jaera albifrons* complex, and in particular about the nature and strength of the isolating barriers between species: ecological isolation due to fine-scale variations in habitat preferences along the seashore, sexual isolation by mate choice based on courtship in which males brush a certain region of the back of females with specialised setae that differ between species, and post-zygotic isolation, all of these barriers being of varying strength between pairs of species, and even between pairs of populations. Although all this took place before the discovery of polymerase chain reaction allowed direct analysis of molecular genetic variation, the work on *Jaera* also provided remarkable advances in genetics, including: estimation of the minimum number of genes responsible for the polymorphism of sexual traits and coloration, fine-scale descriptions of introgressive hybridization in some mixed populations, discovery of a genetic ZW1W2 sex determination system and of complex chromosomal polymorphism across populations, and estimation of the genetic distance between species using allozyme polymorphism. the first French PhD thesis on this type of data was defended in France by M.-L. Carriou in 1977 (Carton, 2014).

C. Bocquet died in 1977, and *Jaera albifrons* was abandoned as a model in 1984 partly because of the difficulty of rearing marine species in Gif-sur-Yvette, where *Drosophila* fruit flies became an important model for empirical investigations of evolutionary genetics. However, The *Jaera albifrons* model was later revived in Roscoff by Thomas Broquet in 2013, on the advice of Franck Gentil (assistant professor at the *Station Biologique de Roscoff* from 1974 to 2013). T. Broquet developed a research program that aims at understanding the genetic basis and evolution of reproductive isolation, basically entirely built upon the inspiring work of C. Bocquet and his students. The eighth PhD thesis on *Jaera albifrons* was defended in Roscoff by Ambre Ribardière in 2017, who described the differential impact of introgression along the genome in the populations first studied by C. Bocquet and M. Solignac about 50 years earlier (Ribardière, 2017), highlighting the role of chromosomal rearrangements in barriers to gene flow.

The research programs dealing with the development of population genetics and speciation originally used the marine station as a base for field surveys, sampling, observations and experiments in the lab, meetings with colleagues, and, last but not least, student training. G. Teissier wrote that the position of *chef de travaux*, responsible for organizing the training of students, was «one of the most beautiful positions that a young naturalist can be given» (Teissier, 1958). But for a long time, there was only little permanent research in Roscoff. Most researchers conducted the largest part of their work in their home laboratories, especially at the university of Paris (later divided into several universities in 1970), Gif-sur-Yvette (from 1950), and Caen. Emile Zuckerkandl, who defended a PhD thesis at Roscoff and then continued to work there on the function and evolution of proteins, left for the United States to work with Linus Pauling in 1959, and the field of population genetics did not generate any resident research activities for some time. Temporary activity hosted there remained dynamic, with for example the visit of J.B.S. Haldane in the summer of 1961, or the one-year stay of François Vuilleumier in 1972, who used his time at the marine station to think about the connections between numerical ecology (population dynamics) and population genetics (Vuilleumier, 1973). F. Vuilleumier was arriving from Lausanne, where he had just founded the *Institut d'écologie animale* (that later became part of the Department of Ecology and Evolution, today a major centre of Evolutionary biology in the university of Lausanne that has organized practical marine biology courses for master students in Roscoff for 35 years).

Roscoff progressively started to host resident research teams in the early 70's. With the strong impetus of successive directors André Toulmond and Bernard Kloareg, a research group dedicated to population genetics (Evolution & Genetics of Marine Populations: EGPM) was founded with the successive arrivals of Didier Jollivet (1996), Frédérique Viard (2000), and Myriam Valero and Christophe Destombe (2002), setting the stage for a renewed interest in speciation research (among many other topics) using marine organisms.

D. Jollivet started his work on the adaptive evolution of deep-sea hydrothermal vent and seep fauna (Fig. 2) in the research team on respiratory pigments led by François Lallier. In the footsteps of E. Zuckerkandl, Xavier Bailly and D. Jollivet re-launched work on the evolution of hemoglobins in marine annelids in relation to adaptation to hypoxia and hydrogen sulfide (Bailly et al., 2003), further developed by S. Hourdez on other species (e.g. Projecto-Garcia et al., 2015). Under the impetus of F. Gentil, D. Jollivet also re-launched population genetics studies on the sandworm *Pectinaria koreni* (Malmgren, 1866), co-supervising the doctoral work of Gudrun Weinmayr initiated by M. Solignac on gene flow between bays and estuaries along the French coast. This work was then resumed with the arrival of F. Viard to better understand the role of the Boreal-Lusitanian transition zone in the speciation processes between the Atlantic and Channel populations. This research was the subject of two PhD theses on *Owenia* and *Pectinaria* worms (Jolly, 2005; Jolly et al., 2006) and the intertidal and coastal forms of the ophiuroid *Acrocnida brachiata* (Montagu, 1804), (Muths, 2006; Muths et al., 2010) using mitochondrial DNA markers and allozymes. The work done by Marc Taimour Jolly and Delphine Muths illustrated the importance of the last glacial episodes on the speciation processes of marine invertebrates in the northern hemisphere through the retreat of marine populations to glacial refuges and their subsequent overlaying after the opening of the English Channel. Moreover, these students also showed that the reconnection of these populations led to a probable repositioning of species along the foreshore, creating depth-ecotypes with local hybridization despite strong genetic divergence accumulated during the last ice age.

At the same time, D. Jollivet continued to study speciation mechanisms in deep hydrothermal species, looking in particular at the role of fragmentation and instability of the environment on the separation of species with high dispersive potential (e.g. Jollivet et al., 1998; Plouviez et al., 2013; Castel et al., 2022). The main outcome of PhD projects completed by Baptiste Faure (Faure, 2008), Sophie Plouviez (Plouviez, 2009) and Marjolaine Matabos (Matabos, 2007) was to show that tectonic movements of plates have had strong effects on the marine fauna associated with oceanic ridges, leading to numerous isolated populations and species crypticism (Matabos & Jollivet, 2019), thus promoting the idea of allopatric speciation processes with potential secondary contact zones where micro-habitats selection could reinforce species separation. Together with other PhD students (Bioy, 2018; Thomas-Bulle, 2019; Castel, 2022), D. Jollivet was the first to use transcriptome sequencing on several vent invertebrates to estimate both divergence and strength of selection using synonymous (d_S) and non-synonymous (d_N) mutations on a collection of annotated orthologous genes between closely-related species living in different thermal habitats (Fontanillas et al., 2017; Castel et al., 2022; Thomas-Bulle et al., 2022). These pioneer studies gave credit to the role of specific gene functions (such as mito-nuclear interacting proteins, cell division/recognition or gametogenesis proteins) promoting species isolation

Figure 2. *Alvinella pompejana* within its parchment-like tube on the wall of a hydrothermal vent chimney of the South East Pacific Rise. The worm (about 75 mm long) is moving outside its tube while opening its branchial crown to take oxygen. Picture obtained from a Nautile dive during the cruise Biospeedo 2004. Copyright IFREMER

but also that these genes may be still positively selected a long time after species separated and congealed their genomes.

Within the EGPM team, M. Valero and C. Destombe arrived at Roscoff to study the evolution of sex and mating system in seaweeds. This project revived the idea of G. Tessier to promote the study of seaweeds at the SBR by the recruitment of a phycologist (Francis Magne) in 1954 (Feldmann, 1972). M. Valero belongs to the school of plant evolutionary genetics founded in Montpellier by Georges Valdeyron, who was among the first students graduated from the genetics and population genetics certificate in France given at the Sorbonne by G. Teissier and L'Héritier in 1947. The circle was thus completed 50 years later by the implementation of seaweed population genetics in Roscoff. Following the pioneer work of Vernet & Harper (1980) on the cost of sex in seaweeds comparing hermaphroditic and dioecious sister

Figure 3. *Fucus vesiculosus* on the wall of the Roscoff seawater reservoir, one of the macro-algae species of interest for the study of speciation. Copyright : Christophe Destombe@ Station Biologique de Roscoff

species of *Fucus*, (Fig. 3), M. Valero and C. Destombe started to investigate the importance of habitat-driven genetic divergence along the intertidal rocky shore in this "*Fucus* species complex" in relation with divergence in their mating system (PhD thesis of Emmanuelle Billard in collaboration with Ester Serrao, University of Algarve, Portugal; Billard, 2007). By comparing the variation in sexual phenotypes and prezygotic fertility between hybrids and the two *Fucus* parental species, Billard et al. (2005) showed that hybrids exhibited all sexual phenotypes and suggested that they were reproductively successful. In addition, using a population genetic approach, Billard et al. (2010) studied the distribution of these species along the vertical gradient of the shore in relation with the variation of their reproductive system. Such gradients of physical and biotic selective pressures have provided classic examples of habitat-driven divergence with gene flow, a first step towards broad sympatric speciation (Johannesson et al., 2010). From the lower to the higher part of the shore, a succession of three well-defined genetic clusters corresponding to *F. vesiculosus* Linnaeus, 1753, "*F. spiralis*-Low", and "*F. spiralis*-High Linnaeus, 1753" were present over less than 100 m. The distribution of genotypes was well correlated with the shore level. However, the distribution of these genetic entities was not totally disjoint, and genetic admixture was detected where individuals from the different entities occurred in sympatry. These results are at the origin of the description of the new species *F. guiryi* Zardi, Nicastro, Serrão Pearson, 2011.

The PhD work done by Florence Tellier (2009) and Valeria Oppliger (2010) illustrated the role of temperature in kelp speciation process (in cotutelle with Chile, in the context of the creation of a CNRS international laboratory with Sylvain Faugeron and Juan Correa from the Pontificia Universidad Católica de Chile). This abiotic factor is one of the most important factors determining the geographic distribution of kelp species, as it affects survival, reproduction and/or growth. F. Tellier, using multilocus barcoding approaches, revealed the existence of two cryptic species in *Lessonia nigrescens* Bory de Saint-Vincent, 1826 along the latitudinal gradient of the coast of Chile (Tellier et al., 2009). These two cryptic species show a strict parapatric distribution with a very narrow overlap in their distribution ranges composed of a mosaic of populations constituted exclusively of individuals from one or the other species, without coexistence. In this contact zone, a total absence of hybrids and mixed populations could be observed based on spatial distribution of microsatellite alleles (Tellier et al., 2011). Using reciprocal transplant experiments in the field and controlled response to different thermal and desiccation stresses in the lab, on both microscopic and macroscopic phases of their life cycle, the two cryptic species were shown to differ in their heat and stress tolerance matching their corresponding latitudinal distributions (Oppliger et al., 2012; López- Cristoffanini et al., 2013).

With the emergence of *Ectocarpus* (Fig. 4) as the genetic and genomic model of Phaeophyceae following the first publication of its genome sequence by the algal genetic team of Mark Cock and Susana Coelho in the *Station Biologique de Roscoff* (Cock et al., 2010), a collaboration between the two groups developed through several research projects in order

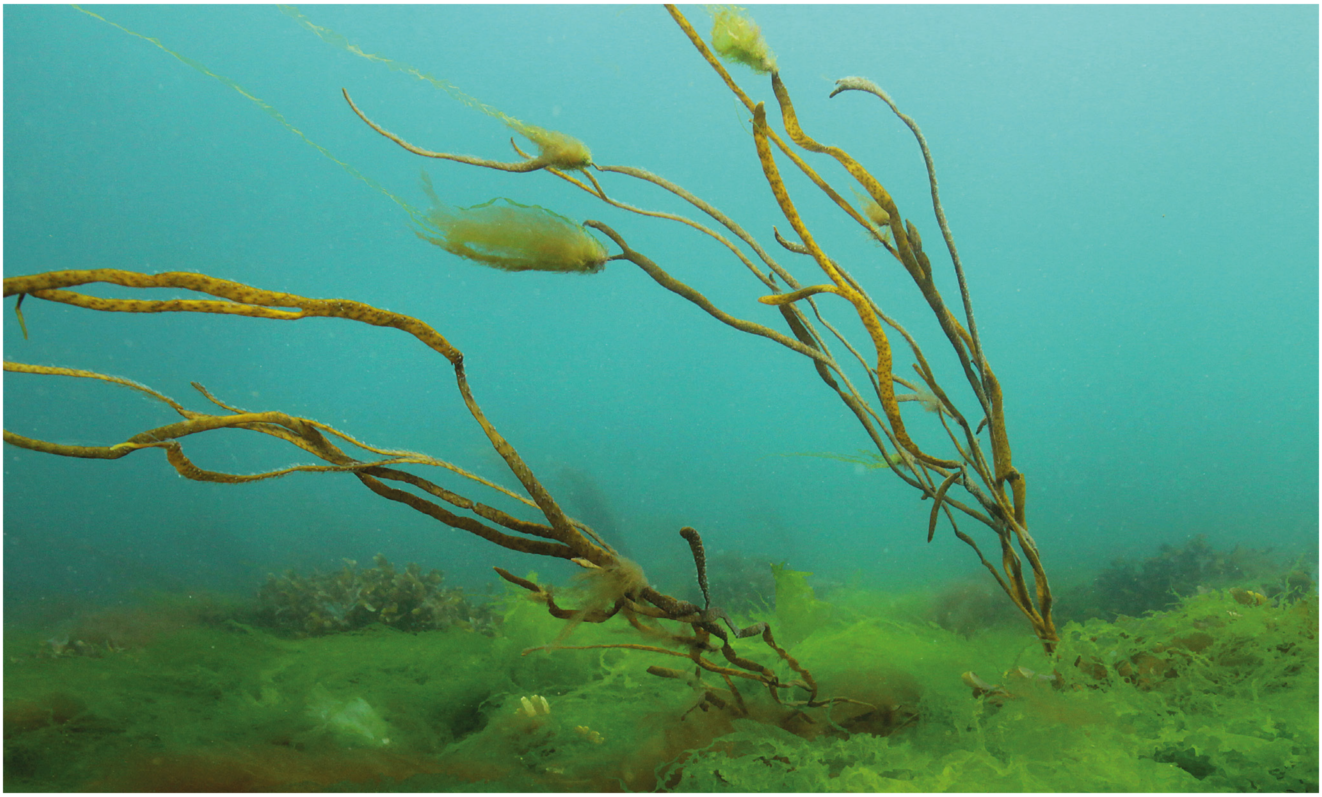

Figure 4. *Ectocarpus siliculosus* as an epiphyte on *Himanthalia elongata* in the Roscoff area. Copyright : Wilfried Thomas@ Station Biologique de Roscoff.

to link functional genetics and genomics to population genetics and ecology. The work of Post-doc Lucia Couceiro and PhD student Alejandro Montecinos (2016, in cotutelle with Marie-Laure Guillemin, Austral University of Chile, Valdivia) was developed in this context. The link between ecological speciation and shifts in mating systems and/or life cycles was also observed in *Ectocarpus* spp. (Couceiro et al., 2015; Montecinos et al., 2017).

These different results highlight the possible role of the complex and variable life cycles of brown algae in promoting speciation without strong geographic isolation. The characteristics of the Ectocarpales cycle, which features alternating haploid gametophytes and diploid sporophytes, provided insight into the importance of pre- and postzygotic barriers in reproductive isolation (Montecinos et al., 2017).

The evolution of reproductive isolation has also been studied by looking at what happens when exotic species are introduced into the area of their native congeners. Beyond their relevance to invasion biology, anthropogenic contact zones provide useful situations to study the strength and evolution of isolating mechanisms, especially in the case of strongly divergent species (Viard et al., 2020). A project led by Frédérique Viard examined the reproductive isolation between *Ciona intestinalis* (Linnaeus, 1767) a solitary ascidian found on the northeast coasts of the Atlantic Ocean, and *Ciona robusta* Hoshino & Tokioka,1967, native to the Pacific Northwest. These species have had a long history of allopatric divergence but now coexist in sympatry in Brittany following human-mediated transport of *C. robusta* (Bouchemousse, 2015). F. Viard's team dissected the nature of reproductive barriers between the two *Ciona* species, and how their genetic divergence was shaped by fluctuations in gene flow. They found no ecological isolation in the area where the two species are sympatric, with only slight differences in optimal growth temperatures but no difference in the timing of gamete production and recruitment (Bouchemousse et al., 2016a). First-generation hybrids also survive equally well in the range of temperatures and salinities encountered naturally in their contact zone (Malfant et al., 2017). Barriers appear later in the life cycle: F1 males have very low fertility, and backcross offspring and F2 have a weakened growth and survival, pointing towards genetic incompatibilities (Malfant, 2017). Analyses based on increasingly detailed genetic data have gradually revealed a complex history of divergence characterized by an episode of ancient introgression followed by a much more recent resurgence of gene flow contemporaneous with the human translocation of *C. robusta* and restricted to a small region of the genome (Bouchemousse et al., 2016b; Le Moan et al., 2021).

The various examples above illustrate that speciation research at Roscoff has been largely based on empirical approaches, taking direct advantage of the proximity of the marine environment, as envisaged by Lacaze-Duthiers when he founded the station 150 years ago. But the station also welcomed the theoretical biologist D. Roze and the mathematician B. Sarels who contributed to several theoretical studies aiming at understanding in particular the evolution of isolation mechanisms due to genetic incompatibilities (Alfaro et al., 2022), and more generally how Fisher's geometric model can be a very efficient tool to approach speciation theory (Fraisse et al., 2016; Schneemann et al., 2020).

Summarizing the research on speciation done at the station in the recent times (say since the establishment of a population genetics team in the early 2000's), we see that we have been collectively interested in two classes of questions: i) exploring the spatial distribution of species, gene flow and hybridization at different spatial scales, from the foreshore through larger geographical areas (Brittany, Chilean coast) up to hydrothermal sources at oceanic scales, and ii) identifying specific pre- and post-zygotic barriers and their underlying genomic bases. This research has benefited from the meteoric progress of sequencing techniques, and population genomics is now at the heart of our work. Yet reading ancient literature is extremely instructive, if only to understand the evolution of ideas and concepts that frame our current thinking. We have also found it to be a good opportunity to learn about methodical observation and the application of the scientific method, and take a step back from the technical advances that tend to influence us a little too much.

Evolutionary biology in France took a decisive turn when G. Teissier, A. Wolf, B. Ephrussi, and P. L'Héritier promoted the field of genetics and its role in evolution. In addition to their routine contacts in Paris, many interactions also took place during the many summers that these researchers spent in the laboratory and on the shores of Roscoff. Although G. Teissier has had a profound impact on evolutionary biology in France as an individual, the raison d'être of the marine laboratory has been, more generally, to provide the best possible conditions for bringing together passionate scientists and students on the field to investigate species diversity in the marine fauna and flora. This was the idea of its bold founder, Henri de Lacaze-Duthier, and it has remained so (and largely developed) to this day. Among other topics, research on the evolution of reproductive isolation has benefited from these premises, mainly through collaborative projects on population genetics of marine algae and invertebrates. Beyond the resident research described in this article, the station has also fully played its role as a relay, host, or sampling site for other speciation studies. To name but a few examples, the station has facilitated sampling of *Littorina* snails (from 1977 to the present! Berger, 1977; Stankowski et al., 2020), blue mussels (Bierne et al., 2003, involving data from genotyping tutorials organized by F. Viard and D. Jollivet for students of the UPMC Master in oceanography), and even... shrews (Taberlet et al., 1994).

The *Station Biologique de Roscoff* was founded as a laboratory of experimental zoology of the Sorbonne in Paris, and today benefits from two affiliations: Sorbonne University & the CNRS. The brief history of speciation research at Roscoff that we have just recounted is obviously inseparable from the work carried out in the Parisian laboratories. Throughout this short historical journey, we have seen that all the researchers, without exception, have had multiple research sites, and an undeniable enrichment of ideas developed internationally (the most striking examples are L'Héritier's stay in the United States in 1931 and the frequent exchanges of G. Teissier and his colleagues with the founders of population genetics and of the synthetic theory of evolution). Although the Roscoff station now has around 120 resident staff, its Parisian tutelage and its national and international collaborations are essential to its involvement in research and higher education. Let us collectively add a few more steps to study the origin of species, facilitate such studies by national and international collaborators, and train students in this field over the next 150 years.

Acknowledgments

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