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BEING HENRI DE LACAZE-DUTHIERS

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MARINE INVERTEBRATES
MALACOLOGY
CORAL
EXPERIMENTAL ZOOLOGY
MARINE LABORATORIES
19TH CENTURY NATURALISM
FIXISM-TRANSFORMISM
HENRI DE LACAZE-DUTHIERS

ABSTRACT. – Why revive, 200 years after his birth, the personality and work of the zoologist Henri de Lacaze-Duthiers (1821-1901)? Did his work have a lasting impact on research until today? In what way can his career enrich the scientists of today? His evocation should bring some answers to these questions. We will follow him from his youth in an austere castle in the southwest of France to Paris where his taste for natural sciences and his republican convictions are affirmed; then in his first scientific expeditions where his passion for the world of marine invertebrates is triggered. We will witness the progression of his scientific work nourished by his multiple trips to the coasts and his university career, from Lille to Paris. Once he reached academic consecration, we will see him conceptualize the refoundation of zoology into a resolutely experimental discipline, by proposing a corpus of pioneering methods. We will leave him as the builder of the first marine stations of Roscoff and Banyuls-sur-Mer which, until today, are at the heart of European marine biology.

In mari via tua, and semitae tuae in acquis multis
Tu te frayas un chemin par la mer, un sentier par les grandes eaux
Your path led through the sea, your way through the mighty waters
Quote written on the blazon of the Arago laboratory, designed by Henri de Lacaze-Duthiers.
(Old Testament, Book of Psalms, Psalm 77:19)

WHO WAS HENRI DE LACAZE-DUTHIERS?

Henri de Lacaze-Duthiers (1821-1901) was one of the great naturalists who dominated zoology in the second half of the 19th century. Born in the south-west of France into an austere aristocratic family and raised under the authority of a father who was opposed to all modern ideas, he escaped this stifling environment and went to Paris after his baccalaureate. Doctor of medicine (1851) and natural sciences (1853), he began his career as a professor in Lille and ended it in a very powerful position in the world of naturalists: in the last quarter of the 19th century, he was a professor at the Sorbonne, a member of the French Academies of Medicine and Sciences, which he chaired, as well as of many foreign academies of Sciences, introduced to the ministries of public education and agriculture, politically influential, grand officer of the Legion of Honor and recipient of numerous decorations, both French and foreign, builder of the first marine laboratories in the world, founder of a new international scientific journal, and finally creator and leader of a school of thought and method that marked a turning point in zoological research, supported by his many pupils. To appreciate such a work, both as a zoologist and as a rebuilder of the discipline, it is interesting to know who he was (Fig. 1).

The image he left among his collaborators, colleagues, subordinates or executives of the Ministry of public education is that of a strict character. He is described as gruff, hot-tempered, relentless, obstinate, demanding, even intransigent, with a caustic sense of humor. If he worked day and night without a break throughout his long life, he expected the same from his collaborators, as well as the same quality and thoroughness from their work as from his own. Let one of his pupils, Yves Delage (1854-1920), tell us about the recruitment interviews that resemble a session in the office of an examining magistrate: "*In a cold and suspicious tone, he questioned you, turned you around and made you say what you would have preferred to keep secret, while an unforgettable eye searched you in your smallest recesses. The most daring came out of there weakened, emptied*." (Delage 1902; translation of the author[1]). As a single man who had broken away from

1 French text: *Sur un ton froid et méfiant, il vous questionnait, vous retournait et vous faisait dire ce que vous auriez préféré*

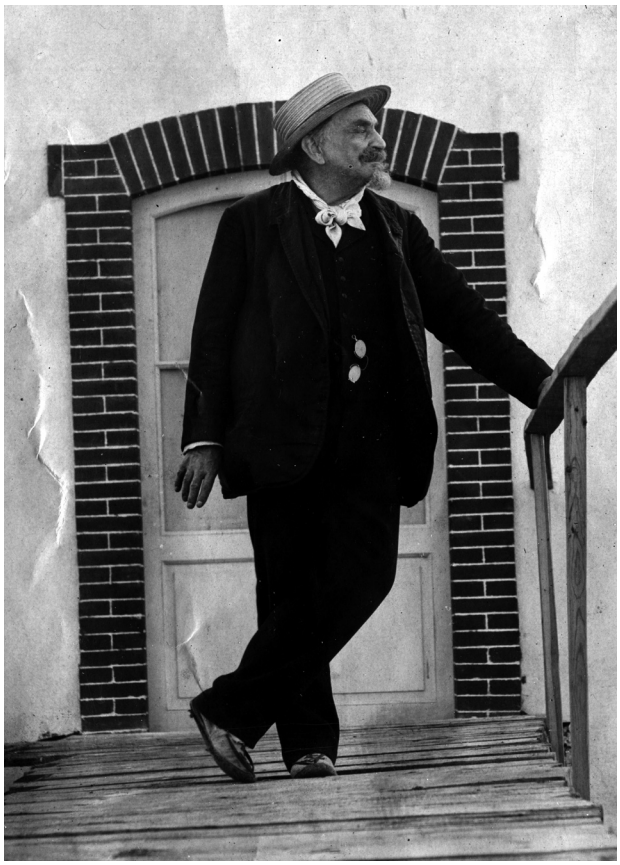

Fig. 1. – Henri Lacaze-Duthiers at the age of 73, photographed in front of the Arago Laboratory (Banyuls) in 1894. © Arago Laboratory, Library of Sorbonne University, Paris.

his closest family after the death of his mother (except for his aunt and cousin) and devoted himself entirely to work without ever taking a break, he was perceived as a solitary man with no private life. Even his scientific approach and reasoning evoked a cold and dispassionate character. He did not like theories or hypotheses, but claimed to focus on the facts, nothing but the facts, without preconceived ideas, without bias prior to observation and experimentation. Was Lacaze-Duthiers really this lonely, cold, severe, demanding character, the authoritarian and sometimes angry mandarin that has often been described?

Let's discover another man through the reading of his diary and his notebooks. And for that, let him speak. Here are the feelings he had during his scientific expeditions, recorded in his personal diary (Lacaze-Duthiers 1848-1858). In Menorca in 1853: "*The weather was beautiful, the water perfectly still, reflecting the blue of the sky and all the shades of the dawn. The calm was complete. I had a few moments of real pleasure; I started to draw one of the numerous rhizostomes which floated in the waters of the gulf with this grace and this nonchalance that I would like to contemplate always*." (translation of the author[2]). It is worth noting that he immortalized the beauty of marine animals through spectacular drawings in line and color, whether they were intended for science or simply for his own pleasure. In 1854, at Saint-Jacut (Brittany): "*I will always think of this quiet life, with no other concern than to make the young of my dentals live and no other sorrow than to see my young oysters die*." (translation of the author[3]). The same year in Saint-Malo, while meditating on the grave of Chateaubriand, he picked some flowers to send to his sister Louise: "*Could the happiness I feel in studying nature ever be lost? Could it be that at some point of my life, I could become indifferent to the wonders that unfold before our eyes the countless beings that populate our seas?* […] *I had only one regret, that of not being attached to a person who was sympathetic to me, the one I dream of having as a companion but whom I will probably never meet. I sometimes found myself alone, very alone, in Saint-Jacut*." (translation of the author[4]). This is a very contemplative character, hedonistic and even epicurean, but also a melancholic one that expresses his suffering from being alone. In his diary and some of his notebooks (Lacaze-Duthiers 1848-1858; 1858-1901), he expressed his heartbreak at the death of his relatives, his young sister Elisabeth in 1851 and his mother in 1863, the only two in his family to whom he was deeply attached. Nevertheless, as we will see, it would be erroneous to view him as a lonely man, with no wife, no children and no family contact.

In 1861, Pierre Lanceplaine, a sailor in military duty, was assigned to Lacaze-Duthiers' service during his coral expedition in Algeria. This was the beginning of an exceptional friendship that lasted throughout Lacaze-Duthiers' life. When Lanceplaine was released from his military obligations, he was hired as manager of all Lacaze-Duthiers' affairs and activities and never left him. Lanceplaine married[5], had three children, and this family

taire, tandis qu'un œil qu'on n'oubliait plus vous fouillait dans vos moindres replis. Les plus hardis sortaient de là assouplis, vidés.

[2] French text: *Le temps était superbe, l'eau d'une tranquillité parfaite reflétait le bleu des cieux et toutes les teintes de l'aurore. Le calme était complet. J'eus quelques moments d'un véritable plaisir ; je commençais le dessin d'un des nombreux rhizostomes qui flottait dans les eaux du golfe avec cette grâce et cette nonchalance que j'aimerais à contempler toujours.*

[3] French text: *Je songerai toujours à cette vie tranquille, sans autre souci que de faire vivre les petits de mes dentales et sans autre chagrin que de voir mourir mes jeunes huîtres.*

[4] French text: *Le bonheur que j'éprouve à étudier la nature pourra-t-il s'émousser jamais ? Se pourrait-il qu'à un moment de mon existence, je pusse devenir indifférent aux merveilles que déroulent devant nos yeux les êtres innombrables qui peuplent nos mers ?* […] *Je n'avais qu'un regret, celui de n'être pas uni à une personne qui me fût sympathique, celle que je rêve d'avoir pour compagne mais que probablement je ne rencontrerai pas. Je me suis parfois trouvé seul, bien seul, à Saint-Jacut.*

[5] Lanceplaine has been married twice. His first wife, Marie d'Autan, died in childbirth in 1868, giving birth to their

Fig. 2. – The residence of Lacaze-Duthiers at Las Fons, Dordogne, in 2022. **A**: Back side. **B**: Side façade. The laboratory was located on the top floor. Lacaze-Duthiers had created a door-window in the center, to gain more light. **C**: View on the Dordogne. On the bank, a water mill that was part of the estate. **D**: The monumental stone staircase in the interior. Note the bust of Lacaze-Duthiers by the sculptor Benlliure, made in 1900. © C. Jessus.

became the family of Lacaze-Duthiers: they lived together in the vast residence of Las Fons, in Dordogne, bought by Lacaze on Lanceplaine's advice in 1873. Lanceplaine or his wife accompanied him on his trips and they frequently stayed in Paris when Lacaze was teaching there. Both in fragile health, Lanceplaine and Lacaze-Duthiers took care of each other. Lacaze-Duthiers was also very busy with Lanceplaine's three children, often taking them with him on his trips to Roscoff and Banyuls-sur-Mer, raising surprise, even suspicion, when his university colleagues saw him traveling with two young girls (Lanceplaine's daughters, Valentine and Antoinette, respective nicknames: *Bébé* and *Tanon*), when he was supposed to have no family. It was to Lacaze-Duthiers that the future husbands of *Bébé* and *Tanon* made their request for marriage, it was on his arm that they were taken to the town hall, and it was he who endowed them. He made Lanceplaine's son, Raymond (nicknamed *Momon*), study medicine, and for a time *Momon* was his assistant at the Sorbonne and in Roscoff. Indeed, Lacaze-Duthiers had a busy and warm family life, a family he had chosen himself, whom he loved dearly and to whom he bequeathed his fortune and his house at Las Fons. Let us return to the latter.

Las Fons is now owned by the Aubriot family, descendants of Lanceplaine, who maintain it in line with Lacaze-Duthiers' vision. The vast residence, built of the local golden stone, is set in an impressive park which was planted by Lacaze-Duthiers with meticulous care: each species was selected from horticultural journals or requested from botanist collaborators from all over the world, the location was carefully chosen according to botanical and esthetic criteria. Terraces shaded by Lacaze-Duthiers' care overlook the green valley of the Dordogne, which flows peacefully at the bottom of the house (Fig. 2). A visit to Las Fons today is enough to enter the intimacy of Lacaze-Duthiers, and to discover a man in love with natural beauty, concerned with calm and serenity, but also with his own comfort! Let us remember that he loved fine

daughter Valentine. He remarried to Marie-Antoinette Darnige, known as Fontille, with whom he had two children, Raymond and Antoinette.

Fig. 3. – Representations of Lacaze-Duthiers offered as a token of admiration. **A**: Portrait of Henri de Lacaze-Duthiers, made by Charles Bellay (1826-1900) in 1886. This engraving was offered to Lacaze-Duthiers in 1887 by many pupils and colleagues, French and foreign. **B**: Bust, made by the Spanish sculptor Mariano Benlliure (1862-1947) in 1900. This bronze bust was offered to Lacaze-Duthiers by the University of Barcelona, at the initiative of Professor Odon de Buen (1863-1945), in recognition of his contribution to science and the fruitful exchanges established between the Arago Laboratory and the University of Barcelona. © Roscoff Biological Station, Library of Sorbonne University Paris (A) and C. Jessus (B).

cooking, wine and beer, and was a champagne expert. Las Fons was his haven of peace, the family home, the center of his life. Teaching in Paris, stays in marine laboratories, travels, everything was organized from Las Fons, where he lived with his adopted family, at least from February to June, then from September to November, and from where he left, then returned, from his frequent trips. For a long time, he was considered an endless traveler, without a home base. Although he travelled extensively, he did have a precious home base, where he found calm, serenity and family happiness. Las Fons was not a secret garden but an open place of which he was very proud. He invited countless colleagues, pupils, students, foreign scientists and friends. The vast laboratory he had installed at the top floor allowed him to work without interruption and to welcome his collaborators. He was so well established in the village that he was its mayor for two mandates, reforming its administrative and financial organization after his republican ideals (d'Hondt 2001, 2002). The annual festival of the village was organized in the gardens of Las Fons!

He was also endowed with a deep affection, solicitude and empathy for many people beyond his adopted family, Lanceplaine's one. On many occasions, he advanced the salaries of young collaborators (several of his assistants, sailors or mechanics, etc.) from his own resources; he regularly offered gifts to his friends, sending them nuts, mushrooms, cold meats or wine from Las Fons; at the end of his life, he even took care to list the personal items (furniture, jewelry, books, souvenirs of his travels, etc.) to be given to his close friends after his death, choosing for each of them what he had appreciated the most. His concern, marked by a great paternalism, was particularly strong for young people, probably because he was marked by the little support he himself received from his father during his youth. He was basically a very good person, absolutely unselfish. A review of his correspondence reveals that the number of people who sought his help and whom he actually obliged is absolutely considerable. He was also constantly concerned about the health of those around him. It must be said that the medicine of the time was still very rudimentary, as Lacaze-Duthiers, himself a physician and suffering from acute rheumatism, was well placed to know, and that cholera, typhoid fever, tuberculosis, influenza and croup were devastating, not to mention the mortality rate among women in childbirth.

Finally, his notebooks also reveal his aversion to ceremonies and approaches to influential people. However, this was one of his permanent occupations, concerned as he was to provide his pupils with interesting professional positions and to collect money for the building and running of his laboratories. But he disliked these actions and he did them with reluctance. The story of the meeting he wanted to have with the Minister of Public Education,

Jules Ferry (1832-1893), who was visiting Perpignan in 1879, to argue for the building of a new laboratory in Port-Vendres (it will become Banyuls-sur-Mer) is quite funny: Lacaze-Duthiers missed the ideal moment of the meeting, did not dare to approach the minister, missed all the opportunities to discuss with him, and only decided to approach him at the very last second. He was simply shy! His modesty, his concern of betraying his emotions perhaps, his lack of taste for large gatherings too, led him to avoid the festivities organized for the happy moments of his relatives, such as the wedding of *Tanon*, Lanceplaine's daughter, whom he accompanied to the town hall and the church, but where he went back to his laboratory rather than taking part in the meal, or that of the wedding of the mechanic Joseph David to the school teacher of Banyuls-sur-Mer, which he had nevertheless planned, but in which he did not participate. However, this did not prevent him from being quite sensitive to honors, especially from people he esteemed, such as his engraved presentation portrait offered by his students in 1887, or his bronze bust commissioned by the University of Barcelona in 1900 (Fig. 3). Nor was he extremely sensitive to the attacks that targeted him, especially when they came from former students in whom he had initially placed his trust, such as Alfred Giard (1846-1908) or Edmond Perrier (1844-1921). Being faithful in friendship, betrayal was totally unbearable for him.

The two impressions of Lacaze-Duthiers that reach us after more than 150 years may seem contradictory: the public image of a cold, solitary, authoritative or even angry man, secret, attached to facts and nothing but facts, which would exclude from his personality any notion of affect; the intimate image of a man who was affectionate, generous, modest, even shy, faithful in friendship, appreciative of calm, of the beauty of things and the pleasures of life, attached to his family life with Lanceplaine. If the portraits are contrasting, they are certainly not contradictory. The intimate Lacaze-Duthiers explains the public Lacaze-Duthiers. As his collaborator Georges Pruvot (1852-1924) summarized in the beautiful speech he gave at his funeral in Banyuls-sur-Mer in 1902 (Pruvot 1902): "*The cause seems to be a sort of modesty, a self-distrust, a need to be encouraged or supported, quite unexpected in a man who passed, and put its efforts to pass, for a rather insensitive, combative, somewhat harsh and difficult character*." (translation of the author[6]). Lacaze-Duthiers simply worked to create an image of himself that did not correspond to his intimate personality, convinced that this artificial image that he had built up, made of insensitivity, coldness, rigidity and authority, was essential to achieve his ambitious scientific objectives. Indeed, the establishment of a new experimental zoology based on the values of scientific impartiality, required bitter struggles, hardly compatible with his intimate self, generous, shy, sometimes melancholic, and deeply attached to the notion of friendship. This explains why the combination of the appearance he displayed and his true intimacy has produced this hard worker who was guided by curiosity, passion and fascination for the richness and beauty of nature, demanding from others what he imposed on himself, determined to fight for the realization of his projects, which made him forget his own doubts, unwaveringly attached to those, many, whom he appreciated and to his reconstituted family, under a gruff exterior which avoided outpourings incompatible with his shyness.

[6] French text: *La cause semble devoir en être cherchée dans une sorte de pudeur, une défiance de lui-même, un besoin d'être encouragé ou soutenu, bien inattendu chez un homme qui passait et mettait sa coquetterie à passer pour peu sensible, d'un caractère combattif, quelque peu âpre et difficile*.

YOUTH: AWAKENING TO NATURALISM AND REPUBLICAN VALUES

Henri de Lacaze-Duthiers was born in 1821 in a family environment that hardly predestined him to become a naturalist. He was the son of a royalist aristocrat, grandson of a baron guillotined in 1793. He received a rigid education from a strict father, in a dark and isolated castle called Stiguederne, in the southwest of France. There, however, he developed a passion for the things of nature. Although Stiguederne was cold and ugly, the charm of the nature that surrounded it worked. In addition to the awakening to naturalism, and in spite of his father's environment, which was committed to the retrograde ideas of the old regime, Lacaze-Duthiers forged republican convictions that would animate him throughout his life. He was also influenced by the family of his mother, daughter of a peer of France, Louis de Cassaignoles. This maternal grandfather was a deputy of the center left party. He signed a motion of no-confidence against the authoritarian policy of King Charles X, which ultimately led to the July Revolution in 1830. His mother's sister, his aunt Laure, married Guillaume Drême, president of the Court of Appeal of Agen, and their home, warm and open to republican ideas, was a refuge far from his father's values. Lacaze-Duthiers was thus at the crossroads of different ideological currents and made his choice very early on. All his life, he displayed his conviction in a republican ideal anchored on the values of laicity, universal suffrage and public education, far from the royalist principles of his father. At the age of 20, driven by his passion for nature and with modern political convictions, Henri de Lacaze-Duthiers, despite his father's opposition, went to Paris to study medicine. Why did he choose medicine when he had no intention of practicing it and was only interested in natural history? It was a very logical choice in 19th century France. The study of natural sciences was not individualized within the faculties but was fragmented and included in physics and chemistry programs. The best way to acquire a complete training as a naturalist was to undertake medical stud-

ies, which included solid training in the natural sciences. Thus, in the middle of the 19th century, the great naturalists were almost all physicians by education (Henri de Blainville, Jean-Victor Audouin, Henri Milne-Edwards, Armand de Quatrefages, Isidore Geoffroy St Hilaire, André and Auguste Duméril, etc). Here was Henri de Lacaze-Duthiers in Paris to study medicine, poorly supported by a small paternal grant.

BETWEEN FIXISM AND TRANSFORMISM, BETWEEN FACTS AND THEORIES

In the 1840s, the French naturalist community emerged from violent debates between supporters of the fixity of species, whose most influential promoter was Georges Cuvier (1769-1832), and supporters of transformism, founded by Lamarck (1744-1829), whose ideas were adopted by Étienne Geoffroy Saint-Hilaire (1772-1844). Cuvier considered species to be static during the periods between two planetary catastrophes, with each catastrophe marking the sudden disappearance of living beings and the creation of new ones, until the next catastrophe. Lamarck, on the contrary, thought that living beings derive from each other by a continuous process in time and bushy in the genesis of new beings, the most complex beings being formed from simpler ones thanks to the acquisition of new hereditary characters under the direct influence of the environment. It is of course this last point that will differentiate him from the theory of natural selection of Darwin (1809-1882) published in 1859.

If Georges Cuvier and Étienne Geoffroy Saint-Hilaire were no longer alive when Lacaze-Duthiers arrived at the Sorbonne, their disciples were there and held important chairs at the Museum. Henri Milne-Edwards was Cuvier's pupil, Isidore Geoffroy Saint-Hilaire that of his own father. They each defended a certain idea of their respective scientific heritages. How was Lacaze-Duthiers' vision forged in the context of these French currents, enriched by the new ideas of Darwinism?

Lacaze-Duthiers was a student of Henri Milne-Edwards. The latter was not the reincarnation of Cuvier. The great question of fixism-catastrophism versus transformism was no longer at the center of passionate debates nor of the lectures given at the Sorbonne and the Museum. Not because the question was resolved, there were followers of both currents. But because the French naturalists of the time, and particularly the successors of Cuvier, were partisans of a scientific method inherited from the empiricism of Aristotle: examining the facts, without *a priori*, without preconceived hypothesis which is not supported by objective data, and from the observation of these facts only, trying to draw general laws. In this case, debating the supremacy of one of the two theories, fixism or transformism, was not a priority, because they remain "theories" insufficiently supported by facts to be validated and gain the status of "law". This method was based on the philosophical current of Auguste Comte (1798-1857), scientific positivism, which promoted a scientific approach aimed at explaining the reality of facts by identifying, through repeated observations and experiments, the relationships and the connections that unite phenomena, without seeking the primary causes. The question was not the "why" but the "how" that allows us to identify scientific laws.

This way of approaching natural sciences deeply influenced Lacaze-Duthiers who remained all his life quite refractory to discuss theories stemming from hypotheses and of carrying out his scientific observations with the aim of validating (or invalidating) such or such theory. On the contrary, he expected from his observations, performed without *a priori*, the logical emergence of general rules. He was therefore cautiously keeping out of the fixism/transformism/Darwinism debates. As he said: "*I am not antagonistic to Darwinism; only I find facts just as difficult to explain by admitting it as I find inexplicable ones by not admitting it*. […] *To be antagonistic and not to be convinced are two different things. I would like nothing better than to accept the evidence; so far I find it insufficient. Besides, going back to the origin of things seems to me to be a problem whose solution is getting further and further away, and which, moreover, does not bother me much. For me, monogenesis or polygenesis are both as difficult to demonstrate one as the other, since the proofs are hypotheses and conjectures*." (Pruvot 1902; translation of the author[7]). What did matter to him is the clarity of observations and their interpretations. Admiring Darwin's naturalist talents, he was a fierce defender for his election as a foreign correspondent to the French academy of sciences. Indeed, incredible as it may seem today, Darwin's election was long and problematic in France. While his work "*On the origin of species*" was published in 1859 and received an enthusiastic reception in Europe, Russia and the United States, it was only in 1870 that Darwin was proposed for election to the French academy of sciences. It took 8 years and 6 presentations before he was finally elected, in 1878, when he was already a member of the most prestigious academies in Europe, Russia and the USA. Surprisingly, he was elected to the botany section, and not to the zoology section! What he will comment in a letter to the botanist Asa Gray (1810-1888) elected at the same time as him: "*It is a pret-*

[7] French text: *Je ne suis pas antagoniste du Darwinisme ; seulement je trouve des faits tout aussi difficiles à expliquer en l'admettant que j'en trouve d'inexplicables en ne l'admettant pas*. […] *Être antagoniste et n'être pas convaincu sont deux choses. Je ne demande pas mieux que de me rendre à l'évidence des preuves, jusqu'ici je les trouve insuffisantes. D'ailleurs, remonter à l'origine des choses me paraît être un problème dont la solution s'éloigne de plus en plus, et qui, du reste, me tourmente peu. La monogenèse ou la polygenèse me paraissent aussi difficiles à démontrer l'une que l'autre, puisque les preuves sont des hypothèses et des conjectures.*

ty good joke that I am elected to the section of botany, the extent of my science in this branch allowing me little more than to know that the daisy is a compositae and the pea a Leguminosae" (Darwin 1888). What happened to make France so resistant to Darwinism, so far behind the rest of the world? The fault lies largely with Cuvier, a fierce supporter of fixism who, during the first part of the 19th century, ridiculed and practically eradicated Lamarck's ideas on the concept of evolution of living beings. It was Darwin who allowed France to rediscover Lamarck's work! But in 1870, the influence of Cuvier's school was still very strong, and Lamarck's transformism, although it introduced the notion of evolution in a visionary way, was opposed to Darwin's theory on the notion of heredity of acquired characters versus natural selection. Stuck between the fixist heritage of Cuvier and the new promotion of Lamarck's transformism, the French academicians were not ready to accept Darwin. These retrograde positions would have long-term repercussions on French science, practically until the middle of the 20th century, hindering in particular the development of genetics in France. As for Lacaze-Duthiers, mocked by some of his former students such as Alfred Giard and Edmond Perrier for his supposed allegiance to Cuvier's fixism, he fought with his usual relentlessness to have Darwin elected. He campaigned, trying to wrest the votes of his fellow academicians, as his correspondence attests. Why did he do this? First, he admired Darwin as a scientific naturalist. Secondly, even if he was not convinced of the validity of Darwin's theory, he did not question the fact that it gave rise to debates of extreme importance and interest, the outcome of which could change the framework of biology. He therefore admired the man whose intellectual power had produced these revolutionary concepts, even though this theory remained unproven, or could even be invalidated, in his opinion. Thus, as soon as he was elected to the French academy in 1872, Lacaze-Duthiers became an ardent defender of Darwin's admission to this institution. He even published a note in the "Archives of experimental and general zoology" on the still unsuccessful election of 1872, where he wrote: "*The secret committee is secret. It is therefore not possible for me, as a member of the Academy and because of the fact that I attended the discussion, to publicly appreciate what was said, to judge the considerations which led to the vote of July 22, 1872 and which caused the failures and defections which with no less pain than astonishment one had to observe. But what is my right, and I want to use it, is the freedom I have to express after the public vote my personal opinion on a fact that now belongs to everyone. Although I am far from sharing all the ideas of Mr. Ch. Darwin, I deeply regret that only fifteen votes were given to his name* […]. *The considerable position, the numerous works, the unquestionable notoriety and the boundless devotion to science of the ILLUSTRATE ENGLISH ZOOLOGIST could have hoped* […] *that the majority would be assured to him whose studies so persevering, whose travels so numerous have given an undeniable and new impulse to the zoological studies,* […] *to the candidate for whom I voted and for whom I shall vote again*." (Lacaze-Duthiers 1872a; translation of the author[8]).

As for his so-called loyalty to Cuvier, it was regularly denied by the rather sharp criticisms he addressed to him in his articles. Louis Boutan (1859-1934), one of Lacaze-Duthiers' pupil and inventor of submarine photography, relates one of his conversations with his master: "*Do you know how my opponents tried to harm me when I was preparing my candidacy for the Institute? Lacaze, they said, is a follower of Cuvier. I don't think it's so bad to be a pupil of Cuvier. He did not lack precision in the observation of facts. He knew how to work. However, in spite of all my admiration for this great man, I fear that I was not his faithful disciple*." (Boutan 1902; translation of the author[9]). Lacaze-Duthiers has never been the fixist he has been accused of being, as a student of Cuvier's pupil. He was not a Lamarckian transformist, nor a Darwinist. He professed all his life his distrust of theories and hypotheses, as he said: "*In the range of hypotheses, there are no limits. Arguably, when one has enough imagination to enter the range of suppositions, one can go very far, but one can also be led to error, especially when one supports all the theories, even the most meaningless. For me I confess, I prefer above all the serious observations, and I stick cautiously to the deductions that wisely follow from them*." (Lacaze-Duthiers 1874; translation of the author[10]). As nothing is simple, he repeatedly for-

[8] French text: *Le comité secret est secret. Il ne m'est donc pas possible, en qualité de membre de l'Académie et par cela même que j'ai assisté à la discussion, d'apprécier publiquement ce qui a été dit, de juger les considérations qui ont conduit au vote du 22 juillet 1872 et qui ont causé les défaillances et les défections qu'avec non moins de peine que d'étonnement on a eu à constater. Mais ce qui est mon droit, et je veux en user, c'est la liberté que j'ai d'exprimer après le vote public mon opinion personnelle sur un fait appartenant désormais à tous. Bien que je sois loin de partager toutes les idées de M. Ch. Darwin, j'ai un profond regret de n'avoir vu porter sur son nom que quinze suffrages* […]. *La position considérable, les travaux nombreux, la notoriété incontestable et le dévouement sans bornes à la science de l'ILLUSTRE ZOOLOGISTE ANGLAIS pouvaient espérer* […] *que la majorité serait assurée à celui dont les études si persévérantes, dont les voyages si nombreux ont donné une impulsion indéniable et nouvelle aux études zoologiques,* […] *au candidat pour lequel j'ai voté et pour lequel je voterai encore.*

[9] French text: *Savez-vous comment mes adversaires essayaient de me nuire lorsque je préparais ma candidature à l'Institut ? Lacaze, disaient-ils, c'est un disciple de Cuvier. Moi, je ne trouve pas cela déjà si mal d'être un élève de Cuvier. Il ne manquait pas de précision dans l'observation des faits. Il savait travailler. Pourtant, malgré toute mon admiration pour ce grand homme, je crains de ne pas avoir été son disciple bien fidèle.*

[10] French text: *Dans le champ des hypothèses, il n'y a pas de limites. Sans doute, quand on a assez d'imagination pour entrer dans la voie des suppositions, on peut aller très loin,*

got his own principles, publishing works whose starting point was, as he said himself, "*a theoretical idea*". One example is his work on the otocysts of molluscs, "acoustic" vesicles sensitive to environmental vibrations. They had been described in some molluscs as being connected to the cerebroid ganglia, which seemed logical for a sense organ. But in other molluscs, they appeared to be connected to the pedal ganglia. How to explain that an acoustic organ is connected to a nervous center controlling motricity? Lacaze-Duthiers could not understand that an organ that is anatomically and functionally similar in all molluscs sends its information to totally different nervous centers, some consistent with its function, the cerebroid ganglia, and others unrelated to this function, the pedal ganglia. This incoherence also challenged the law of connections formulated by Étienne Geoffroy Saint Hilaire, of which Lacaze-Duthiers was a fervent supporter. According to this law, analogous organs (here the otocyst) must have identical relationships with their neighboring parts in all species (but the otocyst connects either to the cerebroid ganglia or to the pedal ganglia). Lacaze-Duthiers decided to embark on a titanic and meticulous work with the objective of testing a hypothesis: the otocysts of all molluscs must be connected to the cerebroid ganglia, because this makes physiological sense; consequently, the works claiming that they are connected to the pedal ganglia in some molluscs must be based on errors. To verify his hypothesis, he undertook careful histological studies, following the acoustic nerve from the cerebroid ganglia in more than thirty species of molluscs. He discovered that, without exception, this nerve is connected to the otocyst. He drew and described in detail the methodology he had used for the dissections and preparations and which explained, according to him, the errors of observation of his colleagues, notably Leydig (1821-1908), Claparède (1832-1871), Gegenbaur (1826-1903) or Huxley (1825-1895). He concluded that his work (a 71-page article) had demonstrated his hypothesis and validated the law of connections (Lacaze-Duthiers 1872b). This approach, marked by a great intellectual rigor based on a theoretical hypothesis, was not the one expected from a follower of the school of facts who prided himself on observing without preconceived ideas, without hypothesis or prior theory!

BETWEEN NATURAL HISTORY, MEDICINE AND AGRONOMY

Once in Paris, the young Lacaze-Duthiers passionately attended the natural history courses given by Henri Milne-Edwards. Even though Milne-Edwards held a chair that was half dedicated to insects, his passion was for marine animals, and more specifically for invertebrates. Milne-Edwards was a pioneer: in the 1820s, he was one of the first to carry out scientific trips to the coasts (Milne-Edwards *et al*. 1845-1848). Until then, scientists studied dead animals, preserved in alcohol, which they had often never seen alive. Milne-Edwards promoted a new approach: field zoology, in which the scientist explores the shore himself, observing and collecting the animals in order to understand how they live in their environment. Behind this idea was the very innovative concept, at the time, according to which physiology completes zoology, which had been descriptive until then. Milne-Edwards had another talent: he was a simple and amazing speaker who fascinated his students, including Henri de Lacaze-Duthiers. In 1845, the latter obtained the licence ès sciences and was hired as Milne-Edwards' assistant, who assigned him a thesis subject: the study of the genitalia of insects.

The idea was to determine if the theory of homologies between insect mouthparts proposed by Savigny (1777-1851) also applied to their genitalia. He undertook a phenomenal work of dissections and comparisons of 170 species (*Hymenoptera*, *Orthoptera*, *Hemiptera*, *Coleoptera*, *Diptera*, *Lepidoptera*, etc.) (Lacaze-Duthiers 1849, 1850, 1852a, b, 1853a, b). This first work of zoology is striking for the absolute meticulousness of the descriptions, which are restricted to the strictest facts, the text not including any discussion or general statement. We see here that Lacaze-Duthiers' reluctance to any generalization and theory is rooted very early in his scientific career! He concluded that all genitalia are organized according to the same pattern, that the changes in shape observed between species reveal an adaptation to a specific function, and that it is always possible to track the origin of extra parts from an abdominal segment. In doing so, Lacaze-Duthiers manipulated both the links based on functional causality introduced by Cuvier and those of family ties between species proposed by Geoffroy Saint-Hilaire. He also allowed himself a physiological interlude thanks to his very original study of insect's galls, which revealed how the metabolism of the egg to the larva, which is nested in each gall, evolves towards the production of fat from plant materials that do not contain any (Lacaze-Duthiers 1854a). This was his first pioneering work in the field he later called "experimental zoology".

This does not mean that Lacaze-Duthiers gave up the study of medicine. He was still determined never to practice it. But it gave him a deeper knowledge of anatomy and physiology than the natural science courses could provide. So he became a medicine resident in Professor Trousseau's department, first at the Necker Hospital and then at La Salpêtrière, an assignment he especially appreciated because it was a stone's throw from the Museum. In 1851, Henri de Lacaze-Duthiers became a doctor of

mais on peut aussi être conduit à l'erreur, surtout quand on soutient toutes les théories, même les plus creuses. Pour moi, je l'avoue, je préfère avant tout les observations sérieuses et je m'en tiens prudemment aux déductions qui sagement en découlent.

medicine. His thesis was on hydrothorax and its treatment by paracentesis (Lacaze-Duthiers 1851). In those years, his publications addressed both human pleural effusions and all the diversity of insects' genitalia!

The young doctor of medicine pursued his thesis of natural history in difficult financial conditions. At his father's castle, the study of insect genitalia provoked only incomprehension and discontent of the baron who sent only a small grant. Lacaze-Duthiers had to make a living. He took a position as a zootechnics instructor at the agronomic institute of Versailles. He had to teach the different breeds of domestic animals and their respective advantages. The study of insects was combined with the study of dairy cows, wool sheep, garrison horses, race-horses or work horses… To learn, he went to slaughter-houses, markets, butcher shops, he even disguised himself as a cowherd. He did not fulfill his task at the agronomic institute for long. He refused to take an oath of loyalty to the head of state, Louis-Napoléon Bonaparte, as the latter demanded of all civil servants following the coup d'état of 1851. This position of loyalty to his republican values cost him his position: he was dismissed in May 1852. He continued his work in poverty and defended his doctorate in science in May 1853.

He was a doctor of medicine, a doctor of science, and practically an agronomist, what path did he follow? He had come to Paris driven by the interest in natural sciences, the reports of the expeditions and discoveries of Milne-Edwards had excited him: "*How many times, at the end of these lessons* […] *did we not repeat to ourselves, after a description full of attractions of some marine animals that we did not see then anywhere, how many times did we not say to ourselves: the sea must be very beautiful to study with its world so varied and so curious! Also, more than one then secretly burned with the desire to make observation trips*." (Lacaze-Duthiers 1885; translation of the author[11]). Although he grew up far from the sea and had only worked on insects, he became fascinated by animals that he practically never saw: marine invertebrates. His desire for a scientific expedition was realized in the summer 1853. One of his friends and colleagues, Jules Haime (1824-1856), also a student and assistant of Henri Milne-Edwards, proposed to Lacaze-Duthiers to accompany him to the Balearic Islands. He left. Did he suspect that this trip would determine the course of his life?

[11] French text: *Combien de fois, en sortant de ces leçons* […] *ne nous sommes-nous pas répétés, après une description pleine d'attraits de quelques animaux marins qu'on ne voyait alors nulle part, combien de fois ne nous sommes pas dit : la mer doit être bien belle à étudier avec son monde si varié et si curieux ! Aussi, plus d'un alors brûlait secrètement du désir de faire des voyages d'observation.*

BIRTH OF A PASSION

The two friends arrived on the small island of Menorca and Lacaze-Duthiers' dream of a naturalist expedition to study marine invertebrates took shape. Housed in a modest inn, they transformed a bedroom into a "laboratory": basins as aquariums, microscopes brought in their luggage, a table as a desk for notes and drawings. The days followed the same schedule: from 5 to 8 am, work on the previous day's harvest; then chocolate time; then a visit to the market to get shells; then lunch and a nap "*under the mosquito net, naked as a worm*"; then work from 2 to 5 pm; then swimming; then harvesting animals, feet in the water, turning over the stones on the shore; return to the hostel at night; dinner; and a digestive walk before bedtime. This 3 months stay was for him a real delight: "*How many times I have been amazed at the stillness of the water and the beauty of the moonlight. How in these moments one tastes life. One would think that one breathes both the well-being of the body and that of the soul*." (Lacaze-Duthiers 1848-1858; translation of the author[12]). There, his vocation was decided: malacology. Cuvier had organized the animal kingdom into 4 phyla: vertebrates, articulates (annelids, arthropods), molluscs and radiates or zoophytes (echinoderms, cnidarians but also protists). Why did Lacaze-Duthiers choose molluscs? Vertebrates did not attract him, they seemed too well known and too studied. The articulates were the domain of the great zoologists of the time, starting with his master Milne-Edwards, whose vassal and competitor he did not want to be. The radiates were a very heterogeneous group. The molluscs remained a vast unexplored field where species abounded. The initial plan of Haime and Lacaze-Duthiers was to study jointly the ascidians, then classified among the molluscs. But the bibliographical bases were very discordant: "*We thought we could start from the memoirs on ascidians that existed in science and, taking them as a basis, add to them the obviously undescribed species that we encountered. But how much it appeared to us immediately that one agreed little for the nomenclature of the species. Our project, first interrupted by the illness of my poor friend Haime, was definitively abandoned due to the untimely death of this distinguished zoologist*[13]." (Lacaze-Duthiers 1874; translation of the author[14]). Nearly 20 years later, Lacaze-Duthiers

[12] French text: *Que de fois je me suis extasié en voyant la tranquillité de l'eau et la beauté du clair de lune. Comme dans ces moments l'on goûte la vie. On croirait qu'on respire à la fois le bien-être du corps et celui de l'âme.*

[13] Jules Haime, zoologist and paleontologist, died from tuberculosis at the age of 32.

[14] French text: *Nous avions cru pouvoir partir des traités sur les ascidies qui existaient dans la science et, les prenant pour base leur ajouter les espèces évidemment non-décrites que nous rencontrions. Mais combien il nous parut tout de suite que l'on s'entendait peu pour la nomenclature des parties ! Notre projet, interrompu d'abord par la maladie de mon pau-*

proposed to share the same subject "ascidians" with his pupil Alfred Giard who, in a very inelegant way, appropriated it alone, sealing a definitive quarrel with his master. Obstinate, Lacaze-Duthiers took up again the study of ascidians, alone at first in 1874-1877, then in 1889-1892 with another of his students, Yves Delage. In Menorca, Lacaze-Duthiers fell back on the multiple species that flourished in the small harbor of Mahon, molluscs such as *Anomia*, *Anodonta* and other bivalves, *Dentalia*, but also sea anemones. He was amazed by the diversity of species, but also by their beauty. About the *Venus cestis* (now *Cestum veneris*, a ctenophore): "*The more one sees them, the more one admires them, the more one is charmed by their delicacy and their elegance. Their edges are furnished with fine pallets which lower and raise unceasingly and seem to walk from one end to the other of this long ribbon; they also decompose the light, and all the colors of the rainbow succeeding one another, extinguishing, relighting, fading again while always walking, give to the sight the sensation of pearls with thousand colors rolling along the edges of this magic belt. These small rainbows, which follow each other and are reborn unceasingly, are elusive. Also, all the drawings that one gives of them are rough and, by seeking to represent them, they can only immobilize the really marvellous spectacle that presents the ceste of Venus, swimming in a jar filled with pure water*." (Lacaze-Duthiers 1888; translation of the author[15]). If Lacaze-Duthiers became a malacologist, it is as much by fascination and amazement in front of the graceful, strange, moving and colored forms of the animals he observed that after a scientific reasoned choice. He never stopped their study and was always delighted by their beauty. Back in France, he went on an expedition, alone, in Brittany. In the small house of a fisherman of Saint-Jacut, he set up again his jars, and the enchantment in front of the elegance of the small molluscs operated again its charm.

The Balearic and Breton journeys were rich in lessons at the methodological level. Lacaze-Duthiers was now convinced that the understanding of a living organism requires the study, not only of its morphology (Linné's precept) and its anatomy (Cuvier's precept), but also of its physiology. As early as 1854, he foresaw the importance of studying the entire life cycle, from the egg to the adult, including the embryo and the larva, whereas until then, most studies focused on the adult. In a short note written afterwards, he demonstrated this by using as example, the tentacles of two species of sea anemones (Lacaze-Duthiers 1866). In mature animals, the tentacles surrounding the mouth are alternately large and small. It was concluded, and this was presented as a proven scientific fact, that the size of the tentacles reflected their age, the largest being the oldest. Lacaze-Duthiers showed that this was not the case by studying the embryonic development. The tentacles form at the same time, so they are all the same age, but they grow in different ways. Similarly, the position of the tentacles in the adult had led to the intuitive proposal of a logical sequence in the positioning of their appearance, which is absolutely not what actually happens in the embryo. These elements, position and size of the tentacles, were used as elements of classification, leading to erroneous connections because of the misinterpretation that had been made. Lacaze-Duthiers insisted throughout his career on the importance of not limiting observations to a given moment in the life of the animal, but to take into account its entire life cycle, from egg to adult, otherwise one can be led to consider the jellyfish and its polyp as two distinct animals (as did Cuvier!).

Above all, he held the pioneering conviction that it is necessary to study living animals, in their living environment on the one hand, which provides information on the functioning but also the classification of the animal, and in the aquarium on the other hand, which allows observations in continuous time and experiments. Until the construction of his marine laboratories, he multiplied the scientific expeditions: Brittany almost every year, the Mediterranean coast and Corsica, the entire French Atlantic coast and the English Channel, the Balearic Islands again, the Algerian and Tunisian coasts on four occasions, staying with local people or in modest inns, taking advice from fishermen, carrying microscopes and dissection instruments with him, improvising laboratories with aquariums in the bedrooms, kitchens or laundry rooms under the sometimes suspicious eyes of the owners of the places, bringing back from his trips jars of animals, dead or alive, and piles of notes and drawings (Fig. 4) that were the material of his more than 250 publications.

SCIENTIFIC DEVELOPMENT, ACADEMIC CAREER

Let's go back to the year 1854. Without resources, Lacaze-Duthiers had to make a living. Napoleon III having relaxed his demands on civil servants, he was appointed professor of natural sciences at the newly created faculty of sciences in Lille, whose dean was Louis Pasteur. It

vre ami Haime, fut définitivement abandonné par suite de la mort si prématurée de cet éminent zoologiste.

[15] French text: *Plus on les voit, plus on les admire, plus on est séduit par leur délicatesse et leur élégance. Leurs bords sont garnis de fines palettes qui s'abaissent et se relèvent sans cesse et semblent marcher d'une extrémité à l'autre de ce long ruban ; elles décomposent aussi la lumière, et toutes les couleurs de l'arc-en-ciel se succédant, s'éteignant, se rallumant, s'effaçant de nouveau en marchant toujours, donnent à la vue la sensation de perles aux mille couleurs roulant le long des bords de cette ceinture magique. Ces petits arcs-en-ciel, qui se suivent et renaissent sans cesse, sont insaisissables. Aussi, tous les dessins qu'on en donne sont grossiers et, en cherchant à les représenter, ils ne peuvent qu'immobiliser le spectacle vraiment merveilleux que présente le ceste de Vénus, nageant dans un bocal rempli d'eau pure.*

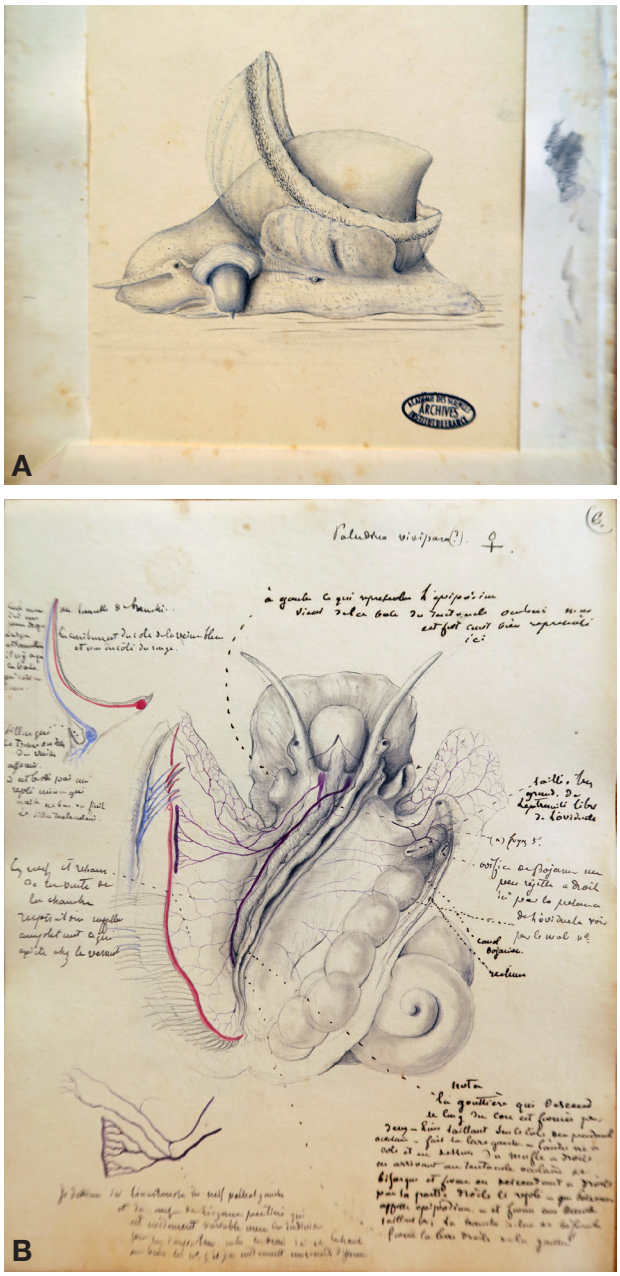

Fig. 4. – Gastropods. **A**: See slug, external view, right side, protruding penis. **B**: Scientific note of Lacaze-Duthiers representing the dissection of the fresh water snail *Paludina vivipara*. Original drawings by Lacaze-Duthiers. © Archives de l'Académie des sciences, Institut de France, Paris.

was not really with pleasure that he took this position. His investigations on the seashore were interrupted, he had to teach, an exercise that he feared even if it also attracted him, and he had to leave Paris, that was to say its libraries, its collections and its laboratories. His beginnings as a teacher were not easy. His shyness and lack of self-confidence made him fear the audience of the amphitheaters. He anxiously assessed the intensity of the applause that traditionally marked the entrance to the lecture hall and the end of the professor's lecture. He worried that the students might abandon his lecture. After an unconvincing start (the minister of public instruction was concerned), he became a remarkable teacher, captivating and innovative, introducing the most modern notions into his lectures (Lami 2022). During the 47 years that he taught, until his last course in 1901, he remained concerned about the quality of his courses, the reception they received, and he rewrote them in their totality every year! After a first year exclusively dedicated to his teaching in Lille, Lacaze-Duthiers resumed his expeditions and his relentless work gave rise to important publications, in particular exhaustive monographs (*Dentalia*, *Anomia*, *Pleurobranchus*, *Muricidae* and purple dye, *Bonellia*, *Vermetidae*…): everything, absolutely everything (morphology, anatomy, physiology, reproduction, embryonic and larval development, ecology) is described, dissected, analyzed by both descriptive and experimental approaches. These comprehensive studies resulted in a totally integrated biological vision of each species studied, whereas at the time there was already a tendency to divide up the publications, scattering observations that were not related to each other. The enormous work of Lacaze-Duthiers not only allowed to understand all the scales of the life of the species in question, but provided a solid base on which to support studies of comparative biology. In 1858, he took advantage of a break granted by the faculty of Lille to undertake a scientific journey to Corsica and again to the Balearics. His work included observations on coral, both zoological and halieutic. As usual, he was fascinated by the beauty of the polypiers which made him forget the seasickness from which he suffered atrociously during his whole life: "*The sight of a magnificent branch whose calyxes were covered with a beautiful anemone blooming of a serene yellow, washed with orange reflections, contrasting with vigor on the beautiful blue of the Mediterranean waves, was a spectacle so new for me that I soon forgot the seasickness which started to weigh me down. If I judge by the sensations that I was able to feel in our seas, the naturalist traveler who goes in the big Ocean, country of the polypiers, must feel very lively enjoyments at the sight of these reefs transformed into flowered and animated bushes*." (Lacaze-Duthiers 1848-1858; translation of the author[16]). He did not restrict his work to zoology; he embarked on the boats of the coral fishermen whose fishing techniques he analyzed. In 1860, this first coral study led to a request from the governor of Algeria for a mission on coral and

[16] French text: *La vue d'un magnifique rameau dont tous les calices étaient couverts d'une belle anémone épanouie d'un jaune serein, lavé de reflets orangés, contrastant avec vigueur sur le beau bleu des flots de la Méditerranée, était un spectacle si nouveau pour moi que j'oubliai bientôt le mal de mer qui commençait à m'alourdir. Si j'en juge par les sensations que j'ai pu ressentir dans nos mers, le naturaliste voyageur qui va dans le grand Océan, pays des polypiers, doit éprouver de bien vives jouissances à la vue de ces écueils transformés en buissons fleuris et animés.*

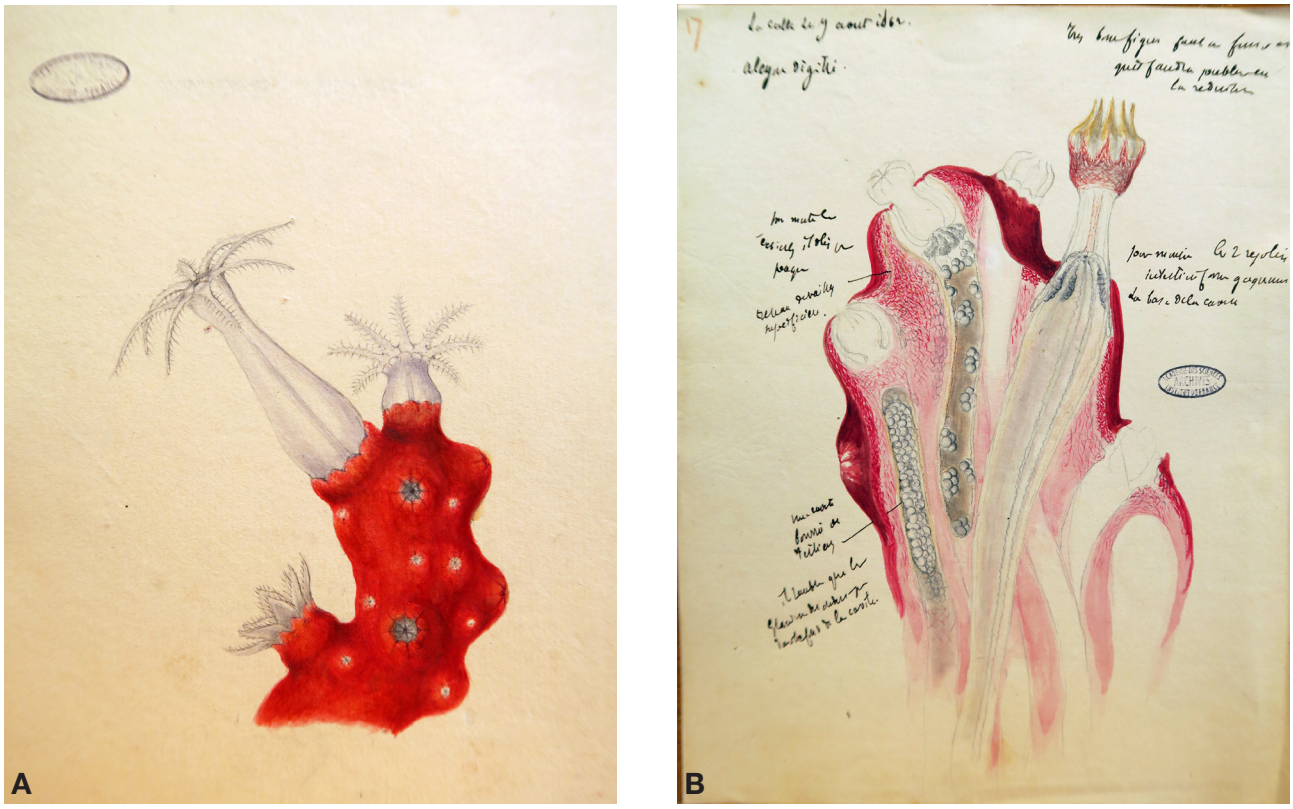

Fig. 5. – Coral. **A**: Three polyps (*Puntarella*) in various stages of development. **B**: Scientific note of Lacaze-Duthiers, written at La Calle (Algeria) in 1862, and representing the dissection of *Alcyonium digitatum*. Original drawings by Lacaze-Duthiers. © Archives de l'Académie des sciences, Institut de France, Paris.

its fishing. From 1860 to 1862, Lacaze-Duthiers spent three long campaigns in La Calle, an Algerian harbor near the Tunisian border. There, he studied all the categories of coral reefs, today *Anthozoa*, but also the techniques of their fishing and industry (Fig. 5).

Let us open a digression. The study of coral that had been commissioned to him by the governor of Algeria embraced everything that concerned coral, including its fishing, processing and trade (see in Vielzeuf *et al*. 2022). Although Lacaze-Duthiers was a researcher with a passion for the most basic questions of zoology, he took a strong interest in fishing techniques (which he criticized because dragging damaged the seabed) and the coral industry, socializing with fishermen, jewelers, and studying trading systems. He produced a very detailed report with many recommendations. This illustrates very well how, curious about the most basic questions, he did not neglect original applied experiments when the species studied was suitable. Thus, in Roscoff, he spent several years developing techniques for farming oysters in tanks, these experiments being carried out with Charles Marty, the manager of the laboratory, in connection with various oyster farmers and the national oyster farming society, techniques on which he devoted 11 publications from 1890 to 1894, in applied journals as the *Bulletin de la Société d'Agriculture de France* (for example: Lacaze-Duthiers 1891) but also in the very severe *Comptes-Rendus de l'Académie des Sciences* (for example: Lacaze-Duthiers 1893a) or in his famous zoological journal, "Archives of experimental and general zoology" (Lacaze-Duthiers 1893b). He considered, rightly, that his sharp knowledge on the biology of oysters, could, even had to be used for the success of the establishment of farms. He also conducted basic research on the molluscs producing the purple dye, sea snails from the Murex genus, and rediscovered that the pigment used in the ancient world to produce the purple dye was derived from these molluscs and not from plants as was thought (Lacaze-Duthiers 1859, 1860). He began experiments to develop the extraction and use of purple dye, including in photography (Fig. 6)! Later, in close collaboration with Alexander Dedekind (1856-1940), an Austrian Egyptologist interested in the purple of the ancient world, with whom he kept up an assiduous correspondence, as much scientific as friendly, for about ten years before his death, he resumed his experiments, with an interest in the practical value of reusing the purple (Lacaze-Duthiers 1896). Hence, this great scientist, passionate and relentless defender of basic research, was particularly open-minded, not neglecting any avenue of application when his basic results could be used in this respect.

To come back to coral, Lacaze-Duthiers recognized in the development of polypiers the application of a law that he called "law of reciprocal destruction", operating between colonies that come into contact, a law very simi-

Fig. 6. – Drawings and photography made with purple by Lacaze-Duthiers in 1859. The material extracted from the animal is colorless. When exposed to light, it takes on a purple color. **A**: Drawings representing the shell of *Purpura haemastoma* (called "Purple with bloody mouth", now *Stramonita haemastoma*) and made with either fresh (top) or desiccated (bottom) material of this animal. **B**: Self-portrait, photography using the purple dye. **C**: Purple drawings made on a silk handkerchief. © Arago Laboratory, Library of Sorbonne University, Paris.

lar to the "struggle for life" that supports Darwin's natural selection. He questioned the axioms posed by Milne-Edwards and Haime in their *Natural History of Coral Reefs* (Milne-Edwards & Haime 1857) because, contrary to his predecessors who had only studied the adult forms, he analyzed the embryonic and larval development, and in particular the transition from the symmetrical state to the radiated state. The important memoirs he produced on the subject from 1861, culminating in a monumental *Natural History of Coral* (Lacaze-Duthiers 1864), propelled him as an expert on *Anthozoa*. The importance of his work opened the doors of the Parisian academic cir-

cles: in 1863, he became a lecturer at the École normale supérieure, in Paris. Two years later, he was a professor at the Museum. In 1869, he was appointed professor at the Sorbonne. In 1871, he joined the French academy of sciences. Holder of one of the two chairs of zoology, he benefited from means, from a Parisian laboratory, from students and from lecturers. It was the consecration and it could have stopped there. This is not the case. The story went on and even took a spectacular turn: the zoologist became a builder of marine laboratories.

THE RISE OF EXPERIMENTAL ZOOLOGY

Three elements motivated Lacaze-Duthiers' new objectives. The first is his conviction that zoology must be refounded on the following basis: (i) a comparative biology approach based on anatomy, physiology and the consideration of the living environment; (ii) the study of living animals; (iii) the exhaustive recording of observations made without preconceived ideas from a large number of species, from which general rules emerge; (iv) the systematic consideration of embryonic and larval development; (v) the study of "abnormal" animals, profoundly divergent from other known organisms that reveals the characteristics, often discrete and larval, specific to the species; he himself studied *Bonellia* (Fig. 7), *Dentalia*, *Anomia*, *Tridacna* (respectively Lacaze-Duthiers 1854b, 1855-1857a, b, 1858, 1902); (vi) the need for experimentation to understand the mechanisms underlying the animal development and physiology (artificial fertilizations, injections of colored fluids to follow circulation (Fig. 8), manipulations to create siamese embryos, etc.; see some examples in his own works: Lacaze-Duthiers 1854a, 1874, 1875). To implement this new concept, two conditions were required: to build real laboratories adapted to experimentation and breeding; and to build such laboratories on the seashore, which is the only option for collecting live animals and knowing their living environment.

The second element was political. In 1870, if Lacaze-Duthiers was happy with the collapse of the empire and the proclamation of the republic, he was extremely affected by the defeat of France by the German coalition. Like many others, he considered that the reasons for this defeat were linked to the weakness of the French educational system considered to be clearly inferior to that of the winner. The German victory was attributed, among other factors, to the quality of education and the richness of the universities in that country. Lacaze-Duthiers decided to devote all his strength to the recovery of the country by the means at his disposal: the revival of the scientific movement. He was confident in his enterprise: "*When, after so many misfortunes, one notices a vitality and a richness as great as that which France has proven, the discouragement, inherent in a terrible crisis such as the one we have just gone through, soon gives way to hope and a profound feeling of confidence*. […] *The revival of the intellectual movement in France is, in our eyes, a fact. It has its reason in our defeat. It must be without limits, like our disasters and our misfortunes*." (Lacaze-Duthiers 1872c; translation of the author[17]). The building of marine laboratories, spearheads of a resolutely modern zoology, was the tool through which he wanted to contribute to the scientific renewal of his country.

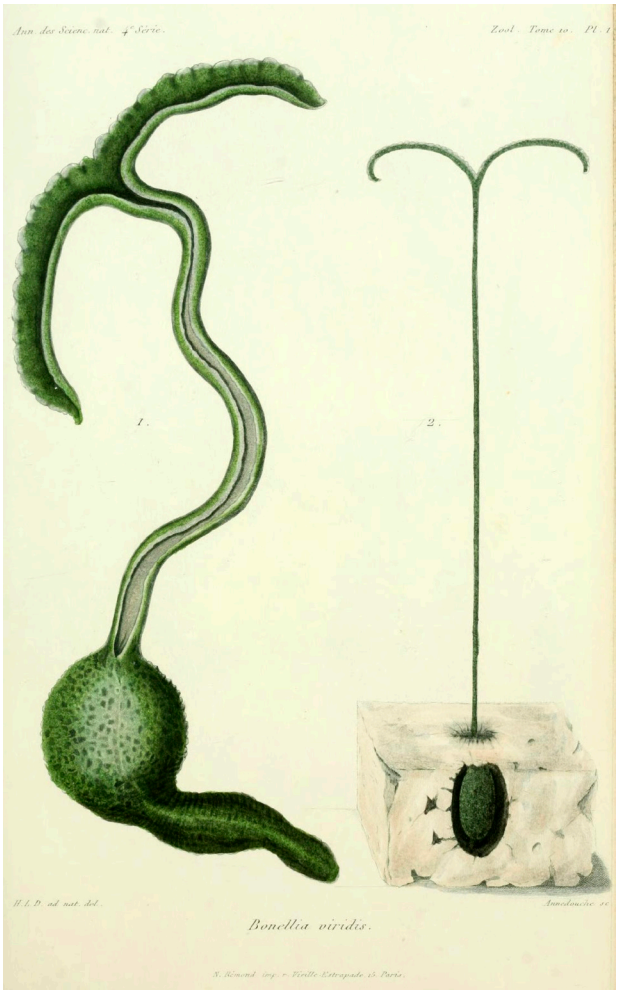

Fig. 7. – *Bonellia viridis*, female, external view, drawing by Lacaze-Duthiers. *Ann Sci Nat Zool* 4th series, volume 10, Plate I.

The third element was related to his Parisian situation, whose development was slowed down by the "Edwards clan". His ex-mentor, Henri Milne-Edwards, and his son Isidore, mobilized all the means, laboratories and publications. They controlled the latter via the influential zoology section of the *Annales des sciences naturelles*.

[17] French text: *Quand on constate après tant de malheurs une vitalité et une richesse aussi grandes que celle dont la France donne la preuve, le découragement, inséparable d'une crise terrible comme celle que nous venons de traverser, fait bientôt place à l'espérance et à un profond sentiment de confiance*. […] *Le réveil du mouvement intellectuel en France est à nos yeux chose assurée. Il a sa raison dans notre défaite. Il doit être sans limites, comme nos désastres et nos malheurs*.

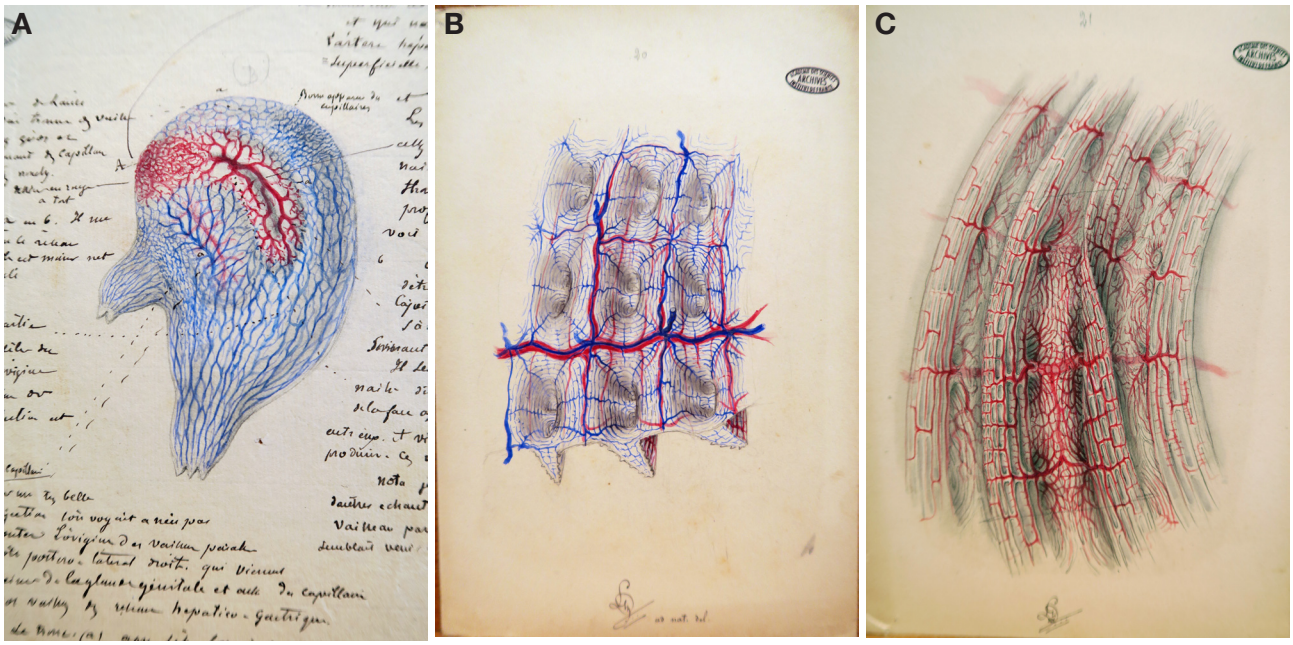

Fig. 8. – The ascidia *Molgula occulta*, blood circulation, original drawings by Lacaze-Duthiers. **A**: Circulation of the tunic, right side. **B, C**: Circulation in the gill. Veins filled in blue, arteries in red. © Archives de l'Académie des sciences, Institut de France, Paris.

Their laboratories at the Museum were spacious, whereas Lacaze-Duthiers' laboratory was only a tiny, dark and poorly heated attic in the rue St Jacques, where it was difficult to properly study dead or living animals. Another radically different trend also opposed his conception of zoology: Claude Bernard (1813-1878), a man he admired, denied that zoology was an experimental science and that it included physiology. The inventor of homeostasis believed that, unlike mammals, invertebrates were not susceptible to regulation. He thus conceived their study only under the angle of the morphological description. Their views also differed on the role of science in society. Claude Bernard, a medical physician, considered it through its applications, especially in human health, while Lacaze-Duthiers defended its function as a basic provider of knowledge, independently of immediate applications. To overcome these oppositions, it was worth leaving the Parisian cenacle. Let's add that Lacaze-Duthiers, hypochondriac and in constant struggle with all sorts of diseases, mainly rheumatism, was convinced that the seaside was more favorable to his health than the Parisian climate. And to free himself from the dictates of the Edwards clan as well as to spread the results of the experimental method, the construction of marine laboratories was not enough. An essential corollary was the foundation of a modern zoological journal.

As early as 1868, he had the idea of setting up a laboratory in Roscoff (Brittany). To do so, he had to convince the Ministry of public education where, as a wise man, he had positioned some of his former pupils in key positions in the direction of higher education. As a result of a complex real estate strategy based on rentals, purchases and refurbishments, the first marine laboratory in Europe, entitled "Laboratory of experimental zoology" was created in Roscoff in 1872. The same year, he founded a journal, the "*Archives of experimental and general zoology*", at his own expense, and almost went bankrupt. The Ministry came to the rescue and by taking out subscriptions for all French faculties of sciences, saved the new review, which took an extraordinary rise. According to the principles of Lacaze-Duthiers, the "*Archives*" published all the works realized in the laboratory of Roscoff (and later that of Banyuls-sur-Mer) ensuring the scientific visibility of these laboratories, but also the works of young researchers and those of foreigners (Jessus & Laudet 2022). As soon as Roscoff was operational, Lacaze-Duthiers launched the project of a second marine laboratory in the Mediterranean, complementary to the first in terms of marine resources. It became the Arago laboratory in Banyuls-sur-Mer, built *ex-nihilo* in 1882, thanks to various private funds (multiple sponsorships among them the city of Banyuls-sur-Mer and Lacaze-Duthiers' own funds), the Ministry having refused to support the real estate project this time.

In addition to setting up a new approach for studying the marine world, Lacaze-Duthiers carefully planned the operating principles of his laboratories. First, their missions were twofold: research and teaching. Students learnt through research, in the laboratory, in contact with their professors, who worked on their research subjects in the same place while teaching. He made his own this injunction of Albert Dumont (1842-1884), director of

higher education of the Ministry: "*make us naturalists*"[18] (Chappuis 1992). In fact, he trained true researchers who were committed to the progress of science. Secondly, everything was free of charge: stay, access to equipment, accommodation, and even travel for students. Thirdly, the visitors: Lacaze favored young people, students and young thesis assistants, and foreigners. His stations had to be international. These principles were very different from the competing German laboratory, opened in Naples in 1874 by Anton Dohrn (1840-1909), whose access was not free, and very expensive indeed, and restricted to qualified researchers. Like the "*Archives*", the laboratories founded by Lacaze-Duthiers were created under a quadruple banner: experimental zoology, training, youth, international dimension; all on a background of equality dear to the republican values of their founder.

WHAT LEGACY?

The life of Lacaze-Duthiers was part of a period marked by two great turning points that metamorphosed naturalism into biology (the latter having been named and defined in a premonitory way by Lamarck). The first is that of theories and concepts; the second is that of approaches and methods. Lacaze-Duthiers has not been one of the major actors, adding masterpieces to the chessboard of the debates on the origin of life and its evolution. But can he be blamed for this, and has this not been the case for the great majority of scientists who have rushed into these debates opened by the genius of a few, such as Lamarck, Darwin, Mendel, Boveri or Morgan? "*The essential questions of a discipline are usually specified by the first competent thinkers to enter it. The intense professional activity of later centuries can often be identified as so many variations on a set of themes. The arrow of history specifies a sequence of changing contents within which the same old questions are endlessly debated*" (Gould 1977). Lacaze-Duthiers was a meticulous zoologist, a remarkable observer, and a tireless worker who unraveled the intimate workings of a fabulous number of marine invertebrates. This sum represented a precious fund for all the questions of comparative biology, which were undertaken by the zoologists of his time. His intellectual approach was based on a simple principle: the detailed and exhaustive study of a given species, published in the form of an imposing monography, possibly supplemented by that of a related but atypical species, providing an enormous database serving to identify all related species, thus jointed in a family, keystone of the classification of the animal kingdom. This approach generated a school of thought that lasted after the death of Lacaze-Duthiers, carried by scientists such as Yves Delage (1854-1920) or Emil Racovitza (1868-1947), and irrigated the research carried out in the marine biology stations. But Lacaze-Duthiers also changed science in a long-lasting way by another type of contribution. It was through his pioneering conception of experimental zoology and the body of methods and infrastructure he established to make it work. By insisting on continuous observation of organisms in conditions where the environment is perfectly controlled by the researcher and on the importance of conducting experiments, he was a pioneer. To implement this new experimental approach, the logic was to build laboratories. There are two remarkable facts in this regard. The first is that he succeeded in building these labs, a real tour de force. For about thirty years, he convinced all the financial sponsors, ministries, private donors, local authorities, etc. He himself checked all the acquisitions, renovations and constructions, all the plans, all the purchases of equipment, from boats to microscopes, all the installations, from aquariums to breeding tanks or electrification, all the recruitment of staff… While continuing the study of the *Tridacna* or the *Molgula* or other molluscs of interest, he walked all over France in all directions, questing for aims as a monk, according to his own expression[19] (Pruvot 1902). A titanic and relentless work. The second remarkable fact is that there was no laboratory of biology in France at that time. Chemists had laboratories and physiological physicians of the Claude Bernard school were beginning to set them up. But there was no pre-existing model in biology. In a visionary way, Lacaze-Duthiers succeeded in designing modern laboratories whose basic ingredients are the same today: equipped with the most efficient instruments (at the time, high quality optical microscopes), with experimental rooms equipped with benches and small aquariums, fish tanks and aquariums for harvesting and breeding (today, an animal facility), technical staff trained in dissection and species recognition, boats and sailors for harvesting, and accommodation areas. Lacaze-Duthiers did not leave us a great doctrine. He left us another sort of precious legacy that has lasted for more than a century without a scratch and for which we are indebted to him: a corpus of methods that has impregnated the way of doing zoology, marine stations that today play a leading role in the European marine biology research system, at the center of current questions concerning the environment and biodiversity.

Let's end this evocation on the same register as its start: the character of Lacaze-Duthiers. As Louis Liard (1846-1917), one of his pupils who became director of higher education at the Ministry of public instruction, said, Lacaze-Duthiers gave to science "*his heart, his time, his effort and his fortune*"[20] (Liard 1902). Without going that far, we can only recommend that young scientists be inspired by this figure who embodied the qualities of the

[18] French text: *Faites-nous des naturalistes!*

[19] French text: *j'aurais dû appartenir à l'ordre des frères-quêteurs*.

[20] French text: *son cœur, son temps, sa peine et sa fortune*.

researcher, past or present: scientific rigor, curiosity, thirst to explore the unknown, taste for risk, freedom of mind, passion, selflessness.

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