

The Arago Laboratory of Banyuls and some of its Academicians

Marie-Odile Soyer-Gobillard

Observatoire Océanologique, Université P. et M. Curie (Paris 6), Banyuls-sur-Mer, France

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Summary. Since its founding in 1881 by Henri de Lacaze-Duthiers (1821–1901), the Arago Laboratory of Banyuls has been one of the three marine stations of the University Pierre and Marie Curie-Paris 6. It is located in Banyuls (Banyuls-sur-Mer) in Northern Catalonia. The center hosts researchers and students from all over the world. Some became famous, including four Nobel Prize winners: André Lwoff (1965), Pierre-Gilles de Gennes (1991), Albert Fert (2007) and Jules Hoffmann (2011). This article focuses on five scientists closely related to the center. The first three are Henri de Lacaze-Duthiers (1821–1901), the founder; Édouard Chatton (1883–1947), eminent director of the center; and André Lwoff (1902–1994), who before being known for his work in bacterial genetics and virology was an outstanding protozoologist under the direction of Chatton. Lynn Margulis (1938–2011), a great friend of the Arago Laboratory and personal friend of the author, is also remembered. Finally, there is a mention of Walter J. Gehring (1939–2014), professor at the University of Basel, Switzerland. [*Int Microbiol* 19(4): 183-190 (2016)]

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Introduction

The Arago Laboratory, currently also known as the Oceanological Observatory at Banyuls-sur-Mer (the village of location), was founded in 1881 by Henri de Lacaze-Duthiers (1821–1901). It opened in 1882 under the French name of

“Laboratoire Arago,” in honor of the French physicist, mathematician, astronomer and politician François Arago. (François Jean Dominique Arago was born in Estagel, near Perpignan, in the Roussillon, Northern Catalonia, in 1786, and died in Paris in 1853, trying to return to his homeland). The location of the Arago Laboratory on the French Mediterranean coast was decided by Lacaze-Duthiers due to his own interest to study the diversity of organisms and habitats offered by the rocky shore surrounding the village of Banyuls (Banyuls-sur-Mer) (Fig. 1). The original mission of the Laboratory, pre-

Correspondence: M-O. Soyer-Gobillard
E-mail: mog66@orange.fr

This article is an homage to my dearest friend Lynn Margulis (1938–2011) at the fifth anniversary of her death. A part of this article has been based on a publication in *Vie et Milieu/Life and Environment* 66(2):107-119 (2016), after a lecture given by the author at the Arago Laboratory (14 May 2016) on the occasion of the 350th Birthday of the French Academy of Sciences (1666–2016), by invitation of Dr. Michel Delseny, Academician of Science, Biology Integrative Section.



Fig. 1. View of the Arago Laboratory of Banyuls (Banyuls-sur-Mer). (Photograph from <http://www.la-clau.net/>).

served by its eleven directors throughout its 135 years of history (Table 1), was that of promoting education and research in marine sciences, and to allow the general public to discover the marine world. For this reason, in 1885 the public aquarium was opened as a part of the Arago Laboratory. Nowadays, the Arago Laboratory comprises several facilities and is one of the three marine stations managed by the Pierre et Marie Curie University (Paris 6) and the CNRS (the French National Center for Scientific Research). The Arago Laboratory is divided into four main research units: Integrative Biology of Marine Organisms (BIOM); the Laboratory of Microbial Biodiversity and Biotechnology (LBBM); the Benthic Ecogeochemistry Laboratory (LECOB), and the Microbial Oceanographic Laboratory (LOMIC).

Some of the researchers and students hosted by the Arago Laboratory became famous, and this paper focuses on five scientists closely related to the center: Henri de Lacaze-Duthiers, founder of the Laboratory and master of experimental zoology [2]. Édouard Chatton (1883–1947), a great protozoologist, pioneer of cell biology, who became

director of the Arago Laboratory, and was the author of splendid painted courseboards passed down to his students. André Lwoff (1902–1994), Chatton's favourite disciple, and winner of the 1965 Nobel Prize in Physiology or Medicine, who before being known for his work on bacterial genetics and virology was an eminent protozoologist. Lynn

Table 1. Directors of the Arago Laboratory of Banyuls

1882–1900	Henri de Lacaze-Duthiers
1900–1923	Georges Pruvot
1923–1937	Octavio Duboscq
1937–1947	Édouard Chatton
1947–1964	Georges Petit
1964–1976	Pierre Drach
1976–1989	Jacques Soyer
1989–1999	Alain Guille
2000–2005	Gilles Boeuf
2005–2015	Philippe Lebaron
2015–current	Vincent Laudet

Margulis (1938–2011), evolutionary microbiologist, distinguished Member of the American National Academy of Sciences (1983), and American National Medal of Science winner (1999), who in 1967 proposed the endosymbiosis theory of the origin of the eukaryotic cell, and Walter J. Gehring (1939–2014), who every year came with his students from the University of Basel to the Arago Laboratory.

Henri de Lacaze-Duthiers (1821–1901)

Félix Joseph Henri de Lacaze-Duthiers (Fig. 2), anatomist, biologist and zoologist, was born in the castle of Stiguederne, Montpezat (Lot-et-Garonne) and died in Las-Fons (Dordogne). He is regarded as a leading authority in malacology of his time. Second son of the baron Etienne de Lacaze-Duthiers (1791–1868), the young Henri faced opposition from his father when he informed him of his will to undertake studies of medicine and biology in Paris. To survive, he became the assistant of Henri Milne-Edwards (1800–1885), famous for his work on molluscs, crustaceans and anthozoans, and then became zootechnician at the Agronomic Institute of Versailles. In 1851, he defended his thesis in Medicine and, in 1853, his doctoral thesis in Science on “the genital frame of the insects”. In 1854, he obtained a position of Professor of Zoology and occupied the first chair of Biology of the Faculty of Science of Lille, whose Dean was Louis Pasteur (1822–1895). Four years later he initiated the study of corals in Corsica and in the Balearic Islands. In 1863 he was appointed lecturer at the École Normale Supérieure in Paris, and in 1864 Professor at the French National Museum of Natural History to occupy the Chair of molluscs, worms and zoophytes. As Professor of Zoology, Comparative anatomy and Physiology at the Sorbonne, he was the first to engage the field of zoology in experimental research and field studies. He coined the term “experimental zoology” and, in 1872, founded the journal *Archives de zoologie expérimentale et générale*, which played a major role in the orientation of zoological research at the time. Lacaze-Duthiers must be regarded as the true founder of marine micro-zoology. Author of more than 250 publications, related in particular to corals, molluscs and the tunicates, he was elected member to the French Academy of Sciences in 1871 (section of Anatomy and Zoology). Known worldwide for his discoveries, he was honored in many countries [24].

To offer his students a close proximity to the marine environment, and to facilitate experimentation on live material,



Fig. 2. Henri de Lacaze-Duthiers (1821–1901) in 1887, bearing the Grand Cross of the Legion of Honour and his Science Academy costume. (© Archives of Laboratoire Arago).

Lacaze-Duthiers founded two marine biology laboratories: the biological station of Roscoff in 1872 and the Arago Laboratory of Banyuls-sur-Mer in 1882.

Edouard Chatton (1883–1947)

Édouard Pierre Léon Chatton was born in Romont, Switzerland and died in Banyuls-sur-Mer. His grandfather introduced him—at a very young age—to biological sciences and was at the origin of his scientific vocation. He completed his high school studies in the area of Belfort, Switzerland and then went to France to study at the Sorbonne, in Paris, with Yves Delage (1854–1920), former assistant of Lacaze-Duthiers and discoverer of artificial fecundation (chemical). In 1905, at the Arago Laboratory, Chatton discovered a group of protists, parasitic peridinians of the gut of pelagic crustacean copepods, named the blastodinides [3,23] (I had myself the honor to continue the work of Chatton during my Ph.D. thesis by studying the ultrastructure and cycle of these parasites with the modern tools of cell biology [7,11,25]). Maurice Caullery (1868–1958), great zoologist, specialized on invertebrates



Fig. 3. Edouard Chatton (1883–1947) and Marie Herre, the day of their wedding in Banyuls (1908). (© Archives of Laboratoire Arago).

and professor at the Faculty of Sciences of Paris, recommended Chatton to enter the Pasteur Institute in the Service of Protozoology and Colonial Microbiology, at that time directed by Felix Mesnil (1868–1938), microbiologist specialized on the sleeping sickness agent, the protozoan *Trypanosoma*. In 1908 Chatton married Marie Herre (Fig. 3), who later became his collaborator.

In 1913, Charles Nicolle (1866–1936), director of the Pasteur Institute in Tunis, awarded with the 1928 Nobel Prize in Physiology or Medicine for his work on typhus, and expert on *Leishmania* (trypanosomid agent of the visceral leishmaniasis, also known as kala-azar), put him in charge of the study of the etiology of toxoplasmosis, a parasitic disease caused by *Toxoplasma gondii*. At the beginning of World War I, Chatton was mobilized and went back to France, where he was injured. In 1916, he returned to Tunisia where, in Gabes, he created and directed the Laboratory of bacteriology for the

troops of Southern Tunisia. In 1918, once the war was over, he worked again at the Pasteur Institute in Tunis. During holidays, he went to the Arago Laboratory, where he achieved his doctoral thesis on the parasitic peridinians, which he defended in 1919 [4]. Also in 1919, Chatton was appointed lecturer at the General Biology Chair of the University of Strasbourg. In 1932, he was appointed Professor of Zoology and General Biology at the University of Montpellier, a position that included the direction of the Marine Biology Station in Sète. In 1937, he was appointed Professor of Zoology and Biology at the Sorbonne in Paris and became director of the Laboratories of Banyuls-sur-Mer and Villefranche-sur-Mer. Some years before, in 1933, he had been elected Corresponding Member of the French National Academy of Sciences (now part of the Institut de France).

Édouard Chatton was the first biologist to distinguish the fundamental differences between unicellular eukaryotes and prokaryotes, and made an enormous scientific production [5,24]. Some of his works were made in collaboration with his pupils, among them André Lwoff, who occupied a very special place in his life, both as a student and as a friend.

André Lwoff (1902–1994)

André Michel Lwoff (Fig. 4) was born in Ainay-le-Chateau (Allier, Auvergne-Rhône-Alpes) where his father was a psychiatrist. He became a fellow at the Institut Pasteur in 1921, as



Fig. 4. André Lwoff (1902–1994) in 1971, when I met him as director of the Villejuif Cancer Research Institute. (Photograph from the personal collection of M.-O. Soyer-Gobillard.)



Fig. 5. Participants in the 5th Meeting of the International Society for Evolutionary Protistology (ISEP), held in the Laboratoire Arago on the Mediterranean seaside, at Banyuls-sur-Mer in June 4-6, 1983. The meeting was directed by Marie-Odile Soyer-Gobillard and hosted some 70 people representing twelve countries (Belgium, Canada, Denmark, England, France, Germany, the Netherlands, Poland, Scotland, Spain, and the USA). Lynn Margulis is the first woman at the right of the picture. Reproduced from [17a,25].

recipient of a grant for his own research [22] and that same year he met Édouard Chatton at the Zoological Station of Roscoff. Chatton was then thirty-eight (Lwoff nineteen) and was lecturer in general biology at the Faculty of Sciences of Strasbourg. This meeting was crucial for both of them. Out of the 151 publications of André Lwoff on protozoology, 55 were carried out in collaboration with Chatton, particularly for major works, i.e., a monograph on apotomes, parasitic ciliates with two hosts, crustaceans and coelenterates, with remarkable metamorphoses of their cilia [6], and a monograph on thigmotrich ciliates in 1949 [13] (Fig. 4).

In 1925, Lwoff became assistant lecturer at the Pasteur Institute, and in 1927 he defended his medical thesis before becoming the head of a laboratory at the Pasteur Institute in 1929. Chatton and Lwoff continued to publish on protozoology. In 1931, they wondered about the genetic continuity of ciliary systems in foettingeriid ciliates; indeed, kinetosome replication requires not only the reconstruction of a microtubule building in particular and stable geometry but also the conservation of its original polarity. The following year, 1932, Lwoff defended a brilliant science thesis entitled

“Biochemical research on the nutrition of Protozoa”. At that time he had already produced 76 publications on protozoology.

In 1938 Lwoff was appointed director of the Department of Microbial Physiology, newly created for him at the Pasteur Institute in Paris, without definitively abandoning his dear protists. In fact, until Chatton’s death, during the summer they worked together on the study of ciliates and other protists either at Banyuls-sur-Mer, Roscoff, Wimereux or Sète. Most of their research on apotome ciliates was carried out in Banyuls [22]. From 1947 to 1950 he regularly taught in the United States at the Harvard Medical School on “Problems of morphogenesis in ciliates”. Many important prizes and honors rewarded his exceptional career and discoveries [24,26], among them the Nobel Prize in Physiology or Medicine, which he shared with Jacques Monod and François Jacob in 1965. Once retired, Lwoff used to spend several months a year in Banyuls. He often visited the Arago Laboratory and was interested in the research on the biology of dinoflagellates and other protists carried out there. André Lwoff died in Paris in 1994.



Fig. 6. Left: Lynn Margulis (1938–2011) and André Adoutte (1947–2002) at the 5th meeting of the International Society for Evolutionary Protistology (ISEP) in Banyuls (1983) [17a]. Right: Lynn Margulis (1938–2011) with Marie-Odile Soyer-Gobillard as jury members of the Doctorate Thesis of Toni Navarrete, a student of Prof. Ricardo Guerrero at the Faculty of Biology, University of Barcelona, in 1999. (Photograph from the personal collection of M-O. Soyer-Gobillard).

Lynn Margulis (1938–2011)

Lynn Margulis (her maiden name was Lynn Petra Alexander) was born in Chicago, Illinois, USA on March 5, 1938 and died in Amherst, Massachusetts, USA on November 22, 2011. She attended the University of Chicago, obtained a Master's degree from the University of Wisconsin at Madison and a Ph.D. from the University of California, Berkeley, where she defended her thesis entitled "An unusual pattern of incorporation of thymidine in *Euglena*," under the direction of Max Alfert, in 1965. In 1966 she moved to Boston University, where she was professor for twenty-two years. While in Boston she wrote her famous work *Classification and Evolution of Prokaryotes and Eukaryotes* [14]. The issue that made her worldwide famous was her interest in the symbiotic origin of the components of the eukaryotic cell, nucleus, chloroplast, mitochondria, cytoskeleton. She was particularly interested in the study of spirochetes, especially those attached to the surface of the symbiont flagellates living in the gut of termites [16].

Symbiosis in Cell Evolution [15], where she explained the theory of the symbiotic origin of the eukaryotic cell, *Handbook of Protoctista* [17b], considered the "Bible" of protistologists, and *Five Kingdoms* [18], which became a bestseller, are three of her best known works. Later, with James Lovelock, she developed the Gaia concept, the Earth and its environment being considered as an entity having generated its own regulating system.

In 1989, Margulis was appointed Commander of the Order

of Academic Palms of France. In 1999 she received the American National Medal of Science, awarded by US President William J. Clinton, followed by the Alexander von Humboldt Prize awarded in Berlin (2002–2005).

She often visited the Arago Laboratory, and played a major role in the organization of the 5th Meeting of the International Society for Evolutionary Protistology (ISEP), which was held in Banyuls in 1983, and also in the preparation of the Proceedings of the meeting, for which she wrote a Foreword with a chronicle of the conference (Fig. 5). It was the first time that the ISEP had met in Europe [19].

Her personal and scientific relationship with Prof. Ricardo Guerrero from 1983 until her death made Margulis to stay for long periods in Barcelona, Spain, where she continued developing her work and collaborating with many Spanish researches and students [1,10]. Among them, Toni Navarrete, who defended his thesis [21] on the microbial mats of the Ebro Delta in 1999 (Fig. 6). In 2006 the *Proceedings of the National Academy of Sciences* published *The last eukaryotic common ancestor (LECA): Acquisition of cytoskeletal motility from aerotolerant spirochetes in the Proterozoic Eon*, a major paper signed by L. Margulis, M. Chapman, R. Guerrero & J. Hall [16]. More than 30 years of fighting were necessary to finally reach conclusions positively cited by W.F. Martin et al. (2015) in the paper *Endosymbiotic theories for eukaryotic origin* [20]. In spite of her sudden death on 22 November 2011, the continuity in the memory and development of her concepts is assured.

Walter J. Gehring (1939–2014)

Walter Jacob Gehring was a Swiss developmental biologist, Professor at the University of Basel, Switzerland (Fig. 7) that every year visited the Arago Laboratory with his students.

Gehring was born in Zurich, Switzerland, and obtained his Ph.D. at the University of Zurich in 1965 with Professor Ernst Hadorn (1902–1976), a pioneer of developmental biology and genetics of *Drosophila*. After two years as an assistant to this geneticist, he joined the group of Alan Garen, Professor of Molecular Biophysics at Yale University in New Haven, Connecticut, USA, as a post-doctoral researcher. In 1969 he was appointed associate professor at the Yale Medical School and in 1972 returned to Switzerland, where he was appointed Professor of Developmental Biology and Genetics at the Basel Biozentrum, University of Basel, and continued to work on *Drosophila*.

While preparing his doctorate, he discovered a new *Drosophila* mutant in which the antennas were replaced by legs and he named it *Antennapedia*. This mutant remained the focus of his work throughout the following thirty years. Once genetic engineering techniques were available, Walter Gehring cloned the gene responsible for the mutation in *Antennapedia*. He discovered that all homeotic genes had a common sequence of 180 nucleotides, to which he gave the name of Homeobox. He first demonstrated that Homeobox genes were conserved during the evolution of metazoans, in which they play a key role in the organization of the body plan. Along with Kurt Wuthrich, he then determined the dimensional structure of the protein domain encoded by the Homeobox and called it the Homeodomain. He showed that the Homeodomain binds to specific DNA sequences of a gene's promoter, which implies that the Homeobox genes encode transcription factors capable of regulating the activity of other genes. It is on this basis that the Homeobox genes were called "Master genes of development" [8].

Walter J. Gehring made a second discovery of fundamental importance in developmental biology when he showed that the *Pax6* gene (which also contains a Homeobox) is essential to the development of the eye [9]. This gene is necessary for the initiation of gene networks used to build the visual system in all animals, including humans. Mutations that lead to loss of function of *Pax6* or its homologues (eyeless in *Drosophila*, *Aniridia* in humans) prevent the development of the eye in the earliest stages.

He received the Kyoto Prize for Basic Research (2000)



Fig. 7. Walter J. Gehring (1939–2014). (Photograph from the collection of Elizabeth Gehring).

and the Balzan Prize for Developmental Biology in 2002 [12] for his fundamental contributions, that is, the discovery of the universal principle underlying the organization of the body plan and that of eye development. He was elected a foreign member of the French Academy of Sciences in 1998 (section Cell Biology, Molecular and Genomics) and of other Academies of Sciences (USA, UK, Sweden, and Germany) and was awarded honorary doctorates by many universities, including University Pierre and Marie Curie. Walter Gehring started visiting the Arago Laboratory in 1960, as a student, and returned later regularly with his own students, until his death, from a car accident, in Greece in 2014. 🇨🇭

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About the author. Marie-Odile Soyer-Gobillard, Director of Research Emeritus Honorary of French CNRS (National Center for the Scientific Research), was greatly aided by the Cell Biology Laboratory team she formed and led from 1974 until 2005 at the Oceanological Observatory, Arago Laboratory, Banyuls-sur-Mer, University Paris 6 Pierre et Marie Curie, France. Until 2000, she was the head of the research team “Genome and cell cycle of the unicellular eukaryotes” and until 1995 the head of both the Department of Cell and Molecular Biology, and the Electron Microscopy Unit (1975–2000). Her research involved cell and molecular studies of protists, including dinoflagellates. She worked to identify and characterize the molecules that govern the cell cycle, including entry into mitosis, sexuality and meiosis, cytoskeletal structure and organization. These molecules, for the most part, were still unknown and the team demonstrated that some are conserved from dinoflagellates to humans. She elucidated the peculiar structure of dinoflagellate chromosomes, the composition of their chromatin and the maintenance of their chromosome structure by divalent cations and structural RNAs. She has published more than 130 publications mainly in peer-reviewed international scientific journals and has contributed more than 100 communications in congresses.