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# Henri de Lacaze-Duthiers and the ascidian hypothesis

Catherine Jessus<sup>1</sup> | Vincent Laudet<sup>2,3</sup> 

<sup>1</sup>Laboratoire de Biologie du Développement-Institut de Biologie Paris Seine, LBD-IBPS, Sorbonne University, CNRS, Paris, France

<sup>2</sup>Okinawa Institute of Science and Technology, Okinawa, Japan

<sup>3</sup>Marine Research Station, Institute of Cellular and Organismic Biology (ICOB), Academia Sinica, Taipei, Taiwan

## Correspondence

Vincent Laudet, Okinawa Institute of Science and Technology, 1919-1 Tancha, Onna-son, 904-0495 Okinawa, Japan.  
Email: [vincent.laudet@oist.jp](mailto:vincent.laudet@oist.jp)

## Abstract

In 1830, Cuvier and Geoffroy Saint-Hilaire confronted each other in a famous debate on the unity of the animal kingdom, which permeated the zoology of the 19th century. From that time, a growing number of naturalists attempted to understand the large-scale relationships among animals. And among all the questions, that of the origin of vertebrates was one of the most controversial. Analytical methods based on comparative anatomy, embryology and paleontology were developed to identify convincing homologies that would reveal a logical sequence of events for the evolution of an invertebrate into the first vertebrate. Within this context, several theories have clashed on the question of the identity of the ancestor of vertebrates. Among the proposals, a group of rather discrete organisms, the ascidians, played a central role. Because he had discovered an ascidian with a particularly atypical larval development, the *Molgula*, Henri de Lacaze-Duthiers, a rigorous and meticulous naturalist, became involved in the ascidian hypothesis. While the visionary mind of Lacaze-Duthiers led him to establish a particularly innovative methodology and the first marine biology station in Europe, at Roscoff, the tailless tadpole of the *Molgula* prevented him from recognizing the ancestor of vertebrates. This old 19th century story echoes the ever-present questions driving the field of Eco-Evo-Devo.

## KEYWORDS

amphioxus, ascidians, history of science, marine stations, *Molgula*, vertebrates

## 1 | THE ORIGIN OF VERTEBRATES: HOW DID THE QUESTION ARISE?

Stephen Jay Gould noted that “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). This applies very well to the history of Evo-Devo and in particular the question of the origin of vertebrates that we are going to tell here by analyzing the role

played therein by Henri de Lacaze-Duthiers (1821–1901), an eminent 19th century French zoologist.

Everything begins in 1830 in France at the *Académie des Sciences*. Georges Cuvier (1769–1832) and Etienne de Geoffroy Saint-Hilaire (1772–1844), two of the most brilliant minds of the time, addressed a central question of zoology at that time: why do some animal organs look alike? Despite a long friendship and mutual esteem, Cuvier and Geoffroy Saint-Hilaire provided radically different answers to this question, and this led to a famous debate which had long-term consequences and provoked a bitter split between them (Appel, 1987; Le Guyader, 2004).

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For Cuvier, the resemblance among organs in different species is explained by their function: the function is the final cause. Cuvier went further by proposing a “*law of correlation of organs*” which suggests that different organs are correlated with each other because their functions are correlated, even if these organs are not directly connected. According to this law, a carnivore will have sharp teeth, fangs, and claws to catch and devour its prey. Therefore, since function alone explains the resemblances among organs, there is no need to seek historical explanations. This was logical because Cuvier was a fixist and opposed Lamarck (1744–1829) on the question of evolution. Cuvier therefore considered that the animals can be grouped into four large categories (“*embranchements*”), the vertebrates, the articulates, the mollusks and the radiates (or zoophytes). His main tenet was that there is no need to look for similarities (one would say today homologies) among these four groups. Cuvier wished to stick to the scientific facts in themselves and was loath to embark on broad hypotheses, as they, he thought, give rise to unnecessary debate and disorder.

By contrast, Geoffroy Saint-Hilaire loved speculations. He did not hesitate to formulate hazardous hypotheses because, for him, it is the ideas more than the facts, which are the engine of discoveries. For him, Cuvier's insistence on not going beyond observable facts threatened scientific progress. Unlike Cuvier, he therefore believed that we must seek the fundamental unity that exists among all living beings because the similarities among organs are explained not by their function but by their history and the relationship they have with neighboring organs or structures. For Geoffroy Saint-Hilaire, there was a sort of “*transcendental morphology*” which allows scientists to group all organisms together and even to retrace their history. The recognition of what he called “*analogies*” (now homologies) makes it possible to organize the living world and make connections among very different organisms, including among Cuvier's 4 “*embranchements*.”

It was a draft article on mollusks that ignited the debate in the spring of 1830. The little-known authors, Meyranx and Laurencet, suggested a link between the internal anatomy of mollusks and that of vertebrates. Geoffroy Saint-Hilaire saw this as support for his idea of a unity of composition that would unite vertebrates and mollusks, two of Cuvier's “*embranchements*.” Of course, Cuvier contested this claim and rejected the idea of the unity of plan: inside each “*embranchement*”, organs can be alike and related, but among “*embranchements*,” they must be seen as fundamentally different. The debate became more and more heated and culminated in a famous series of sessions of the *Académie des Sciences* in Paris. Members of the *Académie* had to take position for one or the other even if many of them quickly grew tired to see the very personal turn that the debate was taking. All Europe followed this debate with passion. In Germany, Goethe who leaned towards Geoffroy Saint-Hilaire wrote a summary for the German public and was delighted that “the synthetic way of considering nature, introduced by [Geoffroy Saint-Hilaire] in France, could no longer be rejected” (cited in Nève, 2019; our translation). In France, the “*Journal des Débats Politiques et Littéraires*” took Cuvier's side, while “*Le Temps*” supported Geoffroy Saint-Hilaire (Nève, 2019).

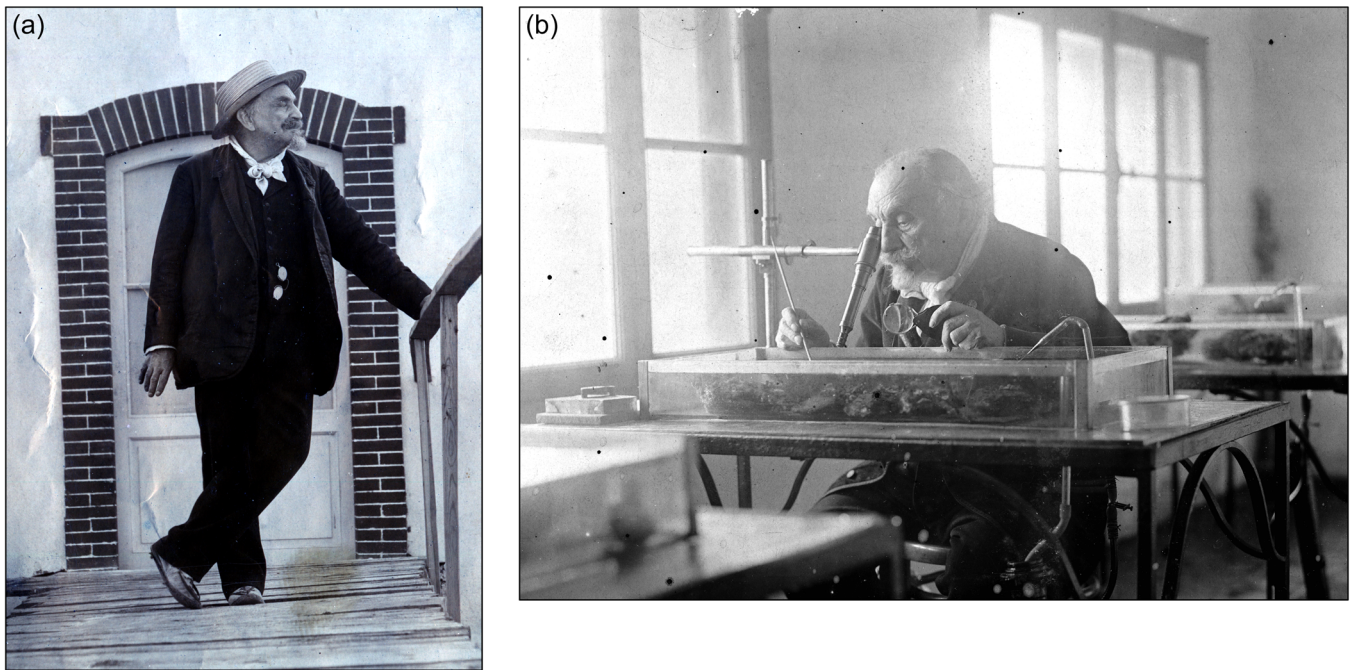
The terms of this debate impacted 19th century zoology, in particular comparative anatomy and embryology. Fundamental questions, such as the relations among living beings, the time scale

of progress or successive divergence in the shape of phylogenetic trees, were addressed during that century (Appel, 1987; Le Guyader, 2004). Of course, the emergence of Darwinism provided a coherent framework through which it would become possible to deepen the fundamental question of the relations among the animal phyla. The theory of recapitulation advocated by Ernst Haeckel (1834–1919) suggesting a deep link between embryonic development and evolutionary divergence, played an important role in these discussions by offering, in addition to Darwinian evolution, a general framework. Today, the recent studies of Evo-Devo and molecular phylogeny continue to address the question of the relationships among animals underlying their fundamental unity. In this respect, the episode reported here echoes the questions currently driving the fields of Evo-Devo and Eco-Evo-Devo (Gilbert & Epel, 2015).

Among the many questions linked to animal phyla relationships that were debated in the 19th century, none occupied a more central position than the origin of vertebrates. This question, its broader implications and the analytical methods that had to be developed to address it (comparative anatomy, embryology, paleontology, etc.) were at the center of debates (Bowler, 1996; Gee, 1996). On the scientific level, vertebrates derived from an invertebrate precursor and the question was: which one? Was their primitive ancestor unsegmented as chaetognaths or arrow-worm (Haeckel, 1866) or segmented as annelids (Dohrn, 1875)? In this debate, a rather discrete group of organisms, the ascidians or tunicates, played a fundamental role, leading to a controversy between the “*ascidian theory*” and the “*annelid theory*.”

We now know that vertebrates have a common ancestor with Urochordates, which contain ascidians, and that the tadpole of ascidians indeed presents homologies with Vertebrata (Satoh et al., 2014). In a linear view of history, we therefore tend today to consider that in the debate between the “*ascidian theory*” and the “*annelid theory*,” there were the “*good ones*,” like Kowalevsky (1840–1901), Huxley (1825–1895), Haeckel and Gegenbaur (1826–1903), who knew how to discern the relevant homologies, and the others such as Dohrn (1840–1909), von Baer (1792–1876), Semper (1832–1893), Metchnikoff (1845–1916) or Patten (1861–1932) who, blinded by their preconceptions, were mistaken. Things are not so simple. Since it could not have been known at the time which hypothesis of the origin of the vertebrates was correct, excellent scientists on both sides were engaged in the debate. Only in retrospect can the question of “how could a good scientist have been so wrong and still be a good scientist” be asked. The analysis of Lacaze-Duthiers's work provides some answers to this question.

The interest of Henri de Lacaze-Duthiers (Figure 1) in ascidians was natural as he was a seasoned malacologist and, at the beginning of his scientific career, ascidians were considered to be part of the mollusks. The question of the ancestor of vertebrates was not part of his interests. He never discussed the hypothesis that annelids may have played such a role. But as a specialist of ascidians, he could not avoid positioning himself on their potential position as ancestors of vertebrates. And he, an undisputed specialist of the mollusks, author of important monographs on the ascidians, a meticulous scientist devoted to long and exhaustive studies, went wrong. How could this happen?



**FIGURE 1** Henri de Lacaze-Duthiers. (a) In 1894, at the age of 73, in front of the Arago Laboratory, founded in Banyuls-sur-Mer (France) in 1882. (b) In 1896, at the age of 75, observing marine invertebrates in the Arago Laboratory (Banyuls-sur-Mer, France). Courtesy of the Bibliothèque du Laboratoire Arago, Sorbonne Université.

## 2 | “THE ASCIDIAN HYPOTHESIS”

To resolve the question of the vertebrate ancestor, it was necessary to identify convincing homologies among the different phyla to be able to determine a logical sequence of events for the evolution of an invertebrate to give rise to the first vertebrate that was admitted looking similar to amphioxus, lampreys or cartilaginous fishes. Initially classed as a mollusk (Pallas, 1772), amphioxus was indeed considered at that time as a primitive type of fish since the publications of Costa (1834) and Yarrell (1836). Very quickly, two different visions were perceptible (Bowler, 1996). Haeckel considered that the vertebrates were an independent offshoot from a primitive unsegmented invertebrate ancestor and proposed in 1866 a theory suggesting that the chaetognaths or arrow-worms which are unsegmented, could be the most similar living animals to what the vertebrate progenitor looked like (Haeckel, 1866). Others, such as Anton Dohrn, believed that segmented worms, annelids, were the precursors from which the ancestor of vertebrates derived, since for him, the segmentation of vertebrates and that of annelids were homologous (Dohrn, 1875). Knowing that the organization along the dorso-ventral axis of the internal organs in the annelids was reversed compared to that of vertebrates, the dorso-ventral axis would have been reversed, as proposed earlier by Geoffroy Saint-Hilaire. Later on, others, like William Patten or Walter Gaskell (1847–1914), went even further and proposed that vertebrates may come from arthropods and in particular from arachnids or crustaceans (Gaskell, 1908; Patten, 1890).

Many scientists of the day, however, believed that the resemblance between vertebrate and annelid segments was only apparent

and could not be taken as a valid argument. Indeed, this “annelid theory” generated secondary complications: as mentioned above, it requires an inversion of the dorso-ventral axis, but this in turn raised many questions about the origin and position of the mouth. The fact that the segmentation was not present in the head of vertebrates was also disquieting and led to a flurry of detailed anatomical and embryological work (Bowler, 1996). All these questions made the proximity between annelids and vertebrates unconvincing for many researchers.

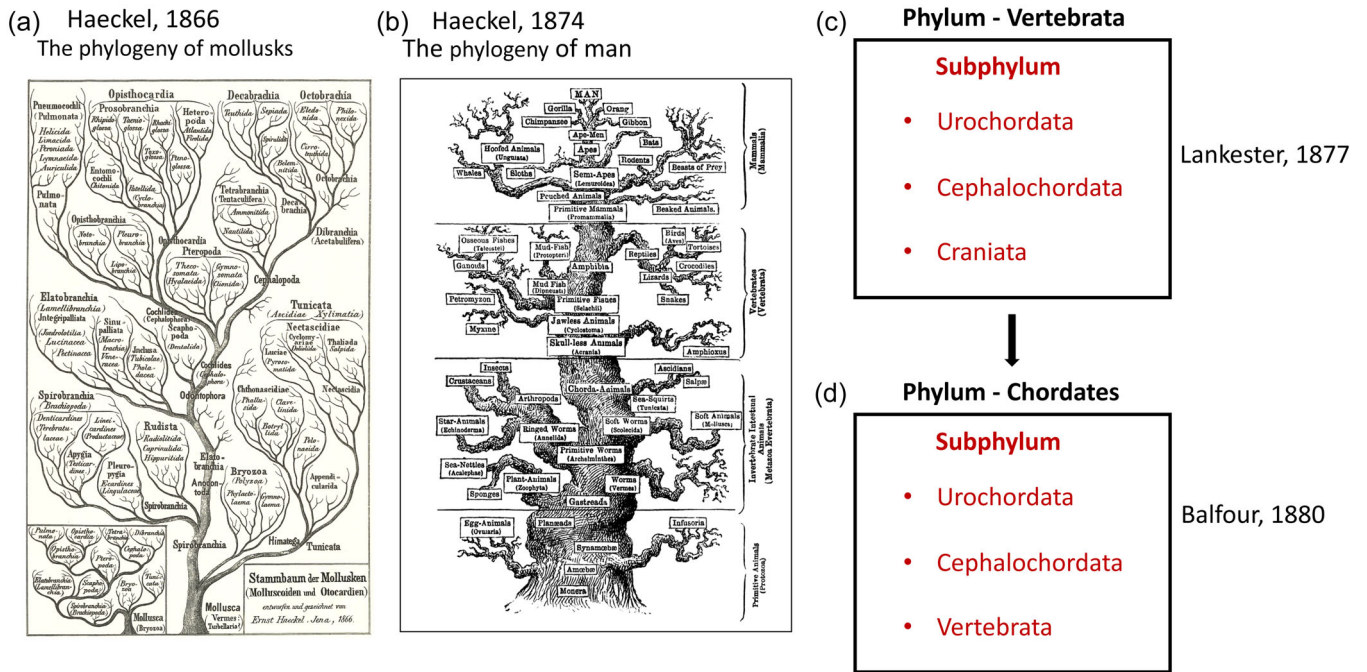
In the meantime, the Russian zoologist Alexander Kowalevsky set the cat among the pigeons by proposing that vertebrates were derived from a relatively insignificant and little-known group of marine organisms, the sea squirts or ascidians. In 1767, Linnaeus (1707–1778) had placed ascidians in mollusks, and this was confirmed by the morphological analysis of Cuvier and Lamarck who recognized ascidians as animals with a tunic (Satoh et al., 2014). This tunic was considered to be a highly derived bivalve shell that would have lost its hardness to form like a garment around the animal (Lemaire & Piette, 2015; Satoh et al., 2014). The fact that ascidians are filter feeders with inhaling and exhaling siphons, quite similar to what is observed in bivalve mollusks, reinforced this interpretation. It became clear that there was quite a diversity in this group that is now divided into three large groups: (i) solitary or colonial ascidians which live fixed to a substrate; (ii) appendicularians, solitary pelagic organisms which retain a tail; and (iii) thaliaceans, also pelagic, but which can be solitary or colonial and which include, for example, salps.

The fact that all these organisms form a single group was established in the middle of the 19th century. In 1804, Cuvier

recognized the proximity between salps and ascidians and Lamarck created the group of Tunicates to separate them more distinctly from other mollusks. In 1834, Quoy and Gaimard, then in 1846, Huxley, but also other authors such as Chamisso or Mertens completed the unification of this group (for a review, see Lemaire & Piette, 2015).

In Naples, Kowalevsky developed methods to analyze the early development of marine invertebrates. He thought in particular that observing the primitive cell layers of embryos, the ectoderm, the endoderm and the mesoderm, could reveal homologies among apparently very different organs and therefore old filiations. In 1866, he published a paper where he showed that certain developmental stages of ascidians resemble those of vertebrates (Kowalevsky, 1866). One year later, he published the first embryological study of amphioxus, showing that its development also resembles that of vertebrates but also that of ascidians (Kowalevsky, 1867). He showed that the tadpole stage of ascidians had many characteristics similar to those of vertebrates, in particular a dorsal neural tube and a dorsal chord. He also found similar axial structures in the amphioxus embryo. He went further and deduced that they are truly homologous because they are formed of cell clusters that share the same embryonic origin. Thus Kowalevsky built a bridge between the ascidians, on the side of the invertebrates, and the amphioxus, the primitive type of the vertebrate. His theory proposed that the larval stage of ascidians could be the true ancestor of vertebrates. This model would later be further elaborated, notably

by Walter Garstang (1868–1949), who suggested that the tadpole stage of an ascidian has acquired an early sexual maturity (Garstang, 1928), a neoteny event crucial for the origin of vertebrates. The work by Kowalevsky had a considerable impact. Based on their adult morphology, amphioxus, ascidians, and vertebrates had never been considered to be linked. For the first time, Kowalevsky proposed that similarities in ontogenic development revealed ancestral connections among the three groups. The developmental parallels highlighted by Kowalevsky captured wide attention among morphologists. Abstracts were published in many of the scientific journals of the time. One of the most important work following Kowalevsky's publications was from Carl von Kupffer (1829–1902) (Kupffer, 1869, 1870). Originally not convinced by Kowalevsky's work, Kupffer intended to repeat his observations to refute them but in fact reversed his initial opinion and became a fierce supporter (Bowler, 1996). In addition, the stars of the time, Haeckel and Darwin (1809–1882), but also Huxley and Ray Lankester (1847–1929) in the United Kingdom, as well as Gegenbaur and Kölliker (1817–1905) in Germany supported this “ascidian theory.” (Haeckel, 1872). Following the work of Kowalevsky, Haeckel moved the tunicates from the mollusks in the phylum called Vermes, in which he also placed the hemichordates (Figure 2a,b) (Haeckel, 1874). It was Ray Lankester who, in 1877, proposed to give the tunicates a status of sub-phylum that he called Urochordata (Lankester, 1877). These, associated with Cephalochordata and Craniata, formed the



**FIGURE 2** Views of ascidian and vertebrate phylogeny. (a) The phylogeny of mollusks. One of the Haeckel's phylogenetic trees (Haeckel, 1866, Vol. 2, Tafel VI). In 1866, tunicates, including ascidians, appendiculars and thaliaceans belong, together with bryozoa, to a sub-phylum of mollusks called Himatega. (b) The phylogeny of man. One of the Haeckel's phylogenetic trees (Haeckel, 1874). In 1874, tunicates are not any longer part of the mollusks. (c) In 1877, Lankester proposed a status of sub-phylum to the tunicates, called Urochordata. Associated with Cephalochordata and Craniata, they form the phylum Vertebrata (Lankester, 1877). (d) In 1880, Balfour renamed the phylum Vertebrata “Chordates.” Craniata were renamed Vertebrata. The phylum of Chordates divided into 3 subphyla was retained until now (Balfour, 1880).

phylum Vertebrata (Figure 2c). In 1880, Francis Balfour (1851–1882) renamed the Vertebrata of Ray Lankester, now called Chordates (Balfour, 1880). The former Craniata were called Vertebrata (Figure 2d). This organization, a phylum of Chordates divided into three sub-parts, was retained for over a century.

However, Anton Dohrn, the champion of the “annelid theory” that was developed in parallel with Carl Gottfried Semper (Dohrn, 1875; Semper, 1875), had many objections, and he was not the only one. Carl Ernst von Baer, the pioneer of comparative embryology, who might have been expected on the side of those who invoked ontogenic similarities to argue for the “ascidian theory,” considered that the demonstration was not convincing. His studies had shown him that early developmental stages are generally very similar and should not be overinterpreted. He believed that, while Kowalevsky's observations were interesting, he went too far and that the similarity between the sea squirt tadpole and the amphibian tadpole was a secondary adaptation due to the similarity of the mode of locomotion of these organisms (Bowler, 1996). Hence, he always considered the ascidians as mollusks, even if he was not a follower of the “annelid theory” either, since, above all, he rejected the priority importance of natural selection for effecting evolution changes (von Baer, 1876; Groeben, 1993). But the most important pitfall for the acceptance of this “ascidian theory” was the lack of segmentation in ascidians and the profound divergence of the body plan of the adults. The controversy continued to grow, leading in particular to a clash between two German schools, Gegenbaur's, which supported the “ascidian theory” and Dohrn's supporters, who were in favor of the annelids.

The debates initiated in 1866 by Kowalevsky were still raging in the 1870s when the French zoologist Henri de Lacaze-Duthiers briefly took part in them by positioning himself unambiguously against the “ascidian theory” (without expressing any opinion on the “annelid theory”). Since his main criticisms focused on the methods and assumptions of the supporters of the “ascidian theory,” it is important to present his own principles and values in terms of scientific approach and method.

### 3 | LACAZE-DUTHIERS'S PRINCIPLES: EXAMINING THE FACTS, STUDYING LIFE CYCLES, PERFORMING EXPERIMENTATION

Born in 1821 in southwest France, Henri de Lacaze-Duthiers went to Paris in 1842 to study natural sciences and medicine. He became a student of Henri Milne-Edward (1800–1885), who was himself a Cuvier's pupil. In 1851, Lacaze-Duthiers became a doctor of medicine (Lacaze-Duthiers, 1851). He completed his PhD in science on the insect genitalia under the supervision of Henri Milne-Edwards in 1853 (Lacaze-Duthiers, 1853a). In 1854, he was appointed Professor at the Faculty of Sciences of Lille, of which Louis Pasteur was then dean, then returned to Paris in 1863, where he became a lecturer at the École Normale Supérieure. He was then appointed Professor at the National Museum of Natural History in Paris in 1865 and then at the Sorbonne in 1869. He became a French academician in 1871. The

following year, he built in Roscoff the first marine laboratory in Europe, entitled “Laboratory of experimental zoology.” The same year, he founded a journal, the “Archives of experimental and general zoology,” whose last issue was published in 1983 (Jesus & Laudet, 2022). In 1882, he created a second marine laboratory in the Mediterranean, the Arago laboratory in Banyuls-sur-Mer. He never stopped his teaching, research and laboratory management activities until his death in 1901 (Jesus, 2022; Jesus et al., 2021).

The 19th century was marked by a deep turn in the field of theories and concepts: creationism and fixism confronted evolution, which was itself rapidly divided in France between the tenants of Lamarckian transformism and those of Darwinian natural selection. Lacaze-Duthiers kept himself out of the debates on fixism and Lamarckian or Darwinian transformism. As he wrote: “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.” (cited in Pruvot, 1902; our translation). Admiring Darwin's talents as a naturalist, Lacaze-Duthiers was also the most relentless defender of his candidacy to the French Academy of Sciences (Lacaze-Duthiers, 1872a). He never posed as a disciple of Cuvier, whose interpretations he regularly criticized (e.g.: Lacaze-Duthiers, 1865b, 1874). In short, Lacaze-Duthiers was never the fixist that he has been accused of being and did not claim to be a Lamarckian nor a Darwinist (Boutan, 1902; Pruvot, 1902).

This mistrust, or even indifference, towards the theories that challenged the 19th century natural sciences is linked to the specific approach to biological questions adopted by Lacaze-Duthiers. When he arrived in Paris, the French naturalists, and particularly the successors of Cuvier, such as his supervisor Milne-Edwards, were partisans of a scientific method inherited from Aristotle empiricism: examining the facts, without any preconceived hypothesis, and from the observation of these facts, trying to draw general laws. This empiricist method was revived by a new philosophical current, the scientific positivism of Auguste Comte (1798–1857), which promoted an approach aimed at explaining the reality of facts by identifying, through repeated observations and experiments, the connections that unite phenomena, but without seeking the primary causes. The question was not the “why” but the “how” that would allow scientists to identify scientific laws. This way of approaching natural sciences deeply influenced Lacaze-Duthiers, who remained all his life reluctant to discuss theories stemming from hypotheses. On the contrary, from his observations, carried out without any a priori assumptions, he expected to see the logical emergence of general rules: “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, p640; our translation). We will see how this position was undermined in the ascidian hypothesis.

Let's address a last critical point to understand Lacaze-Duthiers's scientific positioning: approaches and methods. Lacaze-Duthiers was deeply influenced by his mentor. In the 1820s, Milne-Edwards was one of the first in France to carry out scientific trips to the coasts (Milne-Edwards et al., 1845–1848). Breaking with generations of scientists who studied dead animals preserved in alcohol, Milne-Edwards promoted a new approach: field zoology, in which the scientist observes and collects the animals himself to understand how they live in their environment. Behind this idea was the very innovative concept according to which physiology completes zoology. Moreover, Milne-Edwards also focused on individual development as part of his anatomico-physiological approach (Quatrefages de & Blanchard, 1885). Lacaze-Duthiers became the champion of this method, which he practiced in his own works but also conceptualized and promoted (Lacaze-Duthiers, 1872b, p64), spread to his many pupils, and finally brought to a higher dimension. He was convinced that a scientific study of every animal must be exhaustive, including morphology, anatomy, physiology, knowledge of the environment, all of this carried out on embryonic, larval and adult forms, that is, during the entire life cycle. It should be noted that this vision foreshadowed the corpus of concepts and methods that was to become central to the field of Evo-Eco-Devo (Gilbert & Epel, 2015). Hence, the studies had to be performed on living animals. He went further by claiming a new approach in zoology: experimentation. Observing and describing were not enough to understand the physiological functioning and the interactions with the environment. Even though Lacaze-Duthiers considered that “*experimentation*” starts as soon as the animal is taken out of its natural environment and studied alive in a laboratory, he emphasized the key value to manipulate the animals and to modify some of its parameters to study the consequences. Experimentation on living animals implies maintaining animals in aquariums where they reproduce and where all the forms they adopt during their life cycles can be observed under defined conditions. In short, aquariums are needed in the immediate vicinity of rooms equipped with dissection instruments and microscopes: laboratories! This idea led him to found the first two laboratories dedicated to fundamental research in marine biology, in Roscoff (1872) and Banyuls-sur-Mer (1882) (De Bont, 2015).

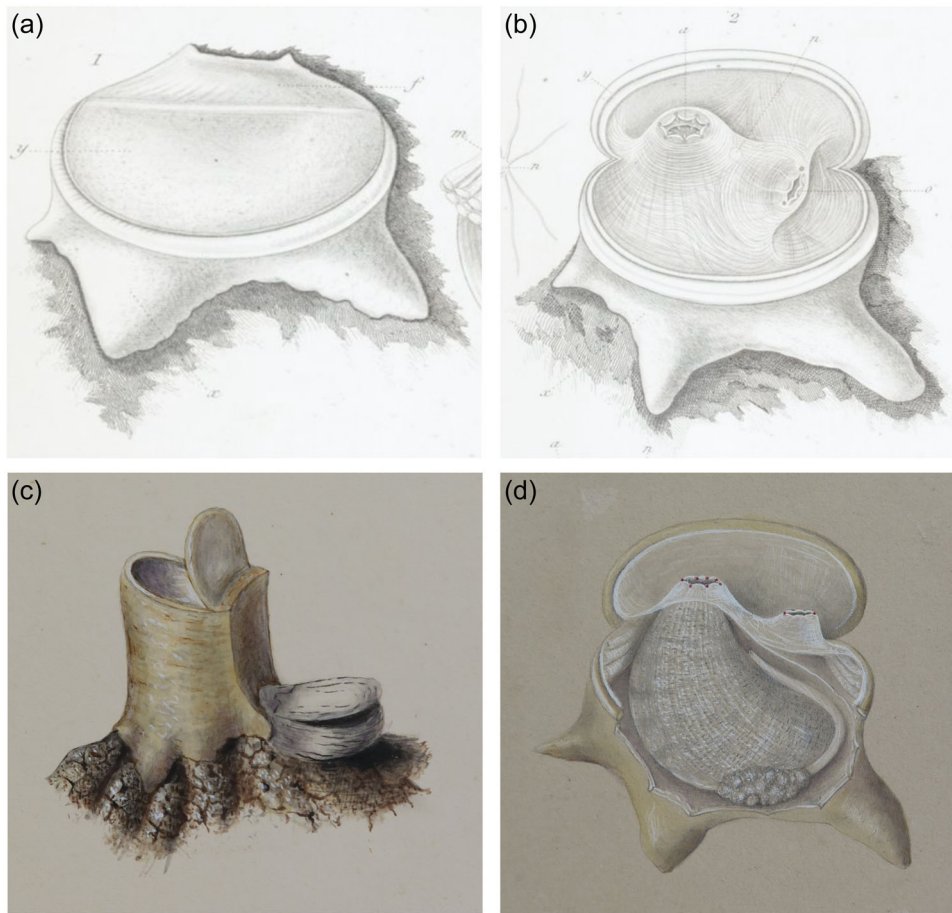
He based his own work on these invariable principles, drawing general rules and even laws from the tireless inventory of observations made without preconceived ideas from a great number of species. Interestingly, he devoted many works to “abnormal” animals, those with no apparent connection or profoundly different from the other known organisms: *Bonellia*, *Dentalium*, *Anomia*, *Tridacna*, etc. (Lacaze-Duthiers, 1854a, 1855a, 1857a, 1857b, 1858, 1902). These he found interesting because, despite the apparent singularity of the adult forms, he always managed to link them to a family thanks to the study of their embryos or their larvae. As he showed in these cases, it is often the embryo or larva that reveals homologies, whereas adult forms may have lost them, or on the contrary may have secondarily acquired characters that make them resemble other organisms with which they have no kinship.

A rule that very surprisingly he did not apply in the case of the ascidians!

## 4 | LACAZE-DUTHIERS'S STUDY OF THE ASCIDIANS

After his thesis on the insect's genitalia, defended in May 1853 (Lacaze-Duthiers, 1853a), the lessons of his mentor, Henri Milne-Edwards, had raised Lacaze-Duthiers's interest in the marine invertebrates, and especially the mollusks, whereas he had practically never studied them. His desire for a scientific expedition devoted to marine invertebrates was realized in the summer 1853. His friend, Jules Haime (1824–1856), who, like Lacaze-Duthiers, was an assistant of Henri Milne-Edwards, suggested he accompanies him to the Balearic Islands. Haime was rather focused on paleontology and geology (Archan & Haime, 1853), while being a knowledgeable zoologist. His idea was to undertake an in-depth study of ascidians. Haime would work on colonial ascidians while Lacaze-Duthiers would focus his research on solitary ascidians. But they immediately came across difficulties that were linked to the great diversity of the group (Lacaze-Duthiers, 1853b; Pruvot, 1902). Finally, Haime studied the geology of the island (Haime, 1855). Lacaze-Duthiers, faced by a diversity which exceeded his imagination, fell under the charm of the beauty of the mollusks and focused on lamellibranches (Lacaze-Duthiers, 1853b; Pruvot, 1902; 18 scientific notes and articles in 1854–1855, among them Lacaze-Duthiers, 1854a, 1854b, 1854c, 1855a, 1855b). Haime died in 1856, aged only 32. This ended the common ascidian project that Lacaze-Duthiers, affected by the death of his friend, did not wish to undertake alone (Jesus, 2022; Jesus et al., 2021).

The topic of ascidians came back naturally as his research on mollusks progressed. During a mission on the coral of the Algerian coasts in 1860–1862, he discovered a strange animal. On the sole criterion of its external form, it resembled a Lamellibranch, except that the bivalve shell was cartilaginous and not limestone (Figure 3). A thorough analysis of the organs and of their functioning left no doubt in Lacaze-Duthiers' mind: it was an ascidian that he called *Chevreulius callensis* (now named *Rhodosoma callense*; Monniot & Zibrowius, 1999). Although this discovery was made before Kowalevsky's seminal publication in 1866 (Lacaze-Duthiers, 1865a, 1865b), it sheds light on the approach that led Lacaze to take a position on the question of ascidians as ancestors of vertebrates. First, he used the example of *Chevreulius* to stress the importance of combining morphological studies with anatomical and physiological examinations. Second, he warned his contemporaries, Hancock (1806–1873) and Huxley, about the importance of multiplying the analytical criteria to support their proposal to group the ascidians with Brachiopods and Bryozoans (Hancock, 1858; Huxley, 1856). Third, he was certain that the new genus, *Chevreulius*, was not an isolated case but, on the contrary, the first representative of a new series. Moreover, this first ascidian study certainly reinforced his conviction of the proximity between mollusks and ascidians.



**FIGURE 3** *Chevreulius callensis*. (a) *Chevreulius* fixed on a rock and closed. (b) Same animal fixed on a rock, valve raised. (c) Another animal, higher than the previous one. (d) *Chevreulius* with a portion of the tunic removed in front. (a, b) Lacaze-Duthiers (1865b), Figures 1 and 2. (c, d) Lacaze-Duthiers's original drawings, courtesy of the Archives de l'Académie des sciences, Paris.

In 1868 and 1869, in Roscoff, he noticed that the beach was full of very diverse ascidians, and he decided to study them. Importantly, Lacaze-Duthiers observed a fascinating ascidian, *Molgula*, which lives in sandy areas unlike most other ascidians, which are fixed on rocks. By studying its embryonic development, he discovered that, unlike other ascidians, this species lacked a tadpole stage. Immediately aware of the importance of this observation, he published in June 1870 a short note in the “Comptes Rendus de l'Académie des Sciences” on the discovery of the peculiar development of *Molgula* that was immediately translated into English (Lacaze-Duthiers, 1870a, 1870b). In this paper, he stressed the previous works of Savigny (1777–1851), Milne-Edwards, Van Beneden (1809–1894), Kölliker, Kowalevsky, Kupffer and others who analyzed the development of ascidians with the spectacular tadpole stage. He underlined in its introduction that “all scientists agree that ascidians, when young, at their escape from the egg have a larval form which makes them comparable, in appearance alone, with the tadpole of the frogs” (underlined by us since he repeated a main argument developed in his articles on *Chevreulius*: do not trust appearances!). In contrast, he observed that the embryo of *Molgula* hatches “like an Amoeba, by flowing like a rounded, plastic, fluid, pasty mass destitute of a tail and

remaining sedentary at the bottom of the vessel” but “never enjoys that agility or activity which is so remarkable in the movements of the life of the other Ascidians.” The importance of his observation did not escape his attention: “I desire particularly to call the attention of naturalists to an exception which is equally remarkable and little known, but which relates to the existence of one of the characters of the class; regarded by all zoologists as one of the most certainly established. A fact so unexpected must show what reserve and prudence should always guide us in zoological generalizations” and he concluded: “to arrive with certainty at the knowledge of characters, we require the concurrence of all morphological as well as of all embryogenic data; for although embryogeny may and must furnish valuable information, by itself it may also in some cases, lead us into the gravest errors.” From then on, his opinion was made and did not change any more: the presence of a tailless embryo in *Molgula* raises questions about the homologies proposed by Kowalevsky between the tadpole of the urodele (provided with a tail) ascidians and that of vertebrates (amphibians).

Finally he published a monumental monograph of more than 700 pages entitled “The simple Ascidians of the French coasts,” organized in two parts (Lacaze-Duthiers, 1874, 1877). The first, “Study of a type

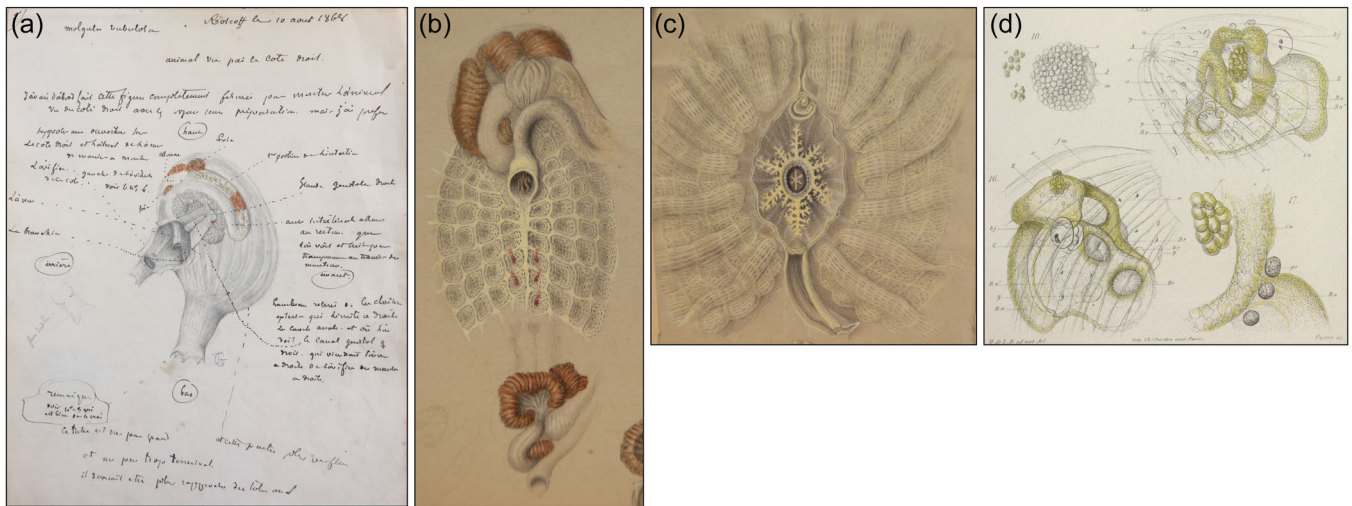


taken in the group of Molgulidae," published in 1874, describes in detail one species, *Molgula tubulosa* (present-day name, *Molgula occulta*). Then, in 1877, the second part, "Study of species," describes the species observed in the Atlantic (with one exception in the Mediterranean). In line with his previous contribution, he made a decision that would have far-reaching consequences: he took the tailless species *Molgula occulta* as a type, as a point of comparison, and not the *Phallusia* with its tailed tadpole. He was of course aware that this choice of a species whose embryogenesis is so unusual was going to bring him criticism, and he justified it in this way: "The Molgulid, having served as a type, presents in its embryogeny a most exceptional abnormality in one of the greatest general facts of the history of metamorphoses. Why choose it? In this, I differ perhaps from the approaches of some zoologists. The types which seem abnormal but which with efforts one can always bring back to the fundamental plan, to the general disposition, seem to me by that very fact infinitely more curious, more interesting, and their history makes a deeper mark in the mind when the efforts to trace it were greater." (Lacaze-Duthiers, 1874, p641; our translation). This remark reflects Lacaze-Duthiers' attachment to the law of connections formulated by Geoffroy Saint-Hilaire, which encourages the search for the fundamental homologies under the diversity/abnormality of the apparent forms. But Lacaze-Duthiers had also established a complementary law called "secondary regularization of parts" stating that original divergences can be found under the acquired resemblances (Pruvot, 1902). Following this law, he also justified his choice of *Molgula* by its very typical ascidian adult form: "the observation related to the embryogeny of our Molgulid does not really concern me; but examining the adult, one sees that it presents a set of the most remarkable organic conditions that particularly supports the reading of the plan of these peculiar beings..." (Lacaze-Duthiers, 1874, p641; our translation). In short, despite the fact that, throughout his work, Lacaze-Duthiers insisted on the importance of analyzing developmental data, in the present case, he considered that the choice of the *Molgula* was relevant because of the greater ease it offers to understand the functional morphology of the adult. In brief, the absence of a tadpole stage during development coupled with an adult form typical of ascidians made the *Molgula* a model case for the search of its homologies with either molluscs or vertebrates.

It was clear that working on ascidians and having discovered *Molgula*'s peculiar development, Lacaze-Duthiers could not escape discussing in full the opinions of Kowalevsky. However, even if the question of the ascidians as potential ancestors of vertebrates is clearly discussed in his work, it was not the primary goal of his large 727 pages monography. From the start, he insisted on his intention to make a general, in-depth and exhaustive study to get a complete understanding of this animal (environment, physiology, life cycle). In his inimitable style he affirmed: "It is, indeed, only by seeking how an animal pursues its existence, how it propagates its species, how it interacts with the outside world, that one can hope to have a correct idea of the relationships among beings and that one can approach the great and serious questions of zoology that are constantly being put on the agenda and regularly reviewed. Without an extensive

knowledge of animals, one falls into general considerations where presumption, sometimes under an appearance of false modesty, often plays the leading role; where vague and hollow theories replace serious ideas and wise opinions which are the consequence of an experience acquired in thorough studies; where one is all talk and uses new words which are taken for explanations, although they say nothing more, and have the disadvantage of cluttering up the science." (Lacaze-Duthiers, 1874, p127; our translation).

He therefore began by describing, for the species he selected, "the biological conditions in which [it] lives" (Lacaze-Duthiers, 1874, p128; our translation). He discussed in detail three localities in Brittany where the animals could be found and even described how to harvest them. He carried out a real ecological study by comparing the harvests he had been able to make over the years with meteorological data; he discussed with local fishermen and confirmed his conclusion of a significant effect of climate on the abundance of this species. He was also interested in their predation by crabs and refuted previous suggestions of mimicry of this species. His work was based on the methods and approaches that were to become those of the Eco-Evo-Devo field and can be compared to certain modern studies in this field by grasping the life of this animal in all its dimensions (Gilbert & Epel, 2015). The morphological analysis is extremely precise. Both the general aspect of the animal and the finest details of anatomical structures, such as the tunic histology, the blood circulation and the gill apparatus, as well as the different stages of development, are presented, to help the reader follow his argument and his conclusions (Figure 4). The accompanying plates with his drawings, made by hand using a camera lucida, compare very well with current photos taken with the best microscopes (Figure 5). On this subject, moreover, he noticed that there was nevertheless a certain imprecision in what he had drawn: "We multiplied the drawings a lot and all of them have been copied exactly with the camera lucida, leaving to the stump [a drawing tool], with its characteristic fuzziness, to delimit what did not seem to us to be clearly defined." (Lacaze-Duthiers, 1874, p632; our translation). But above all, he considered himself an experimentalist. He therefore described how to keep the species in an aquarium, where and when to find mature adults or juveniles in the field and how to obtain in vitro fertilization in the laboratory. He related many experiments he had carried out to understand the functional anatomy, in particular on the circulation. There were divergent opinions in the literature as to whether the circulatory system in ascidians was closed with a dense network of capillaries, or open. His experiments based on injecting colored liquids in various parts of the circulatory system led to the demonstration that the circulation was closed in *Molgula* (Figure 6). He also observed in this species the fascinating potential for reversal of blood circulation occasionally used by the animal, originally observed in salps by Huxley (Huxley, 1851). The zoological interest of the memoir on the *Molgula* and the ascidians is based on the exhaustiveness of the study: everything (morphology, anatomy, physiology, reproduction, development, ecology) is described, dissected, analyzed, by both descriptive and experimental approaches. This results in a totally integrated biological vision of the species



**FIGURE 4** *Molgula occulta*, gills, digestive organs, embryo. (a) Lacaze-Duthiers's notebook, Roscoff, August 10, 1868. The *Molgula* is seen from the right side, tunic open. (b) Portion of the gill and digestive organs seen from the posterior side through the peribranchial cavity. (c) Portion of the gill showing the gill orifice seen from the center of the cavity. (d) On the top left: ovule inside a pluricellular capsule. Other drawings: 3-weeks old embryo, different parts and different magnifications. (a) Courtesy of the Bibliothèque de la Station biologique de Roscoff, Sorbonne Université. (b, c) Lacaze-Duthiers's original drawings, courtesy of the Archives de l'Académie des sciences, Paris. (d) Lacaze-Duthiers (1874), Plate 23, Figures 10 and 15–17.

studied, whereas at the time there was already a tendency to fragment the publications, scattering observations that were not related to each other. The enormous work of Lacaze-Duthiers not only allowed an understanding of all the stages of the life of the species in question, but also represented a solid basis on which to rely for comparative biology studies.

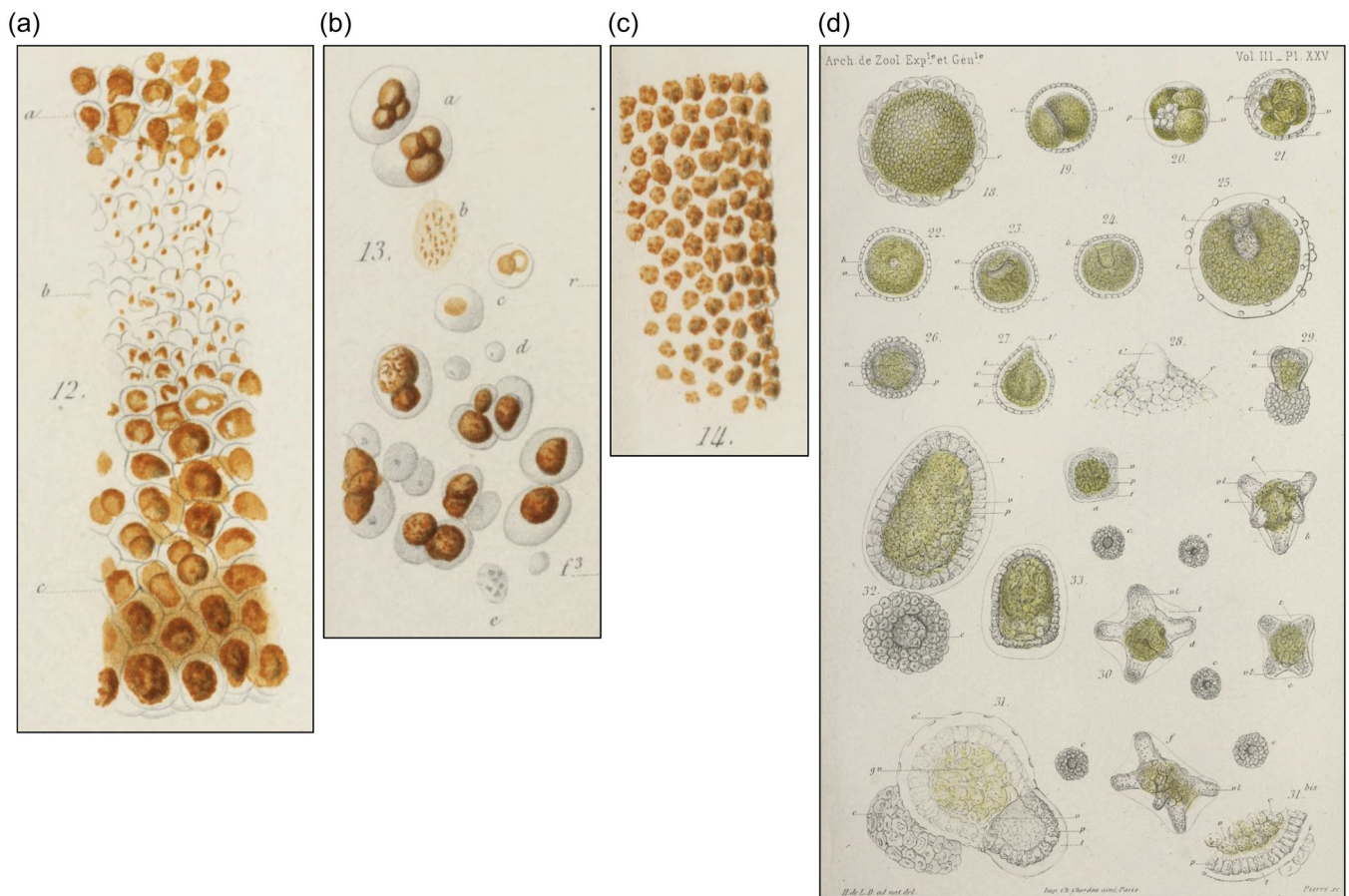
## 5 | LACAZE-DUTHIERS VERSUS THE “ASCIDIAN HYPOTHESIS”

To understand the relationship of *Molgula* with other animals, Lacaze-Duthiers needed to perform a comparative analysis and hence to use a point of comparison. Because of his strong opinion that ascidians were part of the mollusks, he compared his *Molgula* with a lamellibranch without clearly indicating which species he chose (he had clearly in mind a mussel, an oyster or a scallop). This immediately raised a question: how to orient the two animals to allow a relevant comparison? On several pages, he justified the specific orientation that he selected: the siphon inhaling downwards, the fixed part of the ascidian upwards and he compared it with the orientations proposed by his teacher Milne-Edwards (Milne-Edwards, 1841) but also the British zoologist Albany Hancock (Hancock, 1870). There again his concern was to find a relevant point of comparison even if this comparison with a bivalve of course strongly biased his analysis in favor of a proximity to mollusks.

Having a good framework, Lacaze-Duthiers related what he observed with the situation in mollusks and, often, also pointed out the differences he saw with amphioxus, considered, at that time, as the simplest form of vertebrate. About the gills in particular, he

contested the interpretations of the famous German morphologist Carl Gegenbaur, who was puzzled by the differences in the formation of the branchial cavity between mollusks and ascidians (Gegenbaur, 1870). Lacaze-Duthiers pointed out that great differences exist in the way in which the gills of cephalopods, gastropods and lamellibranchs are formed, and yet it would not occur to anyone to take this as an argument for not considering them all as mollusks: “with these principles one would manage [...] to break up the animal kingdom in such a way that it would soon be transformed into a series of secondary groups, and that the great general types would disappear.” (Lacaze-Duthiers, 1874, p298; our translation).

Then, he came to the key question: “Does the embryo of our Molgulid remind us of the vertebrate type?” He first addressed severe criticisms to the methodology used by the proponents of the “ascidian theory,” notably Kupffer, namely: not enough details in the descriptions and drawings, not enough animals studied, lack of details on the experimental protocols used for the observation, observations of phenomena so transient (a few seconds) that they are observable only by chance and only by few other scientists, omission of the names of the species chosen for studies, fragmented observations of continuous phenomena that it is necessary to observe in the long-term, and so forth. These aspects were in total opposition to the methodological principles claimed by Lacaze and previously mentioned. According to him, these weaknesses precluded support of the interpretations and hypotheses of the authors and undermined the reproducibility of their observations. Besides the methodology, let us summarize the 8 pages (Lacaze-Duthiers, 1874, p632–640) in which he developed his main arguments to refute the validity of the link between ascidians and *Amphioxus* or vertebrates.

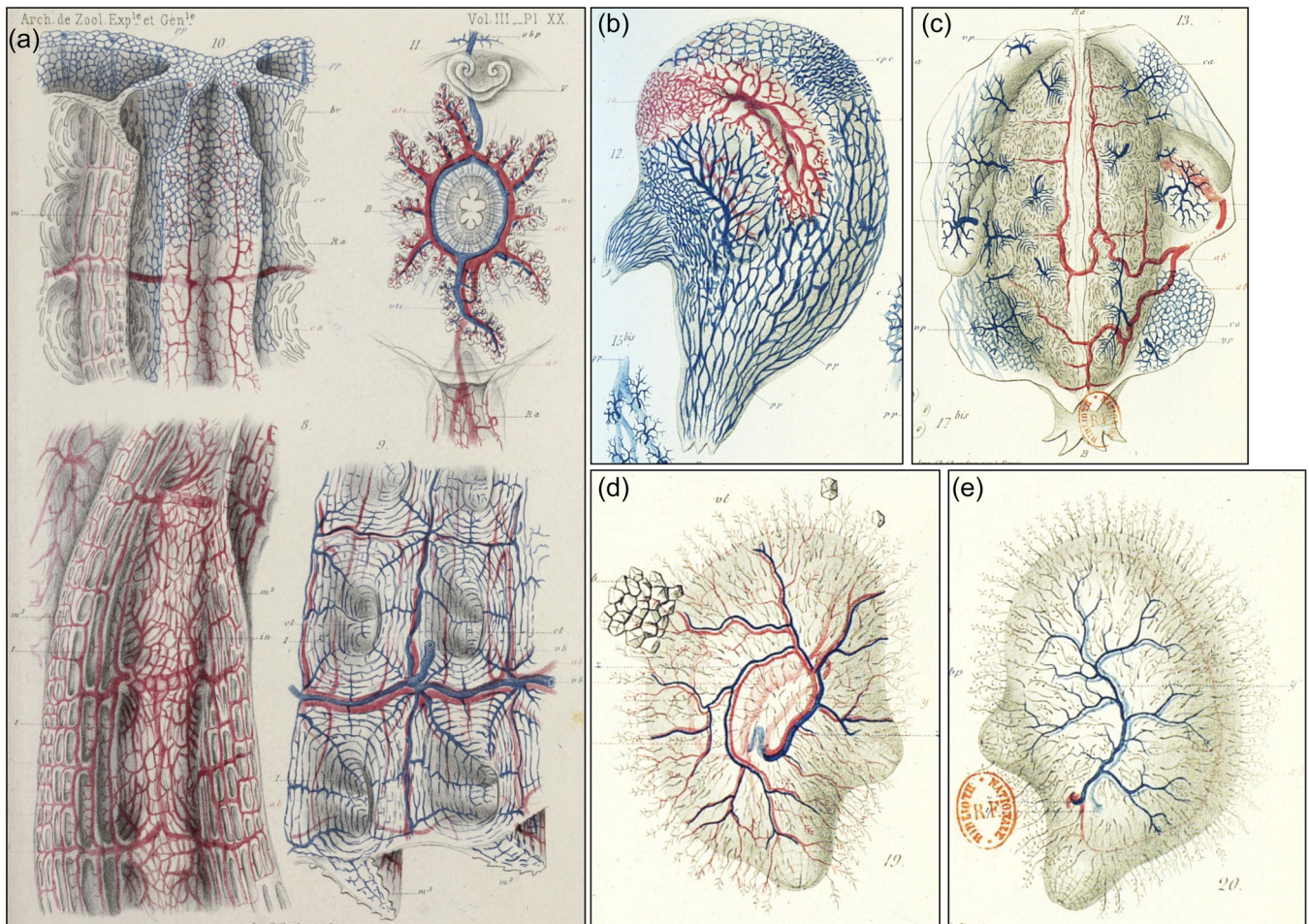


**FIGURE 5** *Molgula occulta*, liver and embryogenesis. (a) Piece of liver tissue. At the top: cells with large nuclei. In the middle: small cells, with punctiform nuclei. At the bottom: huge cells with large nuclei and concretions. (b) Different cell types isolated from the liver. (c) Cells of the hepatic tube located near the intestine. (d) Embryogenesis. 18, the egg; 19–26: embryogenesis inside the shell; 27–29: hatching of the embryo; 31 to 33: embryos outside their shell (c), the tunic (t) is visible; 30: several embryos after hatching. Lacaze-Duthiers (1874). A: Plate 4, Figures 12. B: Plate 4, Figure 13. C: Plate 4, Figure 14. D: Plate 25.

1. His first argument was that, in the species he had chosen as a type, he could not detect any of the similarities with the development of amphioxus or vertebrates pointed out by Kowalevsky (Kowalevsky, 1866) and Kupffer (Kupffer, 1869, 1870, 1872). According to him, the fact that one ascidian, *Molgula*, does not have a tadpole with a tail, denied this tadpole the status of a universal characteristic in all ascidians. Logically, it was no longer possible to use this nonuniversal character as a criterion of homology and as the basis of phylogenetic theories. Moreover, he noted that if the kinship between ascidians and vertebrates was true and relevant with regard to ancestry, it should show up in characters of the embryonic development other than the larval tail. About his drawings of embryos and developing larvae, he wrote: “Which of these drawings is distantly, even very distantly, reminiscent of an embryo, even a state, a period of the vertebrate development? [...] The blindfold that covers my eyes must be too thick for me to be able to find here an analogy, even distant, between *Molgula* and amphioxus, both being embryos.” (Lacaze-Duthiers, 1874, p633; our translation). Rather than similarities, he pointed out important differences, regarding the dorsal chord that is absent in *Molgula*, or

the innervation that is strongly dissimilar in the two cases. Similarly, he did not observe any sense organs, such as the auditory and ocular capsules observed by other authors on urodele ascidians, and he stressed that Kupffer himself had confirmed their absence in *Molgula* (Kupffer, 1872). For him, this is not due to the derived way of life of *Molgula occulta*, in sandy areas, because he discovered other *Molgula* species “tailless and blind” which are fixed on rocks.

2. His second argument was related to a question that was hotly debated at the time: the regression of organs. For the proponents of the “ascidian theory”, the tailless *Molgula* embryo could be explained by a developmental arrest. Contrary to the urodele ascidians, whose embryo develops a tail with a dorsal chord, a nervous system and muscles, the *Molgula* would stop its development before these changes. Then, a regression of the tail brings back the urodele ascidians to the point where the *Molgula* stopped. But Lacaze-Duthiers objected that in this case, one should find in *Molgula* the homolog of the primitive caudal blastema of urodele ascidians, which would not develop in this species. However, such a structure is undetectable. Moreover Lacaze-Duthiers was skeptical



**FIGURE 6** *Molgula occulta*, blood circulation. (a) Circulation in the gill and the tentacle crown. Veins filled in blue, arteries in red. (b) Circulation of the tunic, right side. (c) *Molgula* seen by the anterior face, tunic rejected on the sides. Venous circulation bringing blood to the gill. (d) Circulation in the tunic. Arterial, venous and branchial vessels. (e) Circulation in the tunic, right side. Lacaze-Duthiers (1874). (a) Plate 20, Figures 8–11. (b) Plate 21, Figure 12. (c) Plate 21, Figure 13. (d) Plate 22, Figure 19. (e) Plate 22, Figure 20.

about the supposed developmental arrest of *Molgula*: “Do we see, in the animal kingdom, an interruption of development which is not monstrous when it concerns precisely the fundamental part, the most characteristic of a group, the nervous system?” (Lacaze-Duthiers, 1874, p634; our translation). By emphasizing that “The *Molgula* seems [...] to start where the *Ascidian* urodele ends” (Lacaze-Duthiers, 1874, p620; our translation), he suggests without making it explicit that the opposite could have happened: the secondary appearance of a tail in a model where it is not an ancestral character, that is, the opposite of a secondary regression scenario. Later he pointed out the morphological simplifications of the parasitic trematode worms and drew a provocative parallel with the ascidians. Why not take the tail of cercariae as an argument for establishing this group as the ancestor of vertebrates? The absence of a chord in the cercariae tail could be due, as proposed for *Molgula* by Lacaze-Duthiers's opponents, only to an imperfect primitive state. If one follows the logic of the proponents of the ascidian theory, then trematodes are as good candidates as ancestors of vertebrates as ascidians!

3. Another argument recurred throughout the text of Lacaze-Duthiers. Even if he recognized the importance of embryological studies, he was deeply convinced that, in the present case, they are given too much importance. According to him, an embryonic resemblance outside the general context cannot be taken as a central argument to propose a spectacular parentage, especially when adult morphologies diverge sharply: “The embryogenic studies have the greatest value; but when they are too isolated from the knowledge of the adult body, they can lead to hypothetical interpretations far too distant from the truth.” (Lacaze-Duthiers, 1874, p610; our translation). He stressed that irrespective of the embryo, the adult morphology does not provide any strong argument to link ascidians with *Amphioxus* and vertebrates. He took the gills or the digestive organs as an example but he also discussed at length the general organization of the body and the orientation of the organs relative to each other. He was so unable to discern homologies among adult forms that he suggested that proponents of the “ascidian theory” have relied on “hypothetical data.” Worse, he accused them of having

found similarities only “*pressed by the need to find the ancestral strain of vertebrates in an ascidian*” (Lacaze-Duthiers, 1874, p636; our translation). Further on, he ironically suggested that observations can be used in favor of one theory or another: “Is the reversal of circulation of no value? If joking were allowed in such serious discussions, one might perhaps argue that the heart makes the Tunicate sometimes a Mollusk, sometimes a fish...” (Lacaze-Duthiers, 1874, p637; our translation).

4. His last argument was based on the disagreement between Kowalevsky and Kupffer, both proponents of the “ascidian theory,” about the orientation of the embryo at the beginning of development: “If one accepts this morphological idea of the relationship of an Ascidian embryo with an amphioxus, it is very difficult to understand how one can arrive at an identical result and agree when some considers a specific part to be anterior, while the others consider it to be posterior” (Lacaze-Duthiers, 1874, p592; our translation). As a man of extreme precision, he could not conceive that the proponents of a same theory could diverge on fundamental questions of orientation. Also, many authors disagreed about the position of ascidians within the invertebrates. Gegenbaur considered them to be classed as worms (Gegenbaur, 1870) whereas others placed them among mollusks. How to support as a candidate for the position of ancestor of vertebrates, animals that we do not know how to classify within the invertebrates?

His final conclusion was unambiguous: “Let us not push so far the comparisons and let us say that one took appearances for realities and that, to arrive at establishing homologies, one had to invoke misleading resemblances, one imagined laws which were not confirmed or controlled by facts.” (Lacaze-Duthiers, 1874, p639; our translation). This citation very well exemplifies one strong aspect of Lacaze-Duthiers personality that we commented previously: in science he was prudent, claiming to examine the facts without any preconceived hypothesis. He must see: “I will describe what I saw, and leave undetermined what I could not see clearly.” (Lacaze-Duthiers, 1874, p592; our translation) and he obviously avoided like the plague overinterpretations or preconceived ideas: “As we can see, what kind of exaggerations are we led to when, stating a priori principles without prior demonstration, we do not want to deviate from them!” (Lacaze-Duthiers, 1874, p297; our translation) even if, in the present case, his insistence to keep the comparison between ascidians and mollusks took him away from the truth.

## 6 | WHAT DO WE LEARN FROM THIS?

It is obviously easy to consider Lacaze-Duthiers simply as a conservative mind misled by preconceptions (the ascidians are mollusks) and, therefore, to reject his contribution. In fact, this episode and the work of Lacaze-Duthiers as a whole broke new ground and deserve our attention. Firstly, the debate in question illustrates scientific consensus in the making and reveals the tensions,

the difficulties, in arriving to a widely shared concept. In the context of the time, at the heart of the controversy between the proponents of the ascidian and the annelid theories, Lacaze-Duthiers posed extremely relevant questions. It is not by chance that his work had a strong impact: Lacaze-Duthiers put his finger on a series of questions that had to be solved for the scientists of the time to progress. Today, Kowalevsky is recognized because he detected a relevant homology, the tails of the sea squirt and the frog tadpoles, and drew correct conclusions about the origin of vertebrates. Lacaze-Duthiers is almost forgotten. But yet science could not have advanced without scientists like Lacaze-Duthiers who avoided broad generalizations, stuck to the facts he positively saw, and compelled his colleagues to continue their investigations to strengthen their observations.

On the other hand, this episode also shows that some central questions of Eco-Evo-Devo still very relevant today were asked right at the beginnings of those comparative approaches: What is the link between adaptation to the environment and the emergence of new characters selected by evolution? What role does the regression of certain organs or structures play in the process of evolution? How to properly choose the characters that we can use to infer phylogenies? Because these central questions could not be answered, the interest in evolutionary morphology declined until the beginning of Evo-Devo (Allen, 1978; Nyhart, 1995). The criticisms that Bateson but also Morgan would unleash about this field of research by turning towards genetics, focused precisely on the inability of evolutionary morphology to reach consensus because methods and approaches were inaccurate: “the value of this [...] rests wholly on the hypothesis that the methods of argument are sound. Over it all hung the suspicion that they were not sound. [...] Were we all agreed in our assumptions and as to the canons of interpretation, there might be some excuse, but we are not agreed.” (Bateson, 1893, cited by Hall, 2005).

A last lesson can be drawn from this episode, a lesson which is obviously less favorable to Lacaze-Duthiers: the risks associated with specialization. Lacaze-Duthiers was an internationally renowned zoologist, and in particular a leading expert on mollusks: he knew everything there was to know about these animals at his time, when there were fewer known species than there are today. He was in touch with all the important zoologists of the time: he maintained an extensive correspondence with them (among those cited in this text: Darwin, Gegenbaur, Haeckel, Huxley, Kölliker, Kowalevsky, Lankester, Metchnikoff, Van Beneden and others) and he often received them in the marine stations of Roscoff and Banyuls. However this very knowledge was, together with his unfortunate choice of *Molgula* as a type, the cause of his inability to see and appreciate at its true value what Kowalevsky was able to recognize. Kowalevsky, an excellent naturalist without a doubt, did not attempt to carry out an exhaustive study but, guided by his intuition, decided to focus on the embryonic characters without worrying about the rest. Unfortunately for Lacaze-Duthiers, knowing your subject too well is sometimes an obstacle....

The scientific contribution of Lacaze-Duthiers to this debate about ascidians occupies only a quite modest place in his work. As already noted, he only became involved in this debate because he was studying ascidians in the 1870s and could not avoid the question of

their potential role as vertebrates ancestors at that time. Years after, he turned his attention back to the ascidians and published with one of his students, Yves Delage (1854–1920), two articles describing different new species (Lacaze-Duthiers & Delage, 1889, 1892) without mentioning the hypothetical ascidian origin of vertebrates. Not being an annelid specialist, he took no part in the controversy between “ascidian” versus “annelid” theories. We are not going to discuss here his other works on mollusks and corals, still relevant and cited even today. We end by addressing his role in the establishment in France of a school of experimental zoology, a concept that appears in the background in the ascidian episode. Let Lacaze-Duthiers conclude (Lacaze-Duthiers, 1872b, p64, our translation):

“Descriptive zoology has passed its time: it is now only one of the parts, indispensable, it is true, but insufficient of the GENERAL ZOOLOGY. Also, to have an indisputed value, its results must be:

Based on the precise laws of MORPHOLOGY;

Deduced from the most meticulous research of HISTOLOGY;

Demonstrated by the long and continuous studies of EVOLUTION;

Subjected to the CONTROL OF EXPERIMENTATION, which must always prepare, help and lead the studies of MORPHOLOGY and EVOLUTION.

They must be such, in one word, that GENERAL ZOOLOGY still deserves the name of EXPERIMENTAL ZOOLOGY.”

No doubt that these words establish him as one of the very first pioneers of Eco-Evo-Devo!

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We warmly thank Sandrine Bodin and Véronique Arnaud, from the Library of the Arago Laboratory—Sorbonne University, as well as Isabelle Maurin-Joffre, Curator of the Archives of the Academy of Sciences (Paris), for their help in consulting the abundant archives related to Henri de Lacaze-Duthiers. We thank André Toulmond, Hector Escriva, Christian Sardet and Claire Laudet for helpful discussions, thorough reading of the manuscript and valuable advice. This work was supported by CNRS, Sorbonne University and OIST.

## ORCID

Vincent Laudet  <http://orcid.org/0000-0003-4022-4175>

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