2025, vol. 9, n° spécial UNOC 2025, 46-67 pages, DOI : 10.21494/ISTE.OP.2025.1290 ISTE OpenScience

Two centuries of arts and science in Nice and Villefranche sur Mer: 1) Pioneers: 1800 to 1900

Deux siècles d'arts et de sciences à Nice et Villefranche sur Mer : 1) Les anciens : de 1800 à 1900

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ABSTRACT. We tell the story of exploration of the flora and fauna in the Nice region, and especially pelagic organisms, the work of some twenty biologists associated with painters. In 1800, Antoine Risso, Jean Gabriel Prêtre, François Péron and Alexandre Lesueur described and painted flowers, fish and some marine invertebrates. In the middle of the century, Jean Baptiste Vérany, a naturalist from Nice, welcomed prestigious German and Swiss biologists - Johannes Müller, Rudolf Leuckart, Ernst Haeckel and Carl Vogt - who described andstudied little known organisms such as siphonophores and radiolarians. And in the 1880s, Hermann Fol, Jules Barrois and Alexis Korotneff set up a marine station in Villefranche sur Mer, recognized as an exceptional site for the study of plankton. During this period, the Natural History Museum of Nice was enriched by exceptional collections of flowers, fish and funghi assembled by Risso, Vérany and Jean Baptiste Barla, who employed Vincent Fossat for his talent as painter / illustrator. By the end of the century, the Nice region attracted foreign royalty and aristocrats, visiting biologists and impressionists painters. In a companion article (Sardet 2025 / 2 Modern era: 1970 to 2024) we show that organisms studied in the 19th century are still the subject of research at the Institut de la Mer de Villefranche (IMEV).

RÉSUMÉ. Nous racontons l'histoire de l'évolution des connaissances de la flore et la faune dans la région niçoise et en particulier celle de la faune pélagique. Dans les années 1800, Antoine Risso, Jean Gabriel Prêtre, François Péron et Alexandre Lesueur décrivent et peignent les fleurs, les poissons et des invertébrés marins. Au milieu du siècle, le naturaliste niçois, Jean Baptiste Vérany accueille des savants allemands et suisses
- Johannes Müller, Rudolf Leuckart, Ernst Haeckel et Carl Vogt - qui influencent les recherches et le destin de la biologie dans la région par leurs descriptions illustrées d'organismes jusqu'alors ignorés comme les siphonophores et les radiolaires. Et dans les années 1880, Hermann Fol, Jules Barrois et Alexis Korotneff créent une station marine accueillante à Villefranche sur Mer, reconnue depuis comme un site exceptionel pour l'étude du plancton. A partir du milieu du 19ème, le Muséum d'Histoire Naturelle de Nice s'enrichit des collections de Risso, Vérany et Jean Baptiste Barla épaulés par Vincent Fossat, un peintre / illustrateur talentueux. A la fin du siècle, la région niçoise attire les souverains et aristocrates anglais et russes, des biologistes et des peintres impressionistes. Dans un article compagnon (Sardet 2024 /2 Les modernes – de 1970 à 2024), nous montrons que les organismes explorés au 19ème siècle sont toujours l'objet de recherches à l'Institut de la Mer de Villefranche (IMEV).

KEYWORDS. Nice, Villefranche sur Mer, plankton, protists, Antoine Risso, François Péron, Alexandre Lesueur, Jean Baptiste Vérany, Jean Baptiste Barla, Vincent Fossat, Ernst Haeckel, Johannes Müller, Carl Vogt, Hermann Fol, Jules Barrois, Alexis Korotneff.

MOTS-CLÉS. Nice, Villefranche sur Mer, plankton, protists, Antoine Risso, François Péron, Alexandre Lesueur, Jean Baptiste Vérany, Jean Baptiste Barla, Vincent Fossat, Ernst Haeckel, Johannes Müller, Carl Vogt, Hermann Fol, Jules Barrois, Alexis Korotneff.

Introduction

In the early 1800s, Nice was a provincial town of 40,000 inhabitants, accessible only by stagecoach or boat. In 1860, under Napoleon III, the county of Nice, which previously belonged to the kingdom of Piedmont-Sardinia, became part of France. Four years later, Nice was accessible by rail. Starting in the middle of the century, visitors flocked to the Côte d'Azur, drawn by the presence of Russian, English and Belgian royalties and artistocrats who came with their courts to enjoy the mild winter climate. Artists and biologists were attracted by the diversity of landscapes, flora and marine fauna.

Villefranche sur Mer, situated 7 km east from Nice, was a free port when it was founded, and in the 1800s the bay and city of Villefranche became a place of refuge, supply and rest for ships and their crews. Complicated political agreements brought France and the Kingdom of Piedmont-Sardinia closer to the Russian empire. As a result the bay of Villefranche harbored a large number of Russian, English, French, Italian and even American navies. Today, the bay of Villefranche welcomes cruise ships that flood the French riviera with their passengers (Braconnot & al. 2004).

The Nice region (Figure 1) boasts a remarkable seafront, bordered to the west by the sedimentary delta at the mouth of the Var river, and to the east by the bay of Villefranche sur Mer. This bay opens onto a seabed hundreds of meters deep, through which the Ligurian current flows carrying a variety of planktonic organisms - from bacteria and fish larva to jellyfish - which drift together. Depending on the season and winds, some of these plankton find themselves trapped in the natural receptacle of the bay of Villefranche sur Mer and its deep waters. Here, pelagic organisms, usually found only on the high seas, come close to shore and are accessible with small boats.

From the early 19th century, naturalists from Nice started exploring the local flora and fauna. They befriended and helped European colleagues explore the coast and collect plankton. During this period, anatomical descriptions were illustrated with drawings by professional artists. These illustrations were transformed into engravings for publication in the few scientific journals of the time, or in monographs.

The 19th century was a time when illustrated books and newspapers became popular. Travel was increasingly facilitated by coal-powered ships and trains. In the second half of the 19th century, photography and illustrated publications took off. Biologists developed their networks of universities, academies and publishers across Europe (Jessus & Laudet, 2022). Researchers helped each other, collecting and studying the extraordinary diversity of marine organisms, stimulated by new ideas on classification and evolution and the emerging cell theory. European and Russian professors and students explored the Mediterranean coasts in the 1850s, staying in the Nice region to study and illustrate jellyfish, siphonophores, appendicularians, radiolarians and more. At the end of the 19th century, thanks to young Swiss, French and Russian biologists, set up a marine station in Villefranche sur Mer which permitted scientific research and in-depth exploration of local plankton, a tradition continuing to this day (Anon. 2010, 2024, Trégouboff 1983, Dolan 2014, 2024).

In this article we describes a century-long progression. In a second article, we show how Côte d'Azur organisms described 100 to 200 years ago still inspire the research and pictorial works of researchers at the Villefranche sur Mer marine station (IMEV) in the 21st century (see companion article : Sardet 2025 / 2 Modern era: 1970 to 2024).

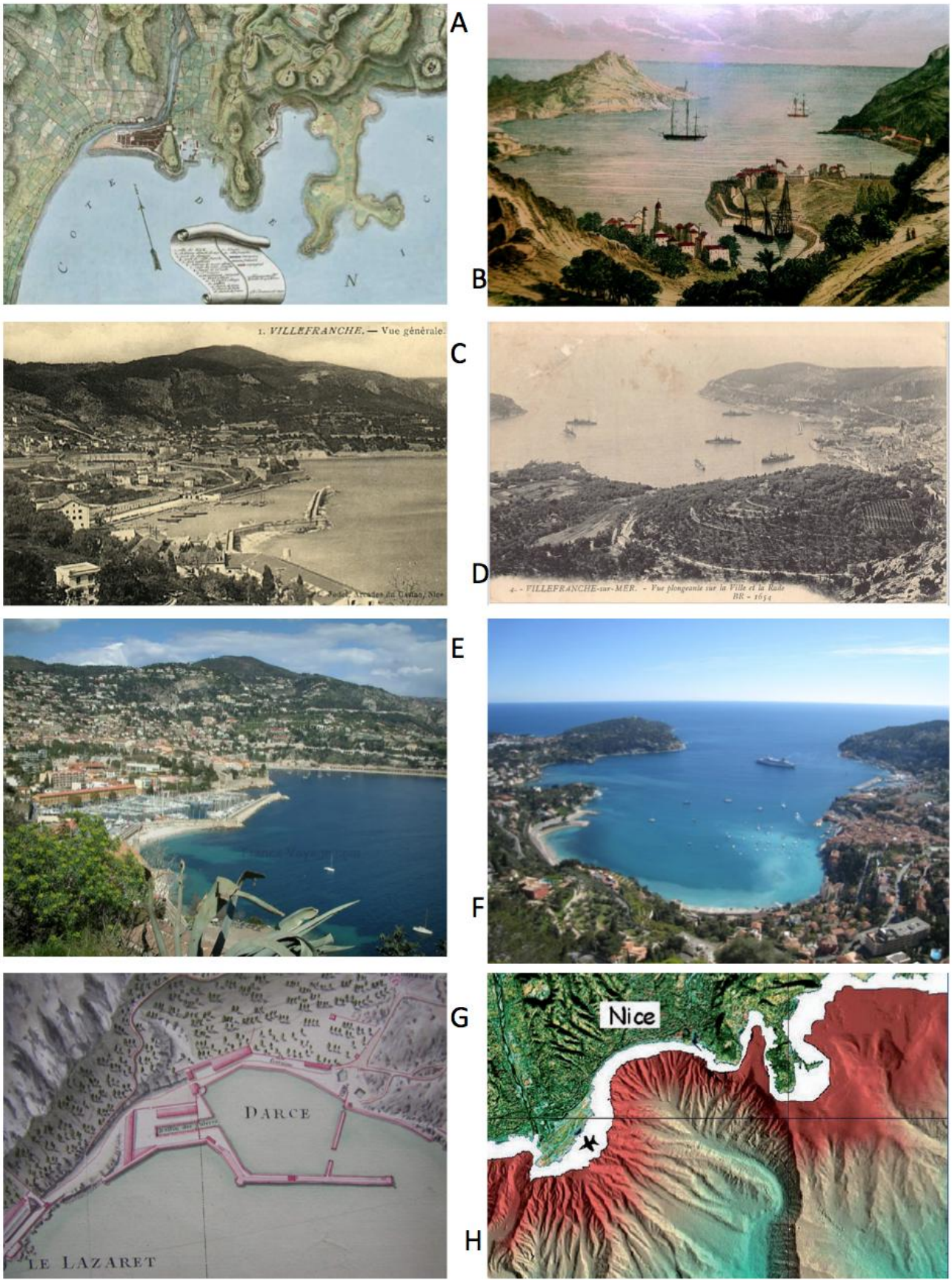

Fig. 1. *Nice region: A - The coast of Nice in the 18th century. B - The bay of Villefranche sur Mer in the 18th century. On the right, buildings on the site of today's port de la Darse.*
C - The port of La Darse in Villefranche sur Mer at the end of the 19th century (postcard)
D - The bay of Villefranche sur Mer at the end of the 19th century (postcard).
E & F - Current views of the bay of Villefranche sur Mer.
G - The port de la Darse (spelled DARCE here) and the Lazaret in 1748
H - Topography of the seabed in the Nice area

1800 - 1900: Naturalists and painters explore Nice's biodiversity

Naturalist began exploring the region in the early 1800s notably Antoine RISSO, author of remarkable publications on the local flora and fauna, illustrated by Jean Gabriel PRÊTRE. In 1809 RISSO welcomed and helped zoologist François PÉRON and watercolorist Charles-Alexandre LESUEUR, visiting Nice, to describe and illustrate gelatinous plankton organisms, jellyfish, mollusks and ctenophores. In the mid-1800s, Jean Baptiste VERANY, along with another Jean Baptiste, BARLA, created the Nice Natural History Museum. With the help of a talented local painter, Vincent FOSSAT, they contributed extraordinary collections. In the 1850s, VÉRANY welcomed and befriended scientists from Germany and Switzerland, attracted by the rich planktonic fauna abundant in the bay of Villefranche sur mer. These visitors - Johannes MÜLLER, Rudolf LEUCKART, Carl VOGT and Ernst HAECKEL - were brilliant and influential biologists who described and artistically illustrated little known pelagic organisms such as siphonophores and radiolarians. Research into marine biodiversity gained momentum with the creation in 1881 of the first laboratory in Villefranche sur Mer by Hermann FOL and Jules BARROIS. In 1886, Alexis KOROTNEFF took over and established the Station Russe de Zoologie in Villefranche sur Mer, the forerunner of IMEV, the Institut de la Mer de Villefranche, today's marine station. All these men, whose dates of birth and death are indicated, succeeded one another over the course of the century (see chronological chart below and Figure 2).

1770 1780 1790 1800 1810 1820 1830 1840 1850 1860 1870

Jean Gabriel PRÊTRE (1768-1849)

Painter-illustrator attached to the Muséum d'Histoire Naturelle, Paris

François PÉRON (1775 - 1810)

Zoologist aboard the Baudin expedition exploring the Austral Lands (1800 -1803)

Antoine RISSO (1777 - 1845)

Pharmacist and botanist from Nice, author of monographs, some illustrated by Prêtre

Charles-Alexandre LESUEUR (1778 - 1846)

Painter and illustrator from Le Havre, who joined Péron for the Baudin expedition

Jean Baptiste VÉRANY (1800 – 1875)

Naturalist from Nice, author of artistic monographs on cephalopods

Johannes MÜLLER (1801 - 1858)

German zoologist and protistologist, Berlin professor and mentor to Haeckel

Jean Baptiste BARLA (1817 - 1890)

Naturalist from Nice who built up collections of mushrooms and fish with Fossat

Carl VOGT (1817 - 1895)

German / Swiss zoologist, professor in Geneva, evolutionist and socialist activist

Vincent FOSSAT (1822 - 1897)

Painter from Nice, employed by Barla to illustrate extraordinary collections

Rudolf LEUCKART (1822 - 1898)

German zoologist, friend of Vérany. Professor in Giessen, then in Leipzig

(1934- 1919) **Ernst HAECKEL**

German zoologist, professor and rector at the University of Jena. Traveller and artist

(1845-1892**) Hermann FOL**

Swiss zoologist, professor in Geneva, founded a laboratory in Villefranche with Barrois

(1851 - 1915) **Alexis KOROTNEFF**

Russian zoologist, professor in Kiev, founded the Villefranche Russian Zoological Station

(1852 - 1943) **Jules BARROIS**

A zoologist and professor in Lille, he founded the first laboratory in Villefranche with Fol

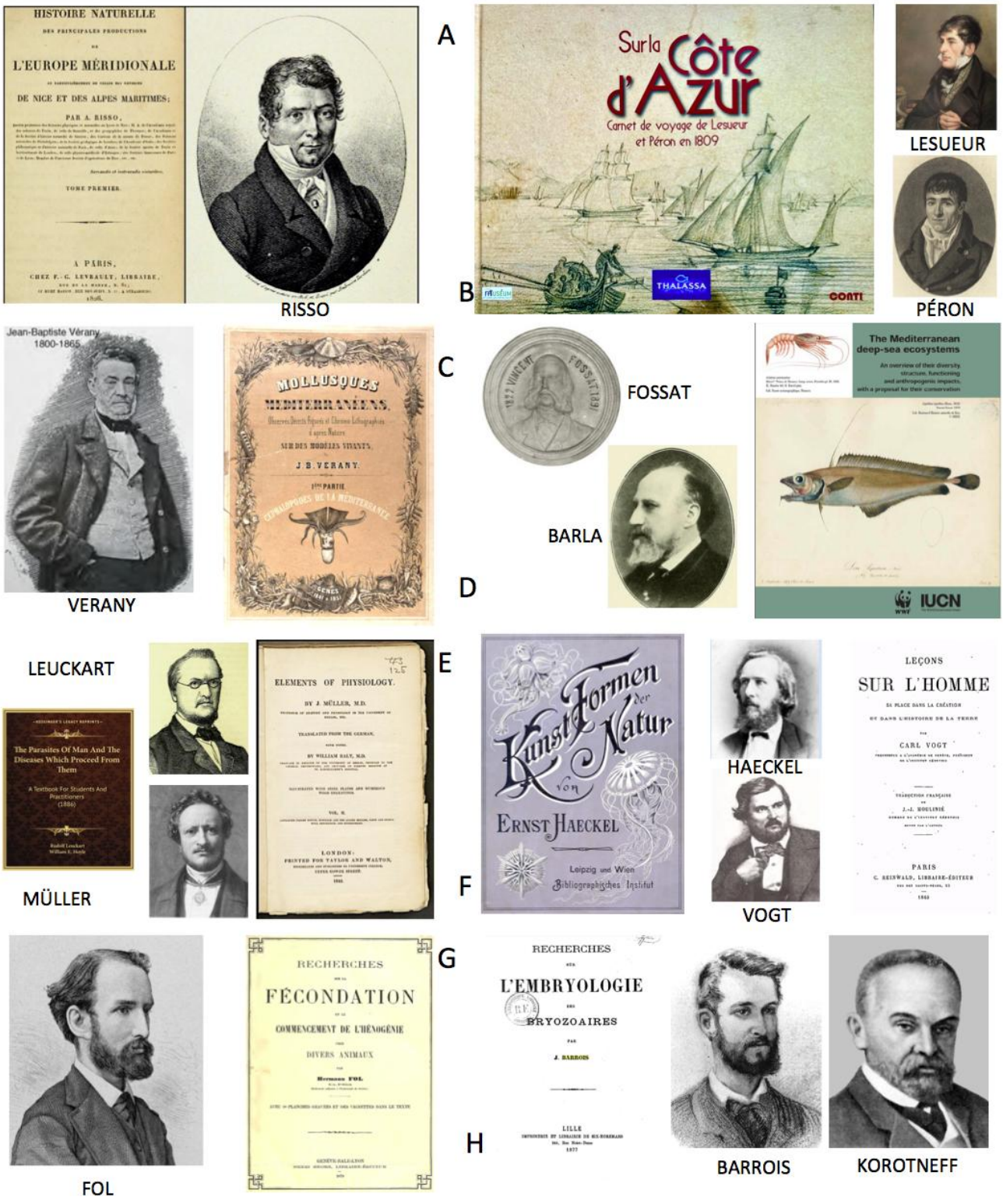

Fig. 2. *The characters in this story and some of their publications:*
A - Antoine RISSO and the first volume his 5-volumes "Histoire Naturelle de Nice et des Alpes Maritimes" (1826)
B - François PÉRON, Alexandre LESUEUR and the book dedicated to theirsojurn on the Côte d'Azur (G. Baglione & J. Goy, 2009)
C - Jean Baptiste VÉRANY and his book of chromolithographs of cephalopods (1851)
D - Jean Baptiste BARLA and Vincent FOSSAT, whose watercolor illustration of a fish illustrates the cover of a recently published book
E - Rudolf LEUCKART and Johannes MÜLLER and their books translated into English
F - Ernst HAECKEL and Carl Vogt and their best-known publications
G - Hermann FOL and his monograph on fertilization (1879)
H - Jules BARROIS and the cover of his thesis (1878) and prtrait of Alexis KOROTNEFF

1800 - 1830: Risso and Prêtre describe and illustrate the flora and fauna of Nice

The history of the naturalist quest in the Nice region began in the early 19th century with Antoine Risso (Gasiglia 1970, Dolan 2023a). Born in Nice in 1777 into a modest family, Risso was orphaned at an early age. He was raised by an uncle who directed him to be an apprentice to a pharmacist and botanist starting at the age 12. Risso managed to open his own pharmacy at age 26 and was appointed assistant curator of the departmental botanical garden. After describing local plants such as olive and citrus trees, Risso turned his attention to the animals that local fishermen brought back in their nets (Risso 1810, 1813). He not only characterized and identified fish, but also the gelatinous catch that fishermen call "carminaria" - literally, sea-meat, a tangle of jellyfish, mollusks and other soft, transparent organisms(Figure 3). Risso revived them in aquariums, carefully observing and describing them. He also caught the organisms from small boats, taking temperature readings at the same time. In 1810, he published "Ichtyologie de Nice", a natural history of fish in the Alpes Maritimes, with 11 unsigned plates.

In 1826, after selling his pharmacy, Risso published an ambitious 5-volume "Histoire Naturelle". The talented illustrator, Jean Gabriel Prêtre produced 44 plates, which were reproduced by half a dozen engravers (Risso 1826). The fifth volume contained descriptions and plates devoted to marine invertebrates (Figure 3). Unfortunately, little is known about the precise dates and conditions under which these first representations of the marine fauna of Nice were produced, and we don't know how Risso and Prêtre worked together or with the publishers. The 5-volume edition must have cost a fortune! From a family of Genevan artists, Prêtre was about ten years older than Risso, and by the time they worked together, Prêtre had already produced some remarkable illustrations of birds and other animals for the books by George Cuvier and his colleagues at the Muséum d'Histoire Naturelle in Paris (Cuvier 1816). Over 700 illustrations by Prêtre are known, an impressive body of work (Dolan 2023a).

Some of the organisms immortalized by Risso and Prêtre, such as jellyfish and sea urchins, were further explored by their successors starting in the 1850s. First by German and Swiss scientists such as Ernst Haeckel and Carl Vogt, who explored Mediterranean coasts in search of planktonic organisms, including unicellular protists (Dolan 2019). This research was amplified in the 1880s, when a laboratory was set up in Villefranche sur Mer (Anon 2010, 2024, Trégouboff 1983). This laboratory was designed to host visiting European researchers, as had already been done at the Roscoff and Banyuls sur Mer marine stations and in Naples (Fischer 2002, Debaz 2005, Groeben C. 2020, Jessus & al. 2021)

In fact, the pioneering research carried out in the 19th century on the anatomy, physiology and reproduction of terrestrial and marine organisms forms the basis of a body of knowledge that continues to this day. Teachers, researchers and members of the region's academic and associative communities continue to study and introduce the public to the rich local marine flora and fauna. Four study centers - the Université de Nice Sophia Antipolis (UNSA), the Institut National de Recherche Agronomique (INRA d'Antibes / Sophia Antipolis), the Centre Scientifique de Monaco and the Institut de la Mer de Villefranche sur Mer (IMEV) - are doing advanced research work in these fields. Some examples of research carried out at IMEV over the last 50 years are described in the companion article (Sardet 2025).

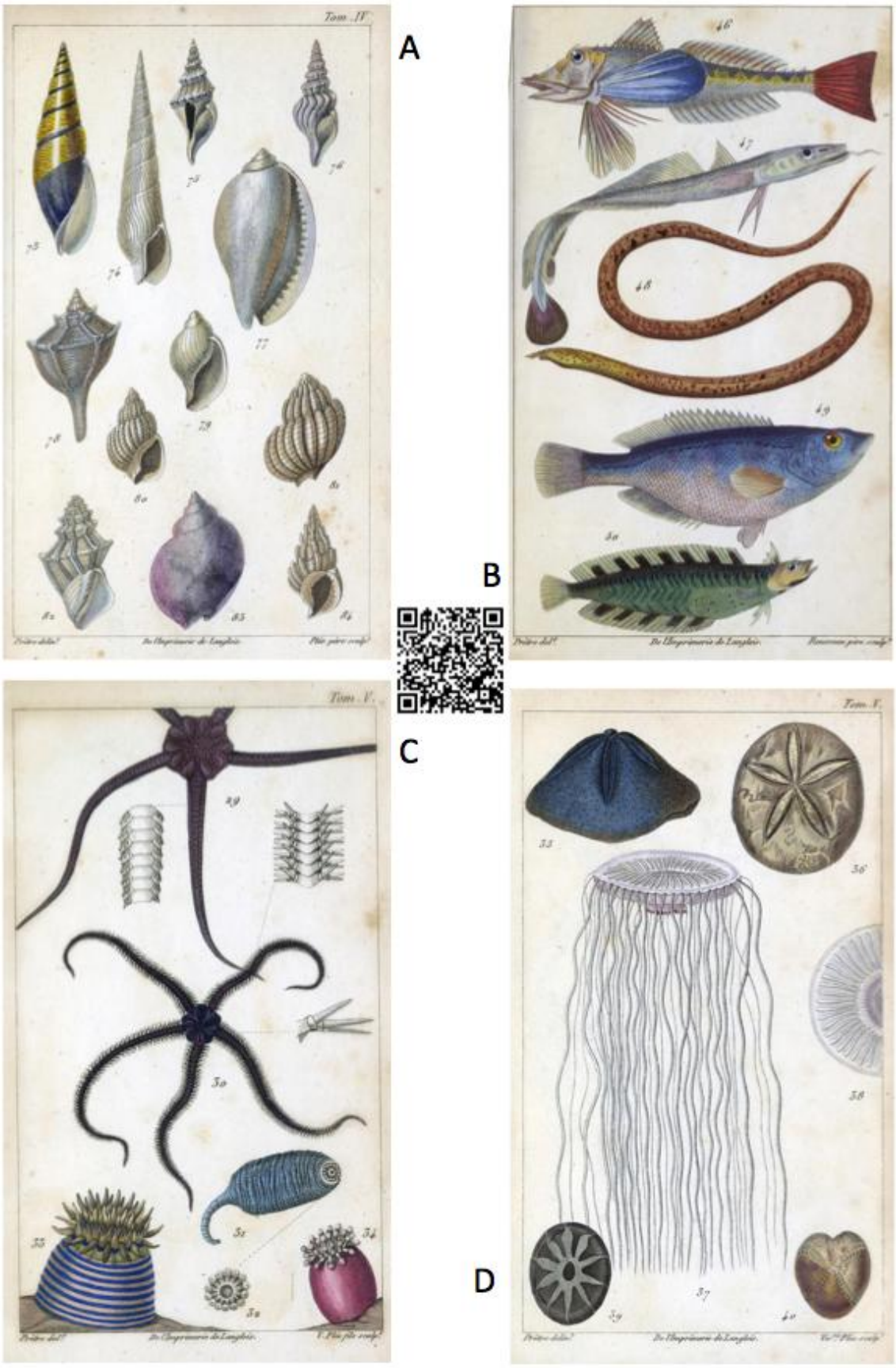

Fig. 3. *Illustrations by painter Jean Gabriel Prêtre for naturalist Antoine Risso*
A - Molluscs in volume 4 of Risso's « Histoire Naturelle » (1826)
B - Fish in volume 3 (plate 16) of the « Histoire Naturelle »
C - Brittle stars and sea anemones in volume 5 (plate 7) of « Histoire Naturelle »
D - The Equorea Rissoana jellyfish and sea urchin tests in volume 5 (plate 7)
QR code: other illustrations available on the Aquaparadox website (John Dolan, IMEV)

1809-1910: Péron and Lesueur discover the Nice area and its marine fauna

Risso's work on the fish of the Alpes-Maritimes region was remarkable. François Péron, a young zoologist, and his painter/illustrator friend Alexandre Lesueur wanted to meet Risso and observe the pelagic fauna they had already observed and described during the Baudin expedition in the Southern Ocean (1800-1804, Baudin 2001). On their return, they lived and worked together in Paris, where they wrote and illustrated a monograph entitled "Voyage de découvertes aux terres australes". This expedition, commissioned by Bonaparte and organized by Nicolas Baudin, took Péron and Lesueur as far as Australia and Tasmania, collecting over 100,000 samples, including 2,500 previously unknown species. The pelagic fauna of the Atlantic and Pacific - jellyfish, molluscs, ctenophores, salps, pyrosomes - was described and illustrated for the first time with accuracy and precision by Péron and Lesueur, who was also an accomplished engraver (Péron & Lesueur 1809).

Lesueur was born into a middle-class family in Le Havre in 1778. Enlisted at the age of 21 as assistant gunner, he quickly established himself as an illustrator for the Baudin expedition, and befriended Péron. Born in Allier in 1775, Péron had a difficult youth. He lost his right eye and was taken prisoner during the French Revolution in 1792. After studying medicine, Péron was hired as a zoologist/anthropologist by the Baudin expedition. This 2-ship voyage cost the lives of many explorers, including Captain Baudin himself, who died of tuberculosis in Mauritius in 1803. Péron also contracted tuberculosis, and on his return to France, his doctor advised him to spend the winter in the south of France for his health.

In 1809, Péron and Lesueur traveled to Nice by stagecoach and boat on the Rhône river, then crossed Provence (Goy & Baglione 2009, Baglione 2024). After a 3-week journey, Péron and Lesueur arrived and then stayed in Nice for 6 months. To collect pelagic organisms, they benefited from the help of Risso and the local authorities. Lesueur recounts: "The Commissioner of Nice provided us with a boat, skipper and four strong sailors chosen from the deserters who were in prison. They came on the day indicated to took us on board, and then we began our experiments on the Mediterranean". Péron and Lesueur collected, then observed some gelatinous organisms in aquariums. They described in particular a remarkable ctenophore, *Cestus veneris* or Venus belt an organism that can still be observed every spring in the bay of Villefranche sur Mer(Figure 4B). They also measured temperatures and noted that gale force winds caused changes in the pelagic fauna, a first step towards oceanography and ecology.

The winter of 1809 was harsh and cold, but Péron and Lesueur managed to get out in the boat and collect, describe and illustrate pelagic fauna and some benthic organisms such as ascidians and mollucs (Figure 4A, 4C). Unfortunately, Péron's health deteriorated rapidly. Lesueur accompanied him to Paris, then to his native Massif Central, where Péron died in 1810, in the hope that Lesueur would publish their observations. Lesueur did so, before leaving for the USA, where he took part in several expeditions exploring and illustrating the fauna, flora, native peoples and landscapes until 1837 (Dolan 2020). Lesueur returned to Le Havre in 1845 to create the Natural History Museum where he was the first director and curator, shortly before his death in 1846. Bequeathed by his family to the Museum after his death, Lesueur's works were forgotten. Rediscovered, his remarkable drawings and watercolors have been the subject of several exhibitions (Baglione & Crémière 2009).

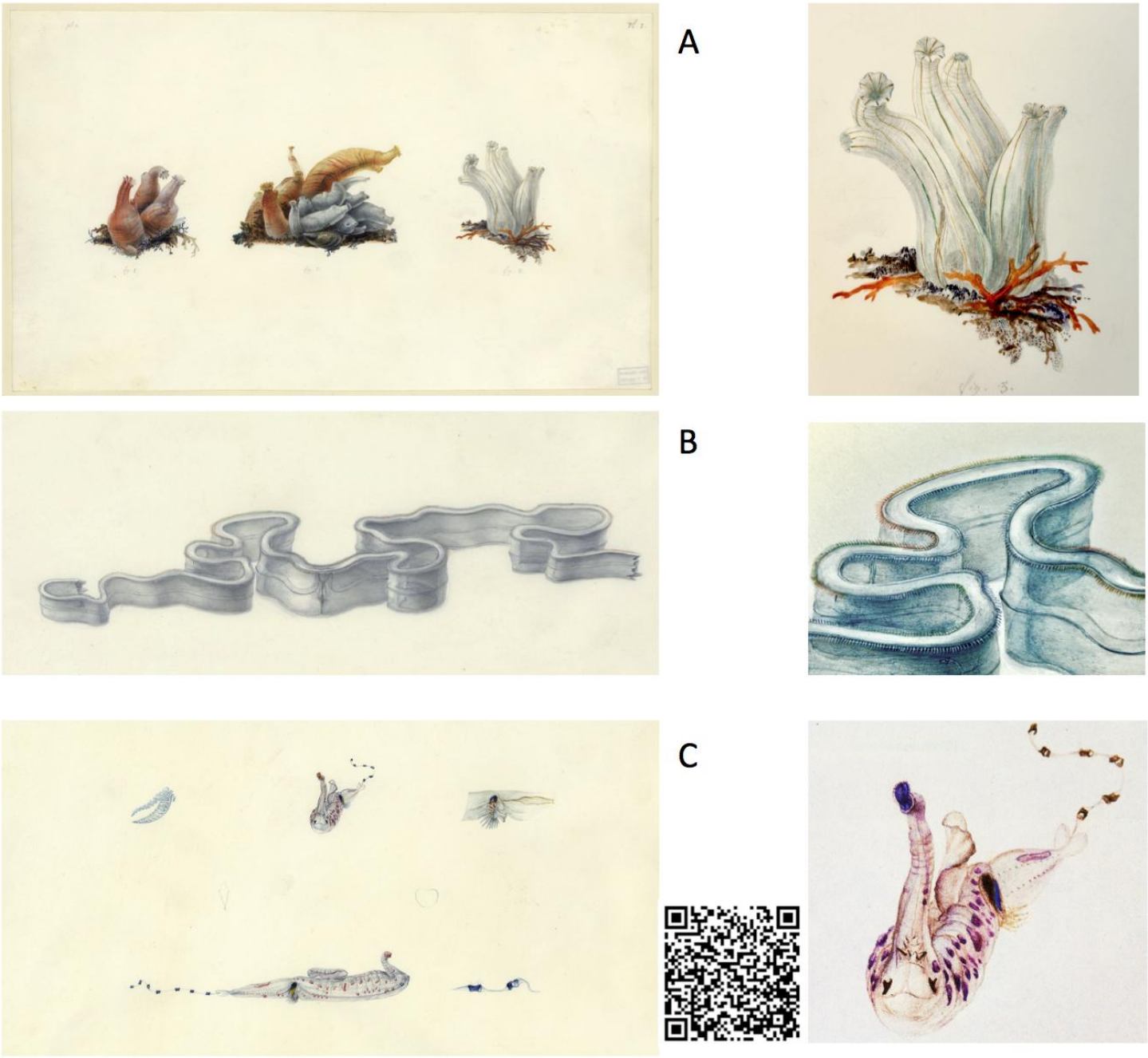

Fig. 4. *Alexandre Lesueur's watercolours on vellum of the marine fauna of Nice*
A - Ciones (Ciona intestinalis), ascidians measuring a few centimeters.
Inv. MHNH 75017, Size of work 24.4x40.8 cm
B - Belt of Venus (Cestus veneris), a ctenophore that can measure up to 80 cm.
Inv. MHNH 67 050, Size of work: 28.0x43.2 cm
C -Firoles (Pterotrachea sp.), planktonic gastropod mollusks belonging to the heteropods. They measure a few centimeters. Inv. MHNH 72010, Size of work: 29.8x43.9

These works are kept at the Natural History Museum of Le Havre (MHNH).
QR code: These and other works can be seenas part of a video interview with MHNH curator Gabrielle Baglione.

Barla, Vérany, Fossat: a new generation completes the biodiversity inventory

Antoine Risso's impetus to study the biodiversity of local flora and fauna was amplified by a new generation of naturalists from Nice. Jean Baptiste Vérany - 23 years younger than Risso, like Risso, was a pharmacist and botanist. He briefly ran the family pharmacy, helped Professor Franco Bonelli build collections for Turin's Natural History Museum, and guided visitors and tourists interested in local flora and fauna. Vérany developed a passion for molluscs, particularly cephalopods. In 1851, he published a monograph whose delicately colored and transparent chromolithographs are considered works of art (Verany 1851, 1862, Dolan 2022a). Vérany's collections formed the basis of the Musée Municipal de la Ville de Nice created in the old town in 1846. Ten years later, under the impetus of another Jean Baptiste, the naturalist Jean Baptiste Barla, a new more ambitious museum was born : the Muséum d'Histoire Naturelle de la Ville de Nice.

Jean Baptiste Barla was from a family which came in Nice from Piedmont and had made their fortune trading in cod liver oil and hemp. He learned botany from his uncle, studied, played the violin, traveled and met naturalists. Barla developed a passion for the region's flora, especially orchids, as well as fish and mushrooms, whose diversity is exceptional in the mountainous back country of Nice (Trimbach 1996). Barla was assisted in his task by a virtuoso gouache and watercolor artist, Vincent Fossat (Defaÿ 1998, Dolan 2022b). As Barla was himself an accomplished artist, it is sometimes difficult to distinguish between Fossat and Barla's paintings. From 1851 onwards, Barla was able to live on his income, since he inherited a substantial fortune from his grandfather. Barla employed Fossat as a painter for 3 to 5 francs a day from 1853 until his death in 1891.

Fossat, born Del Fossat, was the seventh of twelve children in a family that had come to Nice from the Imperia region in the 16th century. Orphaned at the age of 13, with little education, Fossat made a living from various day jobs - fisherman, gardener, coachman, servant. He began to paint Nice and the surrounding area on commission, sometimes under assumed names. Fossat's artistic career took on a new dimension with the naturalistic works he produced for Barla, and also for Vérany. These included thousands of watercolors and gouaches of plants, fish and mushrooms. In 1855, they also published a number of portraits of marine invertebrates, sea urchins, starfish and brittle stars (Figure 5).

Barla and Fossat's best known works are the painted cast/models of mushrooms and cardboard filled, then gouache imprints of fish - the exsiccata - which constitute a kind of fish herbarium (Barla 1892). The painted mushrooms and the 1,500 cardboard fish imprints are a treasure trove preserved at the Muséum d'Histoire Naturelle de la Ville de Nice, a center of intense naturalist activity in the 19th century (Chamagne-Rollier & Defaÿ 2013).

Financed by Barla and supervised by Vérany, the Museum was created in 1865 and directed by Barla. Barla transferred to the City of Nice the imposing building he had built at his own expense. This fine institution regularly exhibits its marvellous collections of works by Risso, Prêtre, Verany, Barla and Fossat and their successors. The Museum has recently entered a new phase: the digitization, restoration and genetic exploration of its conserved works. It also organizes cycles of scholarly conferences paying tribute to its glorious past.

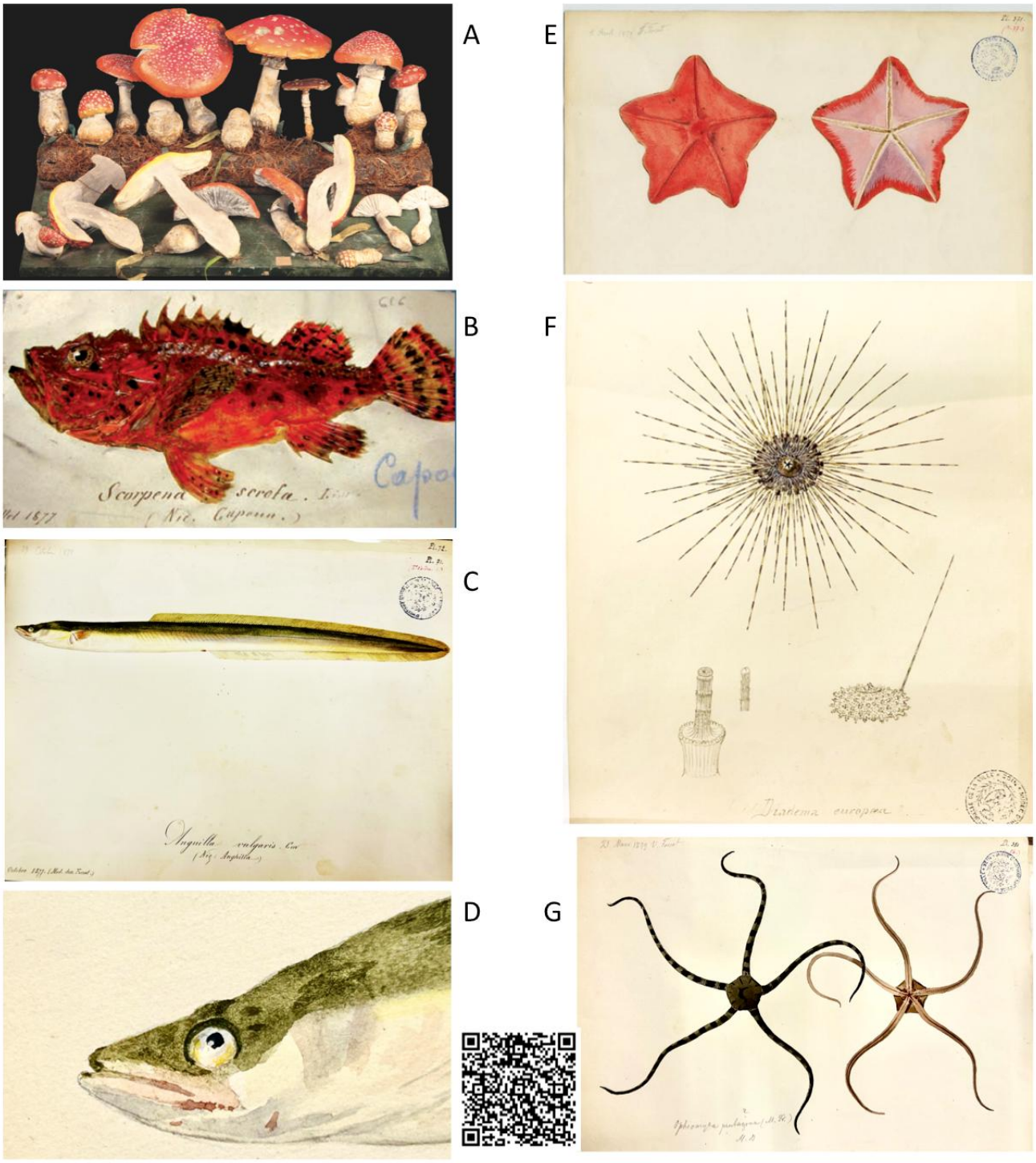

Fig 5. *Moulded and painted works by Jean Baptiste Barla and Vincent Fossat*
A - Painted cast/models of mushrooms (Amanita muscaria), photo @Jean Marc Alpesse
B - Exsiccata (fish skin stretched over cardboard and repainted) of a red scorpion fish (Scorpena scrofa or Capoun in Niçois)
C, D - Eel (Anguila vulgaris, Anghilla in Niçois), watercolor (close-up) by Fossat. Inventory no. 2005.0.730; 71 (plate no.) POP platform, French Ministry of Culture
E - Starfish (Palimpus membranaceus), watercolor by Fossat. Inventory no. 2005.0.1016; 371 (plate no.) POP platform, French Ministry of Culture
F - deep sea urchin (Diadema europea), watercolor by Fossat. Inventory number 2005.0.1011 ;371 (plate no.), POP platform, French Ministry of Culture
G - brittle stars (Ophiomyta pentagona), watercolor by Fossat, size 27.0x 35.2 cm. Inventory no. 2005.0.1025; 380 (plate no.) POP platform, French Ministry of Culture
QR code: gives access to John Dolan's illustrated article on Vincent Fossat (Dolan 2022b)

1850: Visiting foreign scientists and beginnings of the marine station in Villefranche

Our understanding of the principles of life and evolution was revolutionized in the 19th century. From the 1830s onwards, Theodor Schwann, Matthias Schleiden and their microscopist colleagues developed the foundations of a cell theory. It states that animals, plants and all living things are made up of cells that reproduce by division (Sardet 2023). In the 1850s, the identification of natural selection as the driving force behind evolution by Charles Darwin and Alfred Russel Wallace revealed that organisms evolve and are linked by common ancestors. Naturalists, zoologists and botanists began to compare the anatomy and physiology of the organs, tissues, gametes and embryos of animals and plants, as well as unicellular eukaryotes (the type of cells which have a nucleus) known as protists (Jessus & Laudet 2020). Leading figures such as Henri Lacaze-Duthier (Jessus & al. 2021) and Anton Dohrn (Groeben 2020) set up major marine stations (Roscoff in 1872, Naples in 1874) in addition to those already in existence (Concarneau 1859, Arcachon, 1863) or considered such as Messina where Dohrn worked in 1868 before he set up the Naples station. These marine stations gave researchers access to the great diversity of marine flora and fauna.

A new era dawned with the visits to Nice of German and Swiss teachers in the 1850s. One particularly important visitor was Johannes Müller - an influential professor in Berlin and mentor to a whole new generation of cell biologists (Müller 1843). Like his colleague Rudolf Leuckart, a professor in Giessen (Germany), Müller traveled the coasts of Europe with his students, observing marine creatures through the microscopes they carried with them.

Aided by his friend Verany, Rudolf Leuckart stayed in Nice in 1853 to study marine invertebrates - worms, jellyfish and crustaceans. Then, in 1856, Müller and his family visited Nice joined by Swiss biologist Albert Kolliker and students, including Ernst Haeckel, who was 22 years old at the time. They collected plankton in the bay of Villefranche sur Mer, describing and drawing protists and gelatinous organisms (Dolan 2019). In 1864, shortly after the death of his young wife, Haeckel returned to Villefranche for a few months. He produced his first "art and science" drawings of jellyfish and radiolarians (Figure 6). By the end of the 19th century, Haeckel was a celebrated scientist, artist and philosopher, spreading the theory of evolution throughout Europe with his elder compatriot Carl Vogt, one of the most influential biologists of his time (Vogt 1848). After studying medicine in Germany and France, Vogt first drew attention to the phenomenon of programmed cell death in 1842. He stayed in Nice and Villefranche in 1851 - 52 and published extraordinary descriptions and representations of siphonophores in his monograph entitled "Recherches sur les animaux inférieurs de la Méditerranée" (Vogt 1853). Vogt was also a political figure. Nicknamed "the revolutionary scientist" for his socialist ideas and causes, Vogt took refuge in Switzerland. In the early 1850s, he became a professor at the University of Geneva, where he later served as rector.

Praising the merits of plankton in the bay of Villefranche-sur-Mer in 1876, Vogt was the first to advocate the necessary creation of a "marine station" in Villefranche like those already existing elsewhere (Vogt 1876). A few years later, two young biologists - Jules Barrois, from Lille, and Hermann Fol, a zoologist from Geneva inspired by Vogt - set up their first laboratory in Villefranche sur Mer (Anon. 2010, 2024, Dolan 2024).

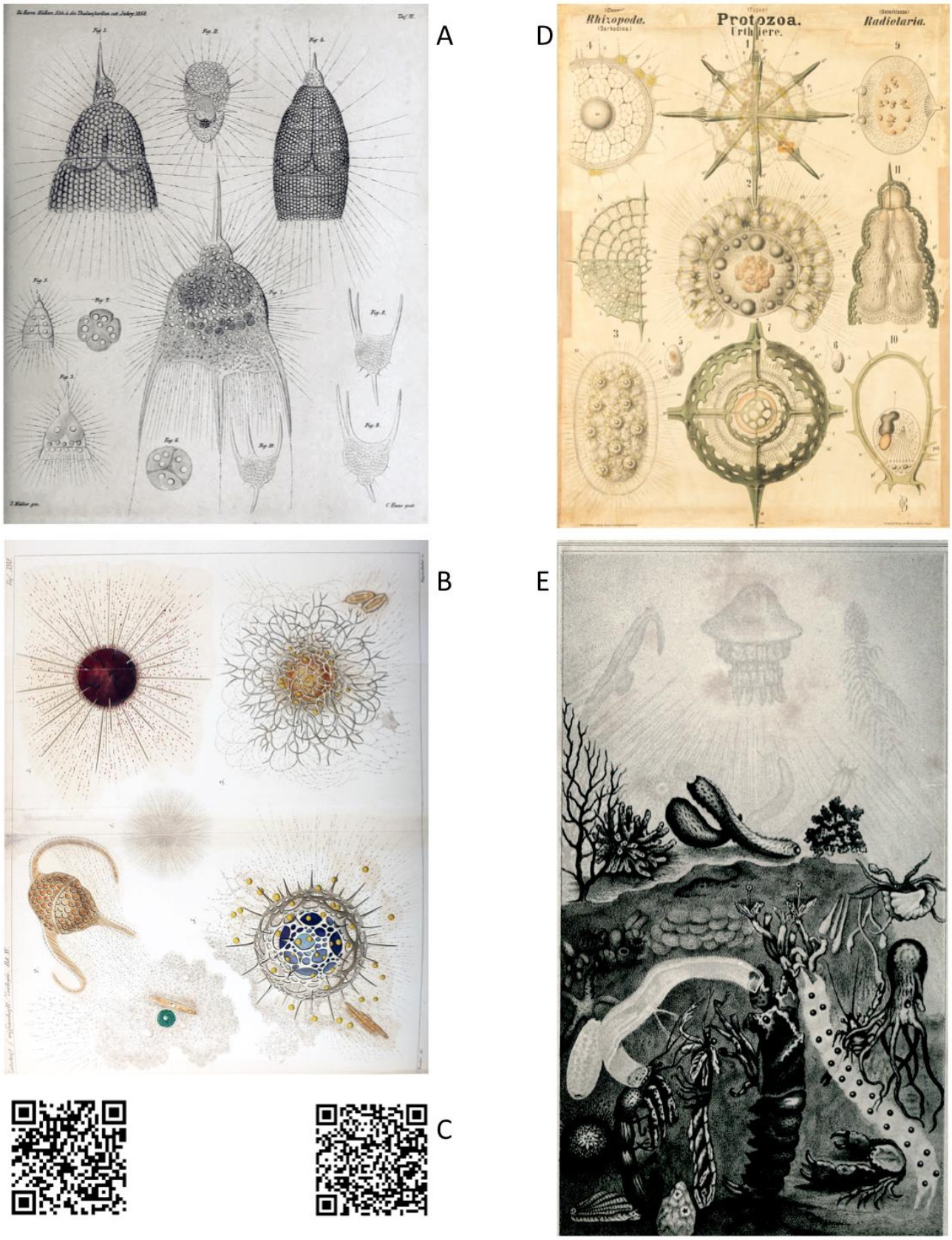

Fig 6. *Plankton works by Johannes Müller, Rudolf Leuckart, Ernst Haeckel and Carl Vogt*
A - Radiolarians discovered in Nice and Villefranche by Müller in 1856
B - Radiolarians observed in Nice and Villefranche in 1864, published by Haeckel (Dolan 2019)
C - QR codes: access to the Aquaparadox website (John Dolan, IMEV)
Left: Species discovered in Villefranche (Dolan 2014). Right: Leuckart poster (Dolan 2023c)
D - Radiolarians, wall poster 29 by Leuckart. Drawing by Otto Bütschli, University of Vienna
E - Drawing of marine fauna by Vogt for his book "Ocean und Mittelmeer (Vogt 1848)"

1880: Fol and Barrois first, then Korotneff - birth of the Villefranche marine station

Five years after Vogt wished for a marine laboratory to be set up in Villefranche sur mer, Jules Barrois, a young PhD from Lille University, and Swiss zoologist Hermann Fol granted this wish. Fol was certainly inspired by his mentor Vogt. In 1878 Fol became Vogt's colleague as a professor at the University of Geneva. Six years earlier, Fol had already spent several months in Nice to take care of his health, while collecting and observing planktonic organisms – mainly appendicularians and pteropods (Dolan 2024).Barrois was only 30 years old when he set up his first laboratory with Fol. We don't know why Barrois was originally attracted to the Nice region, but he seems to have arrived as early as 1879 (Fokin 2008). Barrois had written his thesis on the development of bryozoans and nemerteans at the University of Lille and at the Wimereux marine station created in 1774 (Barrois 1877). In Villefranche, Barrois mainly studied metamorphosis in several species of echinoderms.

Hermann Fol was a brilliant character with a reputation for being quarrelsome (Dolan 2024, Mahé & Sardet 2009). Born in 1845 in the Paris region into a family of Suiss bankers, Fol was sent at an early age to study in Geneva with Edouard Claparède, a zoologist famous for his work on protists and invertebrates. He was also a pupil of Müller and became a colleague and friend of Haeckel. Claparède encouraged Fol to study medicine with Haeckel in Jena, and in 1869 Fol defended his medical thesis working in Zurich and Berlin. The thesis concerned the anatomy and development of ctenophores, considered the most ancestral planktonic animals (Sardet 2013, 2023, Dolan 2024).

When Fol returned to the Nice region in 1879, he was 36 years old. He had already made a major discovery, being the first to describe and illustrate the penetration of spermatozoa into oocytes during fertilization (Fol 1878, Buscaglia & Duboule 2002). Fol made his discoveries in Messina in the 1870s using gametes from starfish, sea urchins and chaetognates. In 1878, he transferred his laboratory from Messina to Villefranche. In extensive correspondence with his other mentor, Henri Lacaze-Duthier, creator and director of the Roscoff and Banyuls marine stations, Fol mentioned the presence in 1879 of other young researchers on the Côte d'Azur as well as a visit from Vogt(Jessus & Laudet 2022). From 1881 onwards, Fol commuted between the Villefranche-sur-Mer laboratory and Geneva, where he taught embryology and carried out various activities - photography, monitoring microbial contamination of drinking water, creation of a scientific journal, etc. (Dolan 2024). Based on his research in Villefranche, Fol published articles on ciliates (tintinnids) and the curious rhizopod protist *Sticholonche zanclea* (Fol 1883). His pioneering work was followed by research carried out over a century later in Villefranche sur Mer (see companion article Sardet 2025 / 2 Modern era: 1970 to 2024).

In 1881-82, Barrois and Fol, encouraged by Charles Darwin and Henri de Lacaze-Duthier, set up the first laboratory in Villefranche sur mer on the site of the former 18th century galley slave prison in the port of Villefranche (port de la Darse : Anon 2010, 2024). Barrois and Fol first occupied a tower in the « lazaretto » (quarantine building) with equipment provided by Fol. Later Barrois and Fol set up the Laboratoire de Zoologie Marine – under the aegis of the Ecole Pratique des Hautes Études – in the larger galley slave prison which also served as a hospital. Fol and Barrois welcomed numerous colleagues: some forty visitors and their research topics are listed year by year from 1881 to 1889 (Barrois & Fol 81-89). One of the visitors, the Russian zoologist Alexis Korotneff, also dreamed of establishing a laboratory in the same building, but under the aegis of the Russian tsarist empire. The Russian navy had for a time docked in the bay of Villefranche and used the premises as a coal depot.

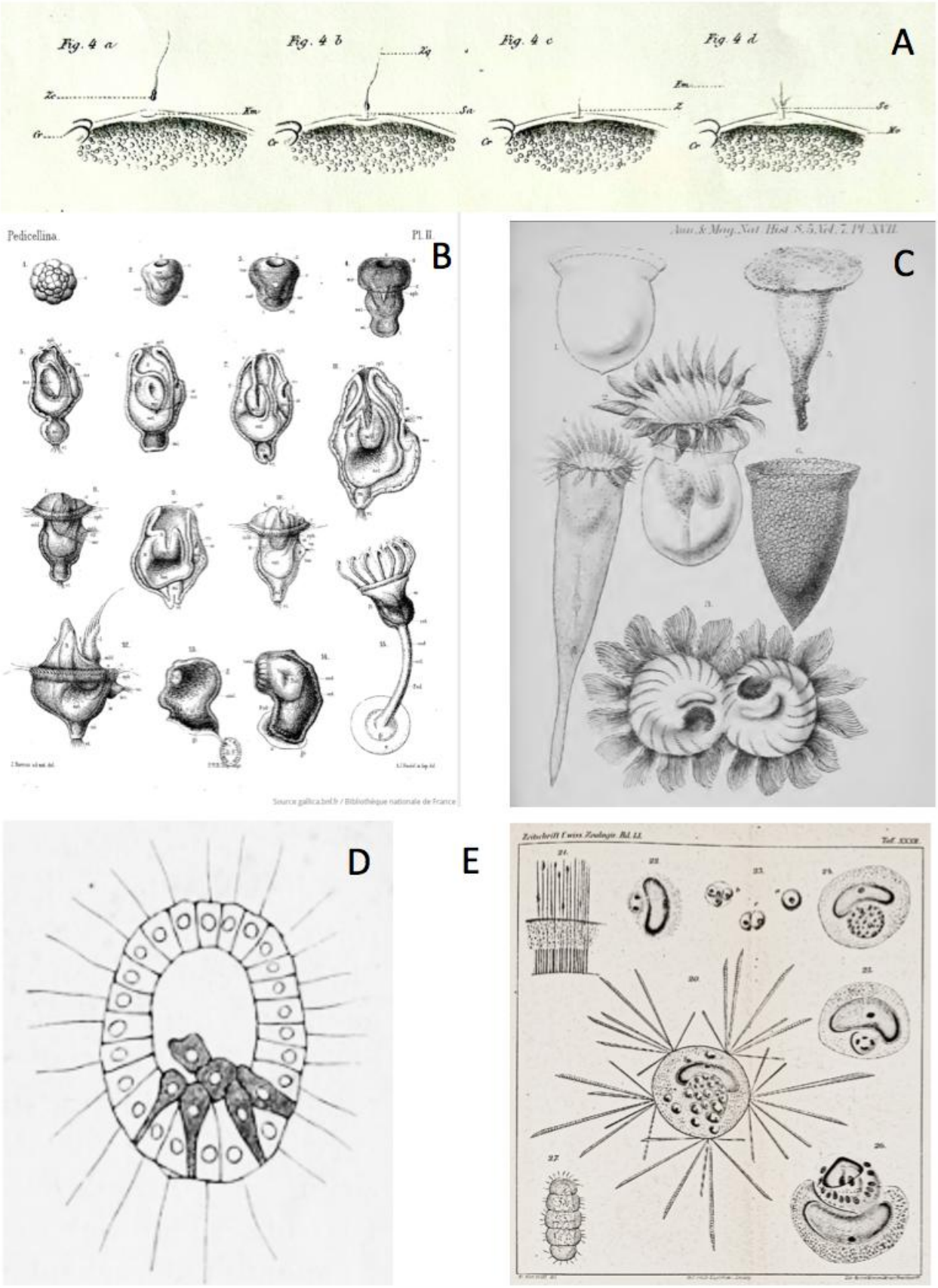

Fig. 7. *Works by Hermann Fol, Jules Barrois, Alexis Korotneff and Elie Metchnikoff*
A – Fol's drawings of sperm penetrating into the oocyte (Fol 1878)
B – Barrois's drawings of the development of the briozoan Pedicellina sp. for his thesis
C – Fol's drawings of tintinnid ciliates in their lorica (see Dolan 2024)
D – Metchnikof's drawing of gastrulation in a jellyfish (Metschnikoff 1886)
E – Korotneff's drawings of the protist Sticholonche zanclea and its intracellular parasites

Two visitors to the Villefranche marine station – Elie Metchnikoff and Alexandre Kowalevski – are famous for their scientific contributions. In 1886, the Russian zoologist Elie Metchnikoff was welcomed to the Villefranche station where he described the formation of the gastrula in jellyfish. His work that would be extended 150 years later at the marine station (see companion article, Sardet 2025). For his research into the mechanisms of immunity, Metchnikoff shared the 1908 Nobel Prize for Medicine with Paul Erlich. The other famous Russian visitor – Kowalevski – is considered the father of evolutionary embryology. In particular, he demonstrated that ascidians are chordates, and as such they were the ancestors of vertebrates. He also demonstarted that all animals undergo a gastrulation phase during embryogenesis (Kowalevsky 1866, Jessus & Laudet 2024). He had already visited the Nice region in 1878 - 79, and was welcomed at the Villefranche marine station in 1882 to study embryogenesis and gastrulation in chitons (molluscs, see visitor lists: Barrois & Fol 1881-1889).

Curiously, Korotneff only appears as one of the visitors in the Barrois and Fol lists from 1882 onwards, although he was probably on site before that. In any case, in 1884, Korotneff founded the « Station Russe de Zoologie » with the support of the Russian government's Ministry of the Navy, which had the use and responsability of the galley slave building which was no longer needed by the Russian war fleet. It was dubbed la " Maison Russe" by the locals (Anon. 2010, 2024, Trégouboff 1983). Korotneff, who had studied zoology in Moscow, was appointed professor in Kiev in 1886. A frequent traveler, he was only present in Villefranche from time to time. He was assisted on site by Michael Davidoff, who succeeded Korotneff in 1915. At the marine station, Korotneff studied the embryology of salps and ascidians. He was also interested in cnidarians and the protist *Sticholonche*, about which Fol had already published (Figure 7, Fol 1883, Korotneff 1891).

Within the Maison Russe, relations between Barrois and Fol on the one hand, and Korotneff on the other were cordial at first, but deteriorated after Korotneff's absence. Korotneff obtained the right to occupy the premises from the French government (a Russian ally) and Fol and Barrois were expelled from the building by the police in 1887 (Trégouboff 1983).

Russian influence and the Villefranche sur Mer marine station

The marine station occupied a large, 70 meter-long building originally constructed in 1769, to serve as a prison/hospital for convicts, and prisoners of war (Figure 8, Anon 2020). It became known as la « Maison Russe » in the mid-19th century at the time of the establishment of a Russian colony in Nice (Braconnot et al. 2004). In 1856, the Treaty of Paris ended the Crimean War, during which France, England and the Kingdom of Piedmont-Sardinia (to which the County of Nice belonged at the time) clashed with Tsarist Russia. In 1856, and again in 1859, the Empress Alexandra Feodorovna, widow of Tsar Nicholas 1er, landed in Villefranche and spent several months in Nice. She met the King of Sardinia, who facilitated negotiations for the galley slave building to become the « Maison Russe ». The building served as a coal depot for the Russian navy, which cruised the Mediterranean and had been based in the bay of Villefranche since the 1770s. The presence of this military base and the empress and her court attracted a Russian colony of over 150 wealthy Russian families to Nice. They built sumptuous villas and an imposing Orthodox church. In 1860, the county of Nice and Savoie became part of France, but the « Maison Russe », although owned by the French state, continued to be used by the Russian navy, until it was banned from the Mediterranean in 1878 by the United Kingdom, France and the Austrian-Hungarian empire at the Congress of Nations in Berlin.

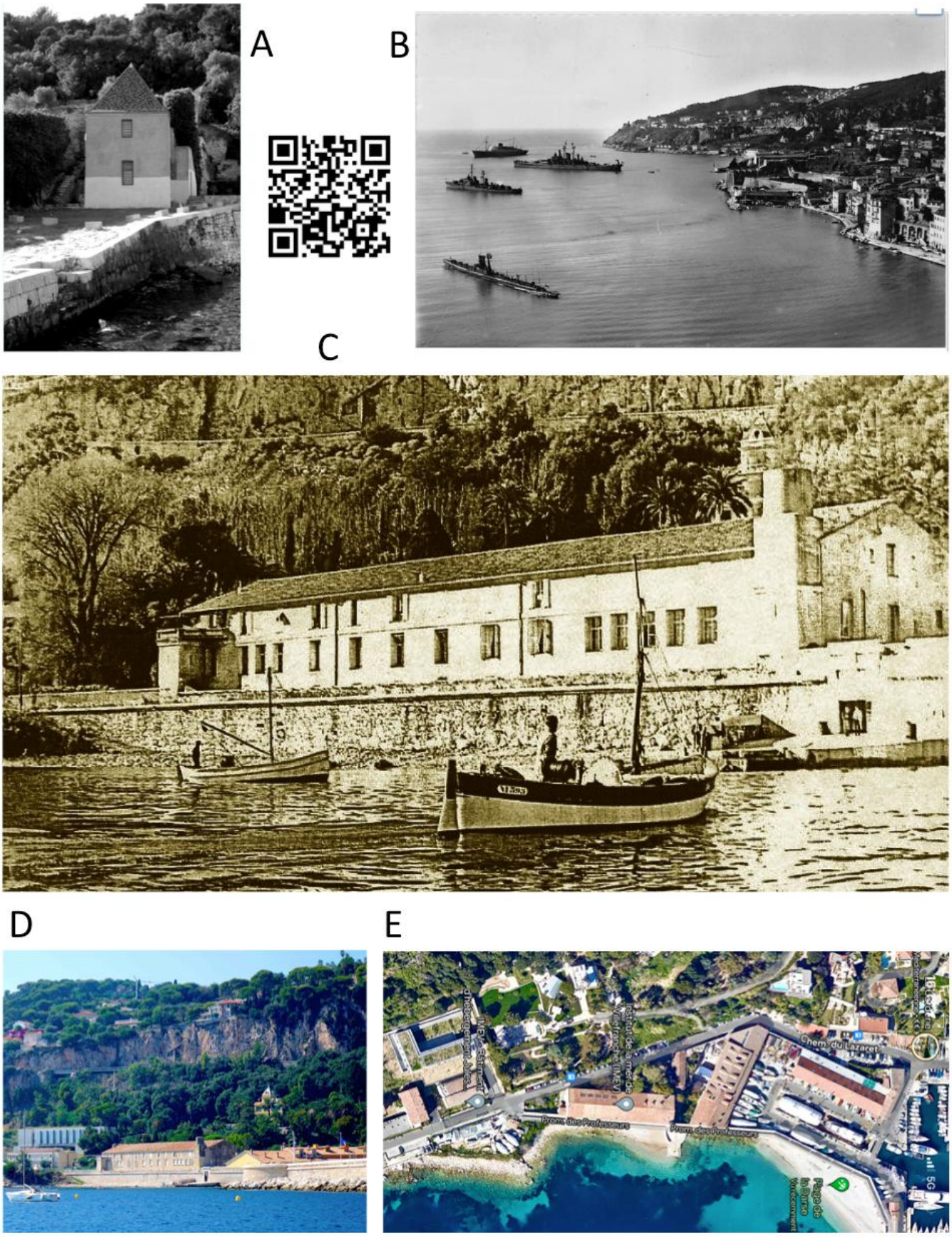

Fig 8. *The Marine Station of Villefranche sur Mer*
A - The lazaret tower in which Fol and Barrois set up their first laboratory in 1880
B - Villefranche Bay was home to navies from the 18th century to the 20th century
C - Villefranche sur Mer zoological station and collecting boats in the 20th century
D, E - Institut de la mer de Villefranche (IMEV) on the port de la Darse
QR code: website (IMEV : Institut de la Mer de Villefranche) (Anon. 2010, 2020).

The galley slave building remained at the disposal of the Russians biologists for a while even after the Bolshevik revolution. Finally, in 1931, the marine station known as la « Station Zoologique » was officially attached to the French Ministry of Education and placed under the authority of the director of the Arago laboratory (the marine station of Banyuls).

The director of the Villefranche sur Mer's « Station Zoologique » was the Russian planktonologist Grégoire Trégouboff, successor of Michael Davidoff. Trégouboff directed the institution until 1956 under the aegis of the University of Paris (Anon. 2010, 2024, Trégouboff 1983, Dolan 2014). Surprisingly, the Station Russe de Zoologie somehow continued to exist until 1930 with a few Russian scientists and a modest Villefranchois staff. After the Bolshevik revolution of 1917, despite financial difficulties, the marine station continued to exist thanks to the support of members of Russian Academy of Sciences in exile. Support also came from members of the large Russian aristocracy and intelligentsia fleeing the Bolshevik revolution to live in Europe and the Côte d'Azur(Trégouboff 1983).

From the naturalist painters of Nice to the visiting impressionist painters

In the 19th century, some twenty well-known painters made a living from their art in the Nice region, painting urban, village scenes, seascapes and landscapes, in watercolor, gouache and oil in modest formats (Giraudy 1998). The people of Nice are familiar with some of these painters: Roassal (1781 - 1850), Fricero (1807 - 1870), Carlone (1812-1873),Trachel (1820-1872), Fossat (1822-1891), Costa (1833-1921), Comba (1834-1872), Mossa (1844-1926), Besset (1861 -1902), since many of the city's main streets, avenues or boulevards are named after them. In connection with our story, two painters, Vincent Fossat and Joseph Fricero, deserve special mention. Fossat, worked with the naturalist Barla and Vérany. He also also painted landscapes and the work of the fishermen he frequented. He made precise paintings of fish as soon as boats arrived (Defaÿ 1998, Dolan 2022). The other painter, Joseph Fricero was a traveler and adventurer born into a large family of winemakers and merchants in the Nice region (Giraudy 1998). A childhood friend of Guiseppe Garibaldi, Fricero began drawing in his youth and studied under the Roman painter Christian Borghese at the Barberi School of Drawing in Nice. What connects Fricero to our story are his extensive travel in Italy, Sicily, Spain, Tunisia, Turkey, Sweden, etc. and his encounters with foreigners. That led him to Saint Petersburg, where he befriended Prince Gagarin, a member of the Russian aristocracy. Adopted as a drawing teacher by the family of Tsar Nicholas 1er, Fricero married Josephine, known as Yousia, the Tsar's natural daughter. Protégés of Empress Alexandra Feodorovna, who stayed in Nice with her court in 1856 and 1858 after the death of Nicholas 1er, Yousia and her husband Joseph Fricero and 4 children, were close to the Russian sovereigns. Fricero and his family settled in Nice on a vast estate where he painted Nice tirelessly. His production slowed down in the 1860s, when Nice became French, and the wintering population became less fond of his academic paintings. Fricero died in 1870 in relative isolation. His paintings were rediscovered and appreciated from the 1920s onwards.

The 1860s-70s were a time of great change in painting, epitomized by the first Impressionist exhibition at the Atelier Nadar in Paris in 1874. The first Impressionist painter on the Côte d'Azur was Berthe Morisot who started painting in Nice and its harbor in 1882 (Lindskog & Mathieu, 2024, Anon. 2024b). She confided to her sister Edma, "I don't understand why this country doesn't serve as a great studio for all the young landscape painters. In addition to its beauty, you enjoy a fixity in time and good weather that allows for more conscientious research" (Giraudy 1998, Anon. 2024b).

Joseph Fricero - Villefranche sur Mer

Berthe Morisot - Port de Nice

Eugène Boudin, Villefranche sur Mer

Fig 9. *Impressionist artists paint in Nice and Villefranche sur Mer*

In early 1888, Claude Monet (1840-1926), inspired by the stories of Guy de Maupassant, set sail for the Côte d'Azur, which he had visited 4 years earlier, and stayed in Antibes to paint. He attracted his friend Auguste Renoir (1841-1919), who settled permanently in Cagnes in 1902. Another impressionist from Le Havre, Eugène Boudin (1824 - 1898), came to paint the bay of Villefranche, crowded with warships, every summer from 1892 until his death (Giraudy 1998). Other famous painters followed - Chagall, Soutine, Modigliani, Matisse, Picasso and others - who appreciated the beauty, light and climate of the region.

Thanks

Many thanks to John Dolan and Elisabeth Christian for encouraging me to write this article. John generously shared his knowledge of the subject and the characters, and provided invaluable help with the history, illustration and referencing. Gabrielle Baglione of the Muséum d'Histoire Naturelle in Le Havre and Joëlle Defaÿ of the Muséum d'Histoire Naturelle de la Ville de Nice were wonderful hosts, allowing me access to and reproduction of works by Lesueur et Péron, Risso, Vérany, Barla and Fossat. I would like to thank them for commenting on and correcting my first manuscript. Catherine Jessus also shared her knowledge of the characters and provided insightful comments.

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