

The Querulous Hermann Fol (1845-1892): His Scientific Work, Art, and Inventions

Le Querelleur Hermann Fol (1845-1892) : Ses travaux Scientifiques, son Art et ses Inventions

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ABSTRACT. Hermann Fol was a very accomplished Swiss naturalist of the late 19th century, but today is largely forgotten. He was a student of the notable biologists Édouard Claparède and Ernst Haeckel, and like them, specialized in the study of marine organisms. Fol is known only among embryologists for his description of fertilization in echinoderms. In reality, his work ranged well beyond such studies to encompass diverse taxa of the marine plankton, illustrated with remarkable scientific artwork, and included designing various scientific devices. Fol worked on human embryology, light penetration in seawater, methods of reducing microbial contamination of drinking water, and development of a rabies vaccine. His career was marked by a long series of disputes with contemporary naturalists and was relatively short, ending at age 47 with a mysterious disappearance. Here I provide a review of his contentious life, his scientific work, his scientific art, his scientific inventions, and his role in establishing Villefranche-sur-Mer as a center of marine science. The life and work of Hermann Fol is shown to be an example of the very wide-ranging activities of 19th century naturalists, and the apparent dangers of an over-sized ego.

KEYWORDS. history of science, scientific illustration, microscopy, marine stations.

Introduction

Few people today know of the 19th century Swiss naturalist Hermann Fol. He mainly worked on fertilization, embryology, and the development of marine invertebrates such as molluscs, starfish, and various gelatinous taxa. Fol is given a place in reviews of the history of fertilization (e.g., Ernst 2011). However, it will be shown here that Fol's activities ranged well beyond developmental biology of invertebrates. His studies encompassed human embryology, bacteriology, protistology, the penetration of light in seawater, and even rabies. Many of his works were magnificently illustrated. Fol developed new methods and devices in microscopy, bacteriology, photography, and oceanography. In his time, his work was very well known, extensively translated, and re-published throughout Europe and in North America. Fol was also known as a difficult character. His publications often contained accusations of others misappropriating priority credit for his observations, or pointing out supposed faults, and otherwise maligning his contemporaries. The obscurity of Fol today is likely due in part to his difficult character resulting in a relative dearth of friends and students despite his fame, and the fact that he worked on a wide variety of topics. In addition his career was cut short with a mysterious disappearance in 1892 when he was only 47 years old.

Here an attempt is made to shine a light on the accomplishments of the difficult but productive Herman Fol. To begin, a biographical account is provided including his role in the establishment of a marine laboratory in Villefranche-sur-Mer, often minimized or overlooked, and an account of his mysterious disappearance at sea, based on reports in the popular press. The biography is followed by a chronological presentation of some of his wide-ranging scientific work with examples of his striking scientific artwork, as well as examples of Fol's diverse disputes and disagreements with his contemporaries. A complete account of Fol's scientific work, with a definitive bibliography, was provided by Bedot (1895). Lastly, the relatively unknown aspects of Fol's work, his diverse inventions and methods developments, are reviewed.

As alluded to above, the first and most complete account of Fol's life and works was by Maurice Bedot, a long-time colleague of Fol (Bedot 1894) with subsequent accounts all largely based on it, either directly or indirectly. These include a long article on Fol in an Italian newspaper (Anon. 1894), the Hermann Fol entry in the *Dictionary of Scientific Biography* (Allen 1981), and in the *Encyclopedia of Life* (Dröscher 2015), the two accounts of Fol in articles focused on Henri Lacaze-Duthiers (Petit & Théorides 1972; Jessus & Laudet 2022), and a short memorial note on Fol (Beuss 1945). The biographical sketch given here is also based on Bedot (1894) except where otherwise noted. Figure one shows the known likenesses of Hermann Fol from the age of 19 to a statue in the University of Genève, donated to the university by Fol's widow in 1905.

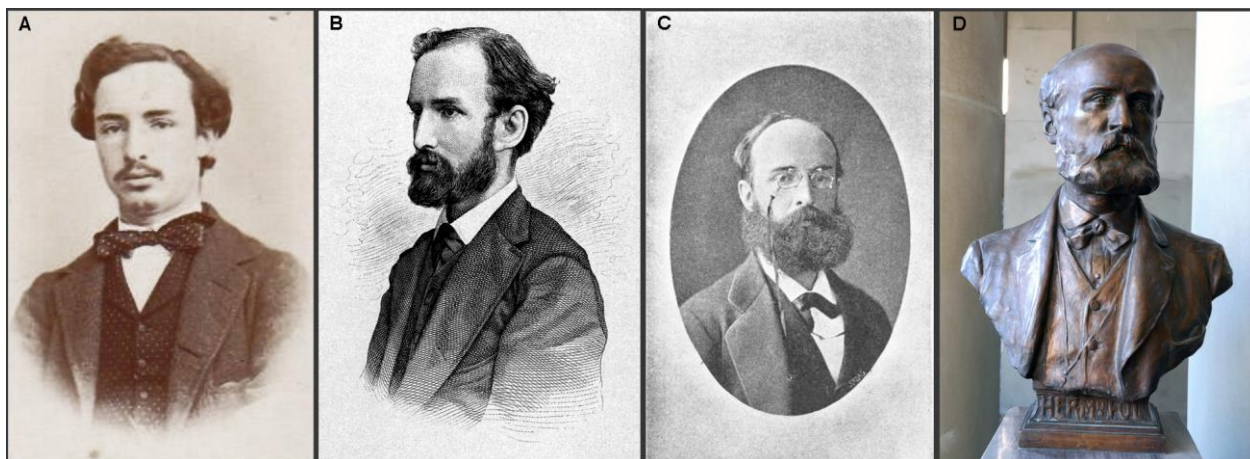


Figure 1. The only existing likenesses of Hermann Fol: **A.** a portrait at age 19 from the author's personal collection. **B.** an engraving dating from ca. 1880, held by the Bibliothèque de Genève. **C.** a portrait ca. 1890 at about age 45 from Bedot 1894. **D.** image of the bust of Fol donated to the University of Geneva in 1905 by his widow, image source <https://commons.wikimedia.org/w/index.php?title=File:UniBastions-1er-buste-Fol-1.jpg&oldid=657602900>.

Hermann Fol was born July 23rd, 1845, into a wealthy family of bankers from Geneva, at the time living in St. Mandé, near Paris. He was sent to Geneva to secondary school and there also took classes in natural history at the Academy of Sciences. At the Academy, Fol became a student of Édouard Claparède, the renowned Swiss naturalist (Hollier & Hollier 2023). Claparède was an expert on protists and invertebrates. He had studied medicine under Johannes Müller in Berlin along with Ernst Haeckel, and was a life-long friend of Haeckel (Dolan 2021). Claparède encouraged Fol to pursue studies in Jena under Haeckel, then a Professor of Medicine. At the time, subjects such as zoology and physiology were taught as part of the curriculum leading to a medical degree.

Fol began his studies in Jena in 1864 (Fol 1869). In 1866, Haeckel chose him, as his most intelligent student, to participate in a zoological expedition to the Canary Islands (Richard 2008). Haeckel's group included another of his students, Nikolai Miklucho, and the zoologist Richard Greeff. Haeckel came to regret the choice of Fol. The group encountered great difficulties in obtaining housing, and supplies, as well as adapting to the isolated community in Lanzerote (Sarmiento Pérez & Batista Rodriguez 2015). In their crowded housing, Haeckel found Fol to be intolerably arrogant (Richard 2008). When they left the Canaries, Haeckel deposited his two students on the Atlantic coast of Morocco to make their own way home, while he and Greeff sailed on to Europe.

Fol subsequently pursued his medical studies, not in Jena, but in multiple institutions, perhaps an early sign of his difficulties with inter-personal relationships. He studied in Heidelberg in 1867, then in Zurich in 1868, and finally in Berlin late 1868 (Fol 1869). In August of 1869 he passed the examinations for his medical degree in Berlin. His doctoral dissertation was on the anatomy and evolutionary history of some ctenophores (Fol 1869), and was based on his studies of the gelatinous

organisms of the marine plankton carried out while he was in the Canaries with Haeckel. Nonetheless, Fol dedicated his dissertation, not to Haeckel but Carl Gegenbauer, another Professor at Jena!

His medical degree in hand, Fol returned to Geneva, but not to practice medicine. As a wealthy man, he had no need to earn an income. Fol continued working on the anatomy and developmental biology of marine invertebrates. Following Haeckel's footsteps who had made his landmark study of radiolarians in Messina (Haeckel 1862), Fol installed a personal laboratory in Messina. Beginning in the winter of 1869, and until 1877, he made extended stays in Messina working on various taxa of the marine plankton. In 1873 he married Emma Bourrit and they soon had a daughter, Alice, who would become, like her father, an expert on marine molluscs (Franc 1972).

By 1877, Fol had become a well-known figure in zoology. He had published widely on the anatomy and development of molluscs and was offered a chair of Embryology in Naples that he refused, preferring to stay in Geneva. With aid of Carl Vogt, Fol was appointed "*Professeur Ordinaire*" of embryology at the University of Geneva in 1878 (Tregobouff 1983). The part-time, low paid, position involved teaching only in the summer, giving him liberty to pursue his research for most of the year. Fol then transferred his site of fieldwork from Messina to Villefranche-sur-Mer, near Nice (France), a site much more easily accessible from Geneva. Villefranche-sur-Mer was where Haeckel had worked a few years before, and before Haeckel, Carl Vogt. Vogt had actually singled out Villefranche-sur-Mer (hereon Villefranche) as an ideal site for a new marine laboratory in an article on laboratories of marine zoology (Vogt 1876); he had made extensive studies of the marine plankton in Villefranche over many years (e.g. Vogt 1853, 1854). Seemingly taking up Vogt's suggestion, Fol announced the establishment of his private laboratory in Villefranche, open to all who wanted to study marine zoology, in 1879 (Wartman 1879), and that year signed his first publication as from Villefranche (Fol 1879). In a letter to Henri de Lacaze-Duthiers from Villefranche, Fol gave his address as *Observatoire Zoologique* (Archival Resources, Hermann Fol letters to Henri de Lacaze-Duthiers, p. 149).

Fol's private laboratory was short-lived. In 1882 Jules Barrois, of the University of Lille, established a modest, but the first officially sanctioned, scientific institution in Villefranche-sur-Mer, the *Laboratoire de Zoologie Marine de Villefranche*. It was established as a field station of the *École Pratique des Hautes Études* in Paris, under the Ministry of Education (Barrois 1882). Fol donated all the material and instruments he had in his private laboratory and began working in Barrois's laboratory. Fol took advantage of the fact that the laboratory was accorded the use of French naval vessels to run experiments, such as those estimating the depth of the penetration of light in the sea (e.g., Fol & Sarrasin 1885).

In 1884 Fol created a new scientific journal, the first Swiss journal devoted to zoology, *Recueil Zoologique Suisse* and its appearance was greeted with lavish compliments (Anon. 1884). 1886 was an eventful year for Fol. He either lost, or resigned, from his position at the University of Geneva for reasons that are unclear today. However, it was a quite public affair. Fol had his resignation letter published in the main newspaper of Geneva, the *Journal de Genève* (Fol 1886a). He claimed he had no choice but to resign as other faculty members attempted to deny him the privileges and rights due him. Although Fol remained quite active in the scientific circles of Geneva, lecturing and writing, it was also in 1886 that he acquired his final official affiliation, not in Geneva but in Villefranche. He became *Directeur Adjoint* of the *Laboratoire de Zoologie Marine de Villefranche* (Barrois & Fol 1886), and he bought a 39-ton steamer yacht, christened the *Amphiaster*, and had it equipped for deep water sampling work for the laboratory. The changes in Fol's official affiliations through the years from none to the University of Geneva, and finally the Villefranche laboratory, were reflected in his letterheads (Fig. 2).

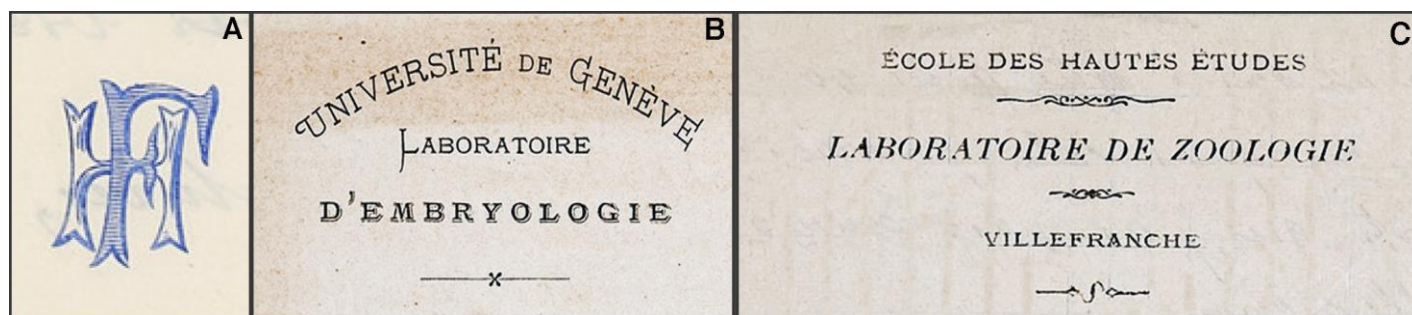


Figure 2. The three letterheads of Fol from his letters to Henri de Lacaze-Duthiers from 1874 to 1898 (see Archival resources: Hermann Fol Letters): **A.** Simple initials until 1877. **B.** Fol's embryology laboratory in University of Geneva from 1877 to 1886. **C.** the Villefranche laboratory.

Despite Fol's material contributions to the *Laboratoire de Zoologie Marine de Villefranche*, his official position in the laboratory, and his considerable international stature, Fol (along with Barrois), was soon to be ousted due to the actions of Alexis Korotneff. The following is based on the account given by Tregobouff (1983). Alexis Korotneff was a Professor of the University of Kiev, and familiar with Villefranche. He had visited in 1881 and had then the idea to establish a Russian zoological laboratory in the large empty buildings known at the time as the "*Maison Russe*". It had been leased to the Russian Navy, for use as coal depot, but had been unused for decades, and was now within the grounds of a French military base, a garrison of the *Chasseurs Alpins*. Establishing a Russian laboratory in France within military grounds was possibly problematic. At the suggestion of Carl Vogt, Korotneff persuaded Barrois to support the establishment of a Franco-Russian laboratory in the *Maison Russe* housing both the French zoological laboratory of Villefranche and a Russian Zoological Station.

Interestingly, in Barrois's official annual report to the *École Pratique des Hautes Études* on the activities of the laboratory for 1884, he stated that the Russian government had ceded the "*Maison Russe*" to the *Laboratoire de Zoologie Marine de Villefranche*, and he made no mention of a Russian zoological station (Barrois 1884). The annual reports from 1886 to 1889 also contain no mentions of a Russian zoological station, and Koronteff is simply listed among visiting scientists (Barrois 1886; Barrois & Fol 1887, 1888). In reports of subsequent years, no mention is made of Korotneff (Barrois & Fol 1889; Barrois 1892; Anon. 1893).

According to Tregobouff's account of the brief period when Fol, Barrois and Korotneff together occupied the *Maison Russe*, Fol's abrasive personality played a large role in the falling out of Fol, Barrois and Korotneff. However, there were apparently no innocents among the three. In reality the property was, in the view of French law, still legitimately leased to the Russian government, and its representative was the legal tenant. In January of 1888, Korotneff had both Fol and Barrois evicted from the *Maison Russe* that then became the *Station Zoologique Russe de Villefranche-sur-Mer* under Korotneff's direction. It remained an independent facility with a Russian director until the 1930's when it was nationalized by the French government and put under the direction of the *Laboratoire Arago* in Banyuls of the *Université de Paris*. Today, it is part of the *Institut de la Mer de Villefranche*, a field station of *Sorbonne Université*.

Following his eviction from the Villefranche laboratory, Fol planned to create a new laboratory in Nice that would include a public aquarium. According to a contemporary press report, the city of Nice had agreed to supply land near the port (Anon. 1890). However, the project was never realized as Hermann Fol mysteriously disappeared, apparently at sea, in 1892. No references exist to any official report concerning Fol's disappearance. The only information available today is from press reports published in 1892.

According to the press reports, on or about March 3, Fol embarked on a recently purchased vessel, the *Aster*, from Le Havre, on the Channel coast of France, to travel to Nice where his sampling gear was stored. He was then to set out to investigate deep-water sponges throughout the Mediterranean

Sea. Although he was not employed in any fashion by the government, Fol's expedition was sanctioned by the *Ministère de l'Instruction Publique* (Ministry of Education). On March 24, about three weeks after departure, was the last confirmed contact with the *Aster*. It was in Bénodet, on the coast of Brittany, a distance of only about 500 km from Le Havre by sea. A crew member asked a lighthouse keeper where water could be obtained. He also stated that the ship's master was not on board, and the crew was taking the ship to the Mediterranean port of Marseille. Informed that only by filling buckets could they have water, the *Aster* apparently left Bénodet without obtaining any water. Subsequently, there were only reports of possible sightings of the *Aster*, near Coruna (Spain), and off the coast of Africa. There were no reports of contacts with the vessel, nor any members of the crew. Surprisingly, it was not until nearly four months after the departure from Le Havre, that an alarm was raised by Fol's wife and his brother-in-law concerning a lack of contact with Fol or any news of the *Aster*.

The press reports which began appearing in late June of 1892 were remarkably widespread, often contradictory and one, singularly odd. The first published were short notices that began to appear June 26, stating that the *Ministère de l'Instruction Publique*, (or in some notices, the *Ministère de la Marine*) were conducting an investigation into the disappearance of Fol and the *Aster* (Fig. 3A). The 'investigation', of which there is no trace, was likely provoked by inquiries from Fol's wife and his brother-in-law. The notices appeared in both Paris and provincial newspapers. On July 1st, advertisements by Fol's wife appeared in the *London Times* and the *New York Herald* (Fig 3B). She stated her fear that an act of 'baratry' (*i.e.*, theft of the *Aster* by the crew) had been committed based on the fact that in the last contact with a crew member, in Bénodet, an unidentified crew member had reportedly said that the owner was no longer on board, and that crew were to sail on their own to the Mediterranean Sea. Simultaneously, her brother, C. Bourrit, sent a letter to the Paris newspaper *La Petite Presse*, stating that his own investigations in Le Havre and Bénodet led him to believe that the crew, too rapidly chosen by Fol in his view, had done away with Fol. Bourrit's letter, in part (e.g. Fig. 3C) or whole, was very widely reprinted in newspapers throughout France, in Switzerland, and even in Algeria. No new information came to light until late August when a brief undocumented report, said to have originated from the *Venice Gazette*, stated that the *Aster* had been captured, and the crew massacred by pirates off the coast of Algeria (Fig. 3D). The notice was widely reprinted. Apparently no attempts were made to verify the singular report; it was often printed with the notice "*nous reproduisons cette information à titre de curiosité*" (we reproduce this information as a curiosity).

NOUVELLES MARITIMES ET COLONIALES A

Brest, 25 juin.

Le ministère de l'instruction publique fait rechercher le yacht à vapeur *Aster*, appartenant à M. Hermann Foll, sujet suisse, naturalisé français, disparu depuis trois mois.

M. Foll, savant professeur, était chargé d'une mission dans la Méditerranée par le ministre. Le yacht *Aster* mouilla à Brest le 19 mars; le 22 mars à Bénodet, le 27, il fut vu en face de la Corogne.

En outre, un capitaine de la Compagnie péninsulaire prétend avoir vu le yacht sur les côtes d'Afrique quelques jours après. Depuis ce temps, on est sans nouvelles du yacht et du professeur Hermann Foll.

En quittant Brest, l'*Aster* devait aller dans la Méditerranée et faire escale à Nice avant de commencer sa mission.

MISSING. B

VERY IMPORTANT NOTICE.

DR. HERMANN FOLL,

Who has been entrusted with a scientific mission to the coasts of Tunis and Dalmatia by the French Government, has, for the purpose of carrying out this mission, purchased and equipped the *Aster*, a 70-ton yacht, on which he embarked at Havre on March 13, for Nice, where he was to have taken on board the instruments needed for his scientific work.

Dr. Hermann Foll's family have received a communication from him, dated at Brest March 17, but since then they have heard nothing from him. According to private advice, the *Aster* was seen off Corunna (La Corogne), Spain. Since then no news has been received of her. M. Foll was to have touched at Vigo for his mail, but the *Aster* has not entered that port. A vessel of the Compagnie Péninsulaire Havrais sighted the *Aster* in Algerian waters in May.

Investigations made at Bénodet (Finistère) by a member of the family on June 24 have led to the following strange discovery.

Before the *Aster* left that port on the morning of March 23, a member of the crew said to one of the lighthouse keepers that the owner of the yacht was no longer on board. According to this statement, it unfortunately seems probable that an act of baratry was committed at Bénodet during the night of March 24-25.

If among the innumerable readers of the "New York Herald" there is any one who can give any news concerning the *Aster*, which continues to navigate without her owner, such news will be gratefully received by MME. HERMANN FOLL, à CHOUGNY, près VANDŒUVRES, Canton de Genève, Suisse.

The *Aster*, whose name may have been changed, was a screw steam yacht, 27 mètres long, and schooner-rigged. Her hull was black above and red below the waterline, and she carried the French flag.

La Disparition de l' « Aster » C

Nous avons déjà parlé à nos lecteurs du yacht *Aster*, monté par M. Hermann Foll, un savant distingué que le Ministre de l'Instruction publique avait chargé d'une mission sur les côtes de la Tunisie et de la Dalmatie.

M. Hermann Foll avait quitté le Havre vers le 5 mars; on avait signalé son passage à Brest vers le 21 mars et, depuis lors, on n'avait eu aucune nouvelle de lui. M. C. Bourit, beau-frère de M. Foll, suppose que son parent a dû être assassiné par son équipage.

En effet, l'explorateur avait l'intention de conduire son yacht à Nice, son port d'attache. Etant un peu pressé par le temps, il a constitué son équipage un peu au hasard, et il est possible que celui-ci se soit débarrassé du propriétaire du navire.

A l'appui de cette assertion, M. Bourit raconte que, en quittant Brest, M. Foll avait écrit à sa femme de lui envoyer son courrier à Vigo. Or, le domestique que M. Foll avait emmené avec lui écrivait à une personne de la domesticité, en date de Bénodet (Finistère), le 24 mars. A Bénodet, le maître de port a déclaré que le seul membre de l'équipage qui eût communiqué avec la terre lui avait affirmé qu'il n'y avait pas de matres à bord... et que l'équipage était chargé de conduire le navire dans la Méditerranée.

Depuis, on sait que le 11 avril l'*Aster* a passé à la Corogne, ce qui prouve que le bateau a marché non pas à la vapeur, mais à la voile.

Il est évident que les réflexions faites par M. Bourit méritent qu'on s'y arrête. Il est fort possible qu'un terrible drame se soit passé en pleine mer et qu'à l'heure actuelle, les coupables cherchent à mettre à l'abri, sur un coin inconnu, le fruit de leur crime.

PIRATES DANS LA MÉDITERRANÉE D

Venise, 27 août.

La Gazette de Venise publie des renseignements d'après lesquels il serait hors de doute, aujourd'hui, que le yacht *Aster*, sur lequel se trouvait le professeur Hermann Foll, et qui a disparu depuis le 17 mars, a été capturé par des pirates au large d'Alger; son équipage aurait été massacré.

Figure 3. The disappearance of Herman Fol and the *Aster* in the popular press in 1892: **A.** The first reports were brief notices that inquiries were being made by the Ministry of Education concerning Fol's yacht having gone missing for 3 months; the example from *Le Rappel* on June 27 (Anon. 1892a) includes a not uncommon misspelling of Fol's name in the press as Foll. **B.** The advertisement, placed by Fol's wife in the *Herald*, contained the allegation that the crew had stolen the *Aster* as a crew member had told an official in Bénodet that the owner of the *Aster* was no longer on board (Fol, E. 1892). **C.** The allegation was repeated in a letter by Fol's brother-in-law that was widely reprinted in early July; the example shown is from the *La Petite Parisien* on July 2nd (Anon. 1892b). **D.** The last wide-spread press accounts were reprints of the brief and unverified report that the *Aster* had been captured by pirates and the crew massacred; the example shown is from *Le XIX Siecle* on the 29th of August (Anon. 1892c).

There was but one article in the press that questioned the very feasibility of Fol's voyage from Le Havre to Nice with the *Aster*. The article was based on a first hand account of the vessel, and the crew, by an anonymous experienced sailor. He claimed to know well both the vessel, and the planned route. According to the sailor, the *Aster*, originally named the *Berta*, was a 25-meter steam-powered, propeller driven vessel. It was designed and built to navigate rivers primarily by steam power, and according to the sailor, it was particularly unsuited to sail in the open ocean. Furthermore, he stated that in any vessel, crossing the Bay of Biscay in the month of March was difficult, but with a vessel such as the *Aster*, was simply "a colossal imprudence" (Anon. 1892d). One other report provided important information concerning the vessel's range. An account of a coal merchant who delivered coal to the *Aster* while it was in Le Havre, stated that the coal storage space of the *Aster* would allow it to steam no further than Brest, indicating a maximum range of about 400 Km under steam power (Anon. 1892e). Thus, for a long distance voyage, re-fueling stops every few days would be necessary. Recall that the last contact with the *Aster* was in Bénodet near Brest in Brittany a few days after the boat was last re-fueled in Brest. A singularly odd press account, entitled the *Le vaisseau fantôme* (the ghost ship), appeared on the first page of the Paris newspaper *Le Public* on June 29th, relatively early in the mystery. It was authored by Victor de Cottens, a drama critic and playwright, who claimed to have been a friend of Fol. Supposedly, a bottle with a message, unsigned but described as clearly by Fol, had been found near a drifting vessel off the west coast of Africa. In the message, the writer states that he avoided a near mutiny of his crew and they had visited a wonderful country (Cotten 1892). No

details are given as to how or when de Cottens acquired the message, perhaps indicating that his story was not to be taken seriously!

Obviously, many questions remain concerning Fol's disappearance. One could begin with why Fol bought a boat in Le Havre, rather than in Nice or Marseille, thereby avoiding the time and expense involved in sailing from Le Havre to Nice. Then there is the basis of the allegations of foul play by the crew based on the statement of a crew member informing an official in Bénodet that the owner of the *Aster* was longer on board. Why would the fact that Fol was not on board necessarily indicate foul play by the crew? Why would a crew member volunteer such supposedly incriminating information? Was there an assumption that Fol would likely have antagonized the crew? It is also worth noting that none of the families of the crew ever heard from any of them, and the families vigorously denied any criminal tendencies among the crew members (Anon 1892f). Nonetheless, the assumption that the crew of the *Aster* did away with Fol was common (e.g. Béthuys 1895) and has been long-lived (e.g., Grassé 1982). It appears most probable that the *Aster* was lost at sea along with the crew in attempting to cross the Gulf of Gascogne. What will likely never be known is whether or not Fol was on board!

The Scientific Work and Scientific Art of Hermann Fol

The first scientific work of Hermann Fol was his doctoral dissertation "*Anatomie und Entwicklungsgeschichte einiger Rippenquallen*" (The Anatomy and Evolutionary History of Some Ctenophores). Despite its title, it was on the embryology of ctenophores, a taxon of gelatinous marine invertebrates of the plankton. As previously mentioned, it was based on observations Fol made in the Canaries during Haeckel's 1868 expedition. Remarkably, Fol's doctoral study was never published in a scientific journal, and in fact he never returned to studies of ctenophores. However, his dissertation did give a good indication of his future career. Development biology would remain Fol's main focus of research, and this first work, while quite short (12 pages of text), was richly illustrated (3 lithographed plates) as many of his future works would be. A portion of one of the plates, using white on black, from his first work is shown in Fig. 4.

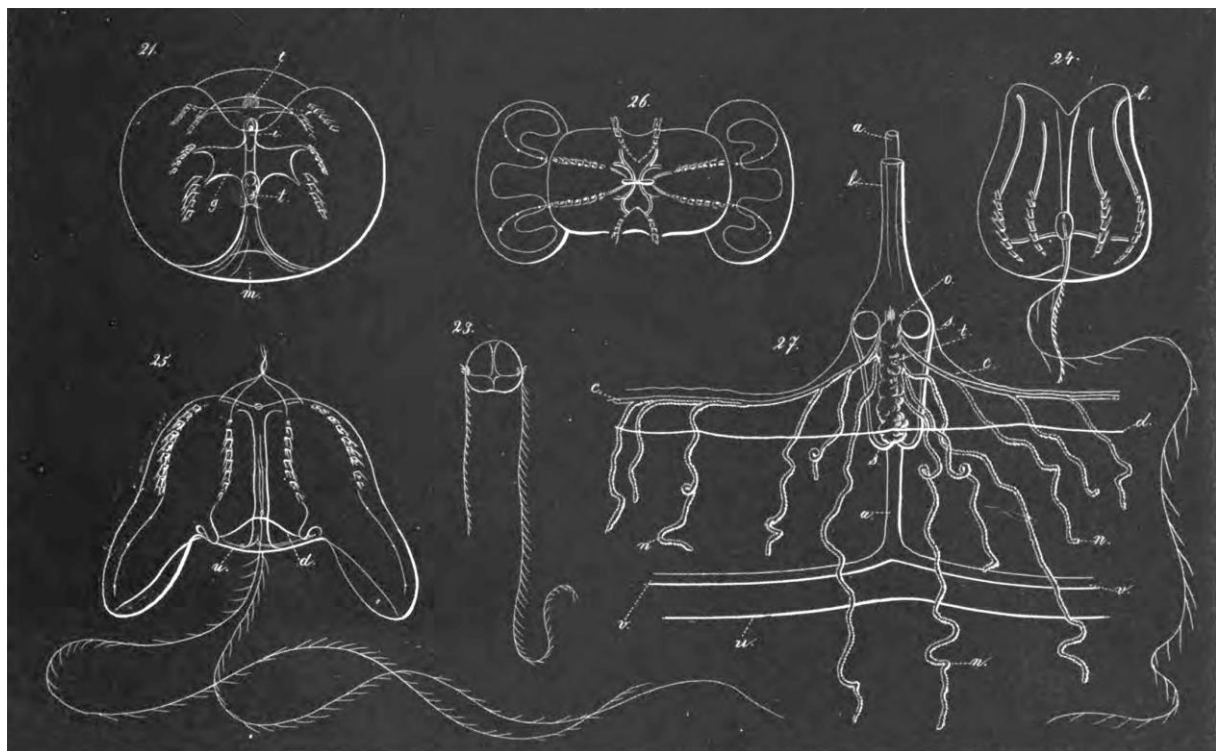


Figure 4. The bottom portion of the first plate in Fol's 1869 dissertation showing different aspects of a four day old embryo of the ctenophore *Eurhamphaea vexilligera*. H. Fol is credited as the artist of the plate and W.A. Meyn as the lithographer.

Following his dissertation, Fol was soon at work on marine invertebrates in Messina. There he first worked on descriptive studies on the anatomy and taxonomy of appendicularians, a taxon of gelatinous marine zooplankton, which yielded his first monographic study "*Etudes sur les appendiculaires du Détroit de Messine*" (Fol 1872). He described nine new species of appendicularians, eight of which are recognized today as valid first descriptions. The illustrations were quite striking (see Fig. 5A). Fol soon returned to studies of development, concerning yet another taxon of gelatinous zooplankton, medusa. He documented and illustrated the development from the egg to feeding larval stage in *Geryonia fungiformis* (fig. 5B), in a German language journal (Fol 1873a). That same year he also published a short summary of his study in French (Fol 1873b). Fol next turned to molluscs with extensive studies on the development of pelagic molluscs. His first reports appeared in the journal of the French Academy of Sciences (Fol 1875a,b) and were translated into English and appeared in the *Annals and Magazine of Natural History* (Fol 1875c,d). These publications were followed by his first large work that appeared in 1875 in the *Archives de Zoologie Experimentale et Générale* (Fol 1875e), focused on the development of the heteropod molluscs of the marine plankton, and it included ten spectacular plates, seven of which were in color (e.g. Fig. 5C). Fol later published a book version of his article and dedicated to his teacher of the Academy of Sciences in Geneva, Édouard Claparède (Fol 1875f). Thus, by the mid-1870's when he was but in his early 30's, Fol, as yet without any academic affiliation, had established himself as a talented developmental biologist. However, by this time he had also established a reputation as a quarrelsome academic with his attacks against his contemporaries.

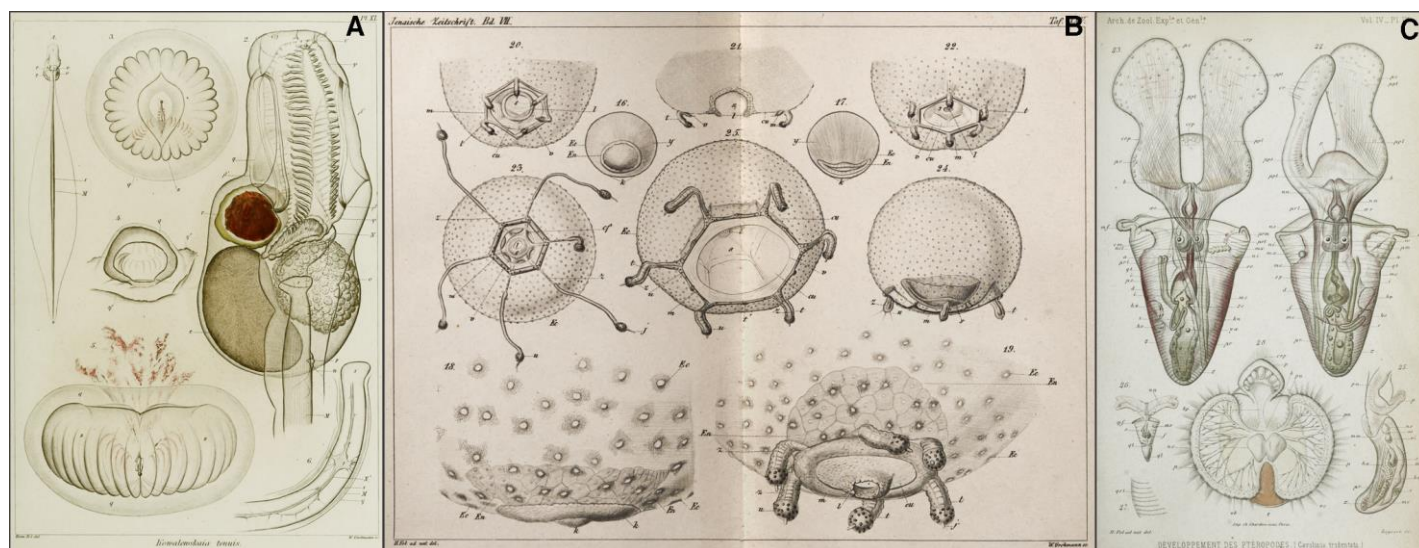


Figure 5. Examples of Fol's illustrations in his publications on marine invertebrates: **A.** from Fol's 1872 study of appendicularians (Fol 1872). Fol is credited as the artist and W. Grohmann as the engraver (Wilhelm Grohman of Berlin). **B.** Plate two from Fol's 1873 study of the development of the medusa *Geryonia fungiformis*. The plate credits H. Fol, ad. nat. (after nature), as the artist and W. Grohmann as the engraver. **C.** Plate IV from Fol's 1875 monograph on the development of the heteropod molluscs (1875e). The plate credits H. Fol, ad. nat. (after nature), as the artist and Lagesse as the engraver.

Fol's first salvo was directed against a summary of his study of the development of the medusa *Geryonia fungiformis* that appeared in the *Journal de Zoologie* (Boulbart 1874). Fol began a short paper, yet again summarizing his results concerning *G. fungiformis* (Fol 1874a), with a sentence stating that the summary in the *Journal de Zoologie* was a singular tissue of absurdities that necessitated a re-publication of his conclusions. Oddly, Fol did not state what in his view was absurd; he simply repeated nearly word for word his previously published digest of the work (Fol 1873b). Next to be subjected to Fol's ire was Alfred Giard. Fol attacked Giard's 1873 study (Giard 1873), charging that he had willfully ignored Fol's priority in attributing a role of an organ in appendicularia in feeding (Fol 1874b). Also in 1874, Fol attacked E. Ray Lankester over a matter of supposed priority in first describing the existence of a shell gland in molluscs. Fol claimed that Lankester learned of the shell gland during visits to Fol's home laboratory in Messina (Fol 1874c). Fol's accusation was hotly

contested by an outraged Lankester who stated that he had once briefly seen Fol (Lankester 1875). Fol replied by claiming that Lankester had apparently forgotten his multiple conversations and visits (Fol 1875g).

Fol's attacks against Giard and Lankester, were typical in that they involved a claim of denied priority of the description of a relatively unimportant detail, and targeted relatively important personalities. In 1874, Giard was a Professor at the University of Lille and he had just founded the *Station Marine de Wimereux*. Jules Barrois, the founder of the *Laboratoire de Zoologie Marine de Villefranche*, was one of his students. Giard would later occupy a chair of Zoology at the Sorbonne, and be elected a member of the Academy of Sciences in Paris (Caullery 1909). In 1874, Lankester was an established scientist and an editor of *Journal of Microscopical Science*, a role he would occupy for nearly fifty years, during which time the journal would become the major English language journal of developmental biology (Bourne 1919). Fol, early on, rather needlessly made enemies of important people.

In 1876 Fol began his studies on fertilization during his stays in Messina, studies that would become his most important contributions. They first appeared in a series of five papers in the journal of the French Academy of Sciences (Fol, 1877a,b,c,d,e). His reports were translated into English (e.g., Fol 1877f) and Italian (e.g., Fol 1877g). In his developmental studies, Fol pointedly took issue with his former teacher Ernst Haeckel's command of Greek. Fol insisted that Haeckel's term for the development, "Ontogeny" was not based on the correct Greek root and should be actually "Henogeny". He made his arguments on the first page of an article he published twice, first in a Swiss journal (Fol 1877h) and again in a French journal (Fol 1877i). Perhaps, needless to say, that Fol's opinion was ignored as the famous dictum of Haeckel, "Ontogeny recapitulates Phylogeny" never became 'Henogeny recapitulates Phylogeny'.

Fol's observations of fertilization contrasted in some details with those of Giard (Giard 1877a). Fol then aggressively countered Giard, claiming that Giard's observations must have been made on abnormally fertilized eggs (Fol 1877d). Once again, Fol's attacks provoked an outraged defense (Giard 1877b). However, Fol actually had the last word as he has long been recognized as the first to have made detailed observations of the process of fertilization in the starfish, describing it as the result of a single sperm cell contributing nuclear material to the ovum (Allen 1959; Ernst 2011; Laubichler and Davidson 2008; Lillie 1916). Fol later published more detailed and illustrated account in a substantial review monograph of nearly 400 pages of text and ten plates (Fol 1878-1879). Fol's now well known illustration, from plate three of his monograph, of a single sperm cell penetrating a cone-shaped structure on the outer membrane of an ovum is shown in Fig. 6. Fol went to considerable trouble with regard to the production of the plates. They are credited to Fol as the artist and Lövendal (Emil Adolf Lövendal) of Copenhagen as the engraver. Fol would later become known for being particular about the production of his plates, preferring to have his plates made by workers chosen by himself, rather than trusting them to the publisher of the journal (Jesus & Laudet 2022).

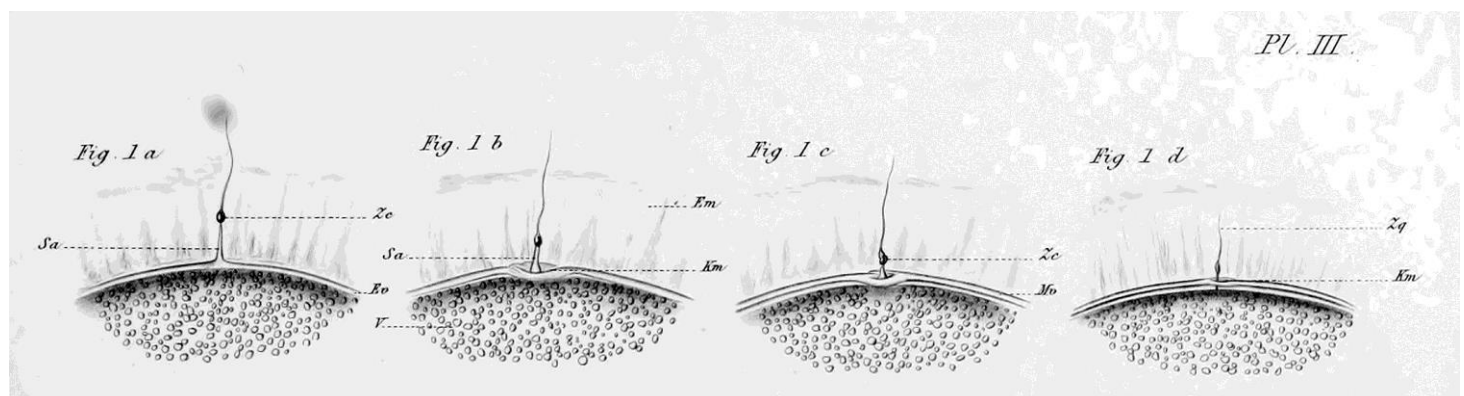


Figure 6. The top panel from plate three of Fol's monograph of 1878-1879 on the fertilization and early development showing the fertilization of a seastar egg. The plate is credited to Fol as the artist and Lövendal (Emil Adolf Lövendal of Copenhagen) as the engraver. Fol's illustrations of fertilization have been called

remarkable (Allen 1959), and have been reproduced in recent years (e.g., Buscaglia & Duboule 2002; Sardet, 2023).

When Fol transferred his private laboratory to Villefranche in 1879, his fieldwork went in new directions. At first, Fol began working on microscopic organisms of the marine plankton, protists, rather than the invertebrates he had studied in Messina. While Fol was an expert microscopist, he previously had shown no interest in microscopic organisms. The protists Fol studied are taxa that can be collected easily with a fine net in shallow waters, and they display eye-catching motility. Planktonic protists were perhaps an object of study by default in his early stays in Villefranche as he apparently did not have access to a boat nor contacts among the local fishermen. His studies concerned tintinnid ciliates (Fol 1881a, 1883a) and the enigmatic rhizopod *Sticholonche zanclea* (Fol 1883b). Fol's articles contained valuable new information on behaviours, details of morphology, and for tintinnid ciliates, descriptions of new species. However, they also contain lengthy critiques of previous studies. The plates of the studies (Fig. 7) illustrated morphological details that were previously undescribed. For the second study of tintinnid ciliates (Fol 1883a) and the article on *S. zanclea* (Fol 1883b), Fol again went to considerable trouble with regard to his plates. He had them produced by the firm of Werner and Winter in Frankfort, the premier lithographers of their time (Goldschmidt 1956). Fol's articles on tintinnid ciliates were also published in English (Anon. 1881; Fol 1881b; 1883c).

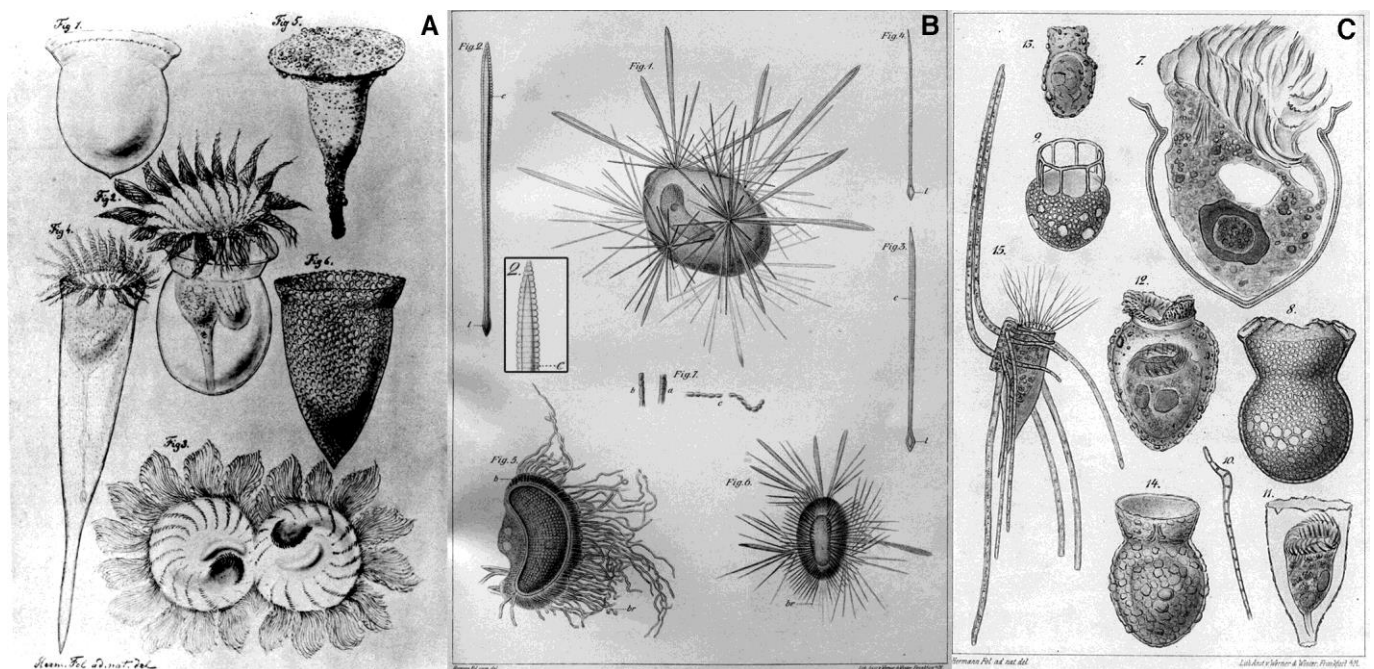


Figure 7. Plates from Fol's studies in Villefranche on protists of the marine plankton, during his early winter stays, 1879 to 1881 when he was working in his private laboratory: **A.** The plate from Fol 1881, showing new species of tintinnid ciliates in their loricae or shells (center and lower left figures) and a pair of conjugating cells, exchanging genetic material (lower right figure). The plate credits Fol as the artist but no engraver or lithographer is given. **B.** One of the plates from Fol's study of the enigmatic rhizopod species *Sticholonche zanclea* (Fol 1883b); he erected an order for it alone declaring it to have no close relatives among known rhizopod taxa and it remains today a species with its own genus and order. The plate credits Fol as the author and as lithographer Werner & Winter of Frankfort. The inset (added) shows the detailed structure of one of the 'oar' spicules, about 5 μm across. **C.** The plate from Fol's study of tintinnid ciliates during the winter of 1881 published in 1883 (Fol 1883a) on systematics, the chemical composition of the lorica, and the descriptions of new species. As in the *Sticholonche* paper, the plate credits Fol as the author, and as lithographer, Werner & Winter of Frankfort. In the three plates the actual sizes of the organisms shown range from about 75 to 200 μm .

Back in Geneva, Fol began working on human embryology. He published his first study on the anatomy of a 3-week-old fetus in a short report to the French Academy of Sciences in late 1883 (Fol 1883d). It was followed by a much more detailed and illustrated reports in the *Revue Médicale de la Suisse Romande* (Fol 1884a) and Fol's new journal *Recueil Zoologique Suisse* (1884b). The plates were, once again, produced by Werner and Winter of Frankfort (Fig. 8A). Fol's next, and last, report on human embryology created a stir. Fol first described the transitory existence of a tail in the human embryo during the 5th and 6th weeks of development during a meeting of the *Société de Physique et d'Histoire Naturelle de Genève* (1885a) and a short version of his report was read before to the French Academy of Sciences, a few days later (Fol 1885b). His findings were widely disseminated (e.g. Anon. 1885a; Minot 1885). Fol did not return to studies of human embryology. However, interestingly, his textbook on histology contained only 1 photomicrograph. It was in the first part of the textbook, published a few years before his disappearance (Fol 1884c). The photomicrograph, an arresting image of a human embryo (Fig. 8B), was in a discussion of the great difficulty of showing detail and the depth of field in photomicrographs.

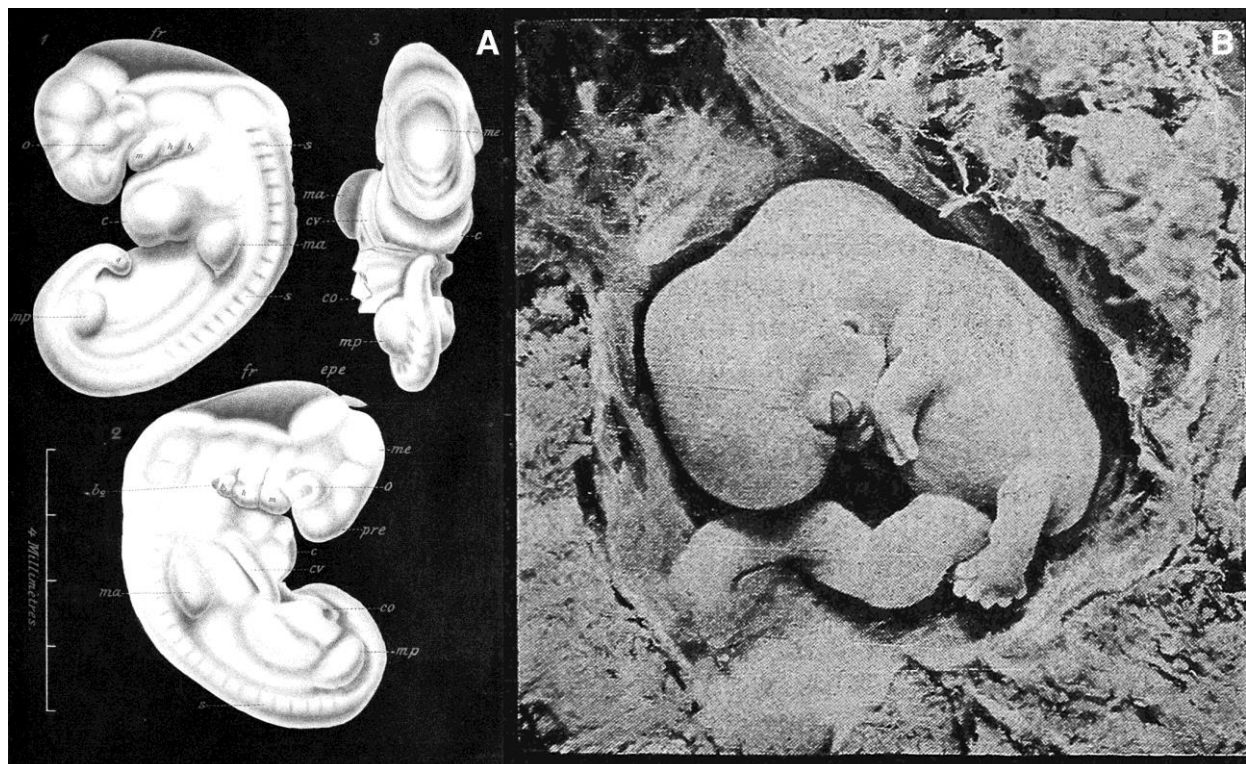


Figure 8. Fol's illustrations of human embryos: **A.** Plate 1 from Fol's 1884 article on the anatomy of a 3-week old fetus (Fol 1884c). The plate credits Fol as the artist and Werner and Winter as lithographers. **B.** Fol's only published photomicrograph, a human embryo, about 21 mm long (about 9 weeks of age), from the first part of Fol's textbook on histology (Fol 1884c).

During this same period in Geneva, Fol became interested in both bacteriology and infectious diseases. He published articles in the popular press on "microbes" (e.g. Fol 1883e, 1884d), some of which were translated and published in the American journal *Science* (e.g. Fol 1884e,f) and he gave lectures (Fig. 9). Fol conducted studies on the 'numbers of living germs' in the drinking water of Geneva (Fol & Dunat 1884), and methods of purifying water (Fol & Dunat 1885). After a visit to Louis Pasteur's laboratory in Paris, Fol turned his attention to the unidentified infectious microbe, the causal agent of canine rabies (Anon. 1886a). Fol's histological studies led him to believe that he might have found an infectious agent (Fol 1885c). Fol attempted to culture the agent and supplied Pasteur with the suspected agent (Fol 1886b,c). Fol's experiments were widely reported upon (e.g., Anon 1886b) and Pasteur himself was inclined to believe (for a time) that Fol had actually isolated the infectious agent (Vignal 1886).

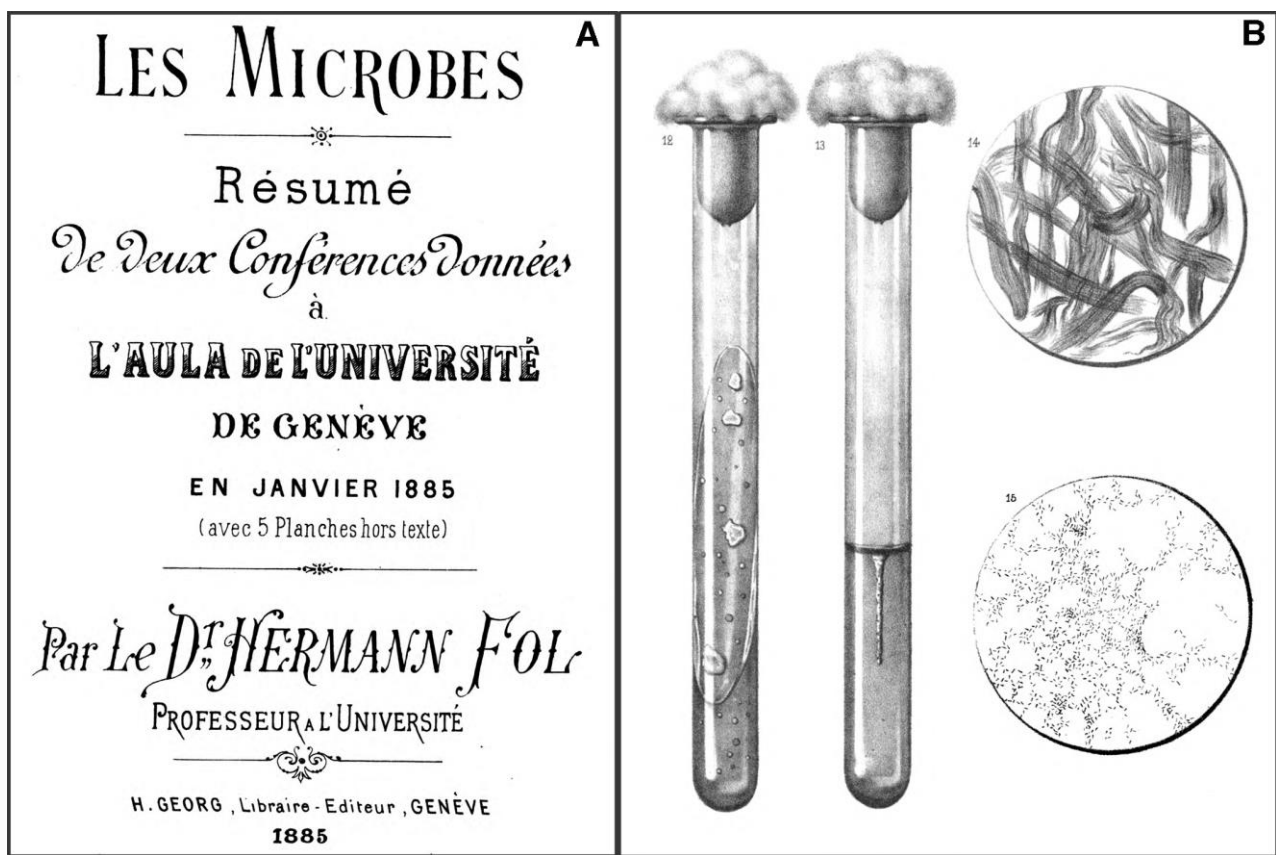


Figure 9. A. The cover and **B.** plate 3 "methods of culture and sterilization" from Fol's 1885 booklet derived from public lectures he gave on "microbes" in January of 1885 (Fol 1885d). Note the use of elaborate Art Nouveau fonts in the cover. The plates are all credited to S. Balicki as artist rather than Fol. It appears to be the only publication by Fol with plates showing drawings not by Fol himself.

Meanwhile, during Fol's stays in Villefranche during these same years, he transferred some fieldwork he had begun with the Swiss engineer Edouard Sarasin in Lake Geneva on the penetration of light into lake water (Fol & Sarasin 1884, 1885a), to studies of seawater. With his integration into Barrois's *Laboratoire de Zoologie Marine de Villefranche*, Fol and Sarasin gained access to the use of French naval vessels to study the penetration of daylight in Mediterranean waters. They used a device that exposed a photographic plate for 10 minutes at a desired depth and found that in the month of March on cloudless day, at midday, light penetration regularly declined with depth to maximum depth of 400 m (Fol & Sarasin 1885b CRAS). Their results were translated into English (Fol & Sarasin 1885c) and reported upon (e.g., Anon. 1885b). In Fol's last Villefranche-based study, Fol and Sarasin examined the penetration of light at different times of day. They found that light was detectable from shortly after dawn until sunset, not just at mid-day, at 300 m depth (Fol & Sarasin 1886). In their article they also needlessly launched an attack against Carl Chun, and once again, a major scientific figure was targeted over a detail.

Chun had reported that light could be detected at 550 m depth near Capri off the coast near Naples (Italy), deeper than the 400 m measurement by Fol and Sarasin, using a similar technique. His results appeared in a brief section in a long (65 pages) article focused on the existence of deep-water fauna, not light in seawater (Chun 1887). Fol and Sarasin claimed that the deeper value reported by Chun was likely an artifact of the device not actually being at 550 m, but a shallower depth. They asserted that the cable was likely at an angle because the Naples boat crew was incapable of correctly manipulating cables. Regardless of any matter of cable angle, oddly overlooked by Fol and Sarasin were quite simple explanations of the differences. Measurements of a parameter in different sites, using different devices would likely yield different figures. Furthermore, Chun's figures were from exposing a photographic plate for 30 minutes rather than the 10 minutes used by Fol and Sarasin. Fol repeated his attack on Chun, at length, in two of his last articles (Fol 1889, 1891a). Fol proclaimed his own priority in measures of light at depth in the sea, actually not denied by Chun, and oddly claimed that Chun had

stated that Fol and Sarasin had copied the design of their devices from others. Chun was at the time a Professor at the University of Königsburg. His 1887 article was dedicated to his father-in-law, Carl Vogt, Fol's former mentor. Chun would later organize and head the Valdivia Deep-Sea Expedition of 1898-1899, the most important post-*Challenger* oceanographic expedition of the 19th century (Dolan 2023).

The Diverse Inventions of Herman Fol

Fol published frequently on inventions of new devices, instruments and methods. With regard to most, his innovations were likely incited by problems he encountered or perceptions of a need to fill. These include a trawl for collecting benthic fauna, designed to function regardless of how it landed on the sea floor (Fig. 10.A.), a portable aquarium (Fol 1879), a portable microscope (Fol 1885e), a chamber for making time-course microscopic observations (fig. 10.D.), and the devices for measuring light penetration in the sea (Fig.10.C.). Fol developed protocols for anesthetizing marine vertebrates to facilitate observations (Fol 1882), and procedures for histological studies (Fol 1883f), understandable, given his considerable work on developmental biology of invertebrates. Fol also published on protocols and equipment needed for sterile transfers of microbial cultures (Fol 1884g), again understandable as he worked for a time on bacteriology. However, with regard to some of his inventions, the motivation appeared to have been simply ideas he had as they are devices that had no relationship to his published work. Examples of this are his design for a manometer to measure great depths in the oceans (Fig. 10.E.). Fol himself never worked on soundings; he was working on the developmental biology of invertebrates in Messina when he first proposed his design in 1874 (Fol 1874). Another is a camera (Fig. 10.B.), designed to take pictures in rapid succession, to capture images of animals in action (Fol 1884h,i,j). Yet another is his plankton net. While Fol never worked on deep-sea plankton, his last 'invention' was the proposal of a new closing plankton net (Fig. 10.F.), closing resembling the net of Albert of Monaco (Monaco 1889), that could be mounted in a depth series to collect plankton in discrete depth strata (Fol 1891). All in all, Fol's inventions characterize an imaginative man, and also one who proposed new devices for endeavors in which he had no apparent experience. Notably, there appear no references attesting to the actual construction of some of his inventions such as the closing net array and camera, nor the use of any of his inventions or protocols, by anyone other than himself. In his papers on new devices and methods, Fol did not do the drawings, in contrast with the illustrations of his research articles.

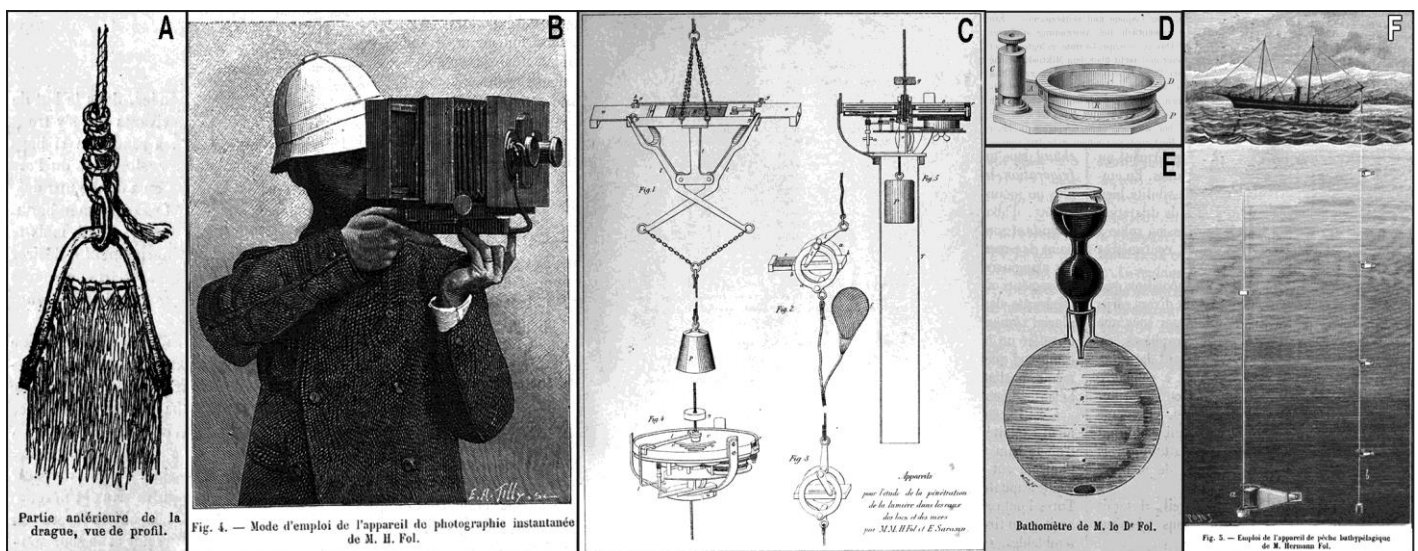


Figure 10. Examples of the diverse inventions of Hermann Fol: **A.** Fol's double arc trawl that sampled bottom fauna regardless of which side landed on the bottom (Fol 1883f). The drawing is not credited. **B.** Fol's camera designed to take in quick succession a series of images and to be easily carried in the field (Fol 1884i). The drawing is by Auguste Tilly. **C.** The devices of Fol and Sarasin used to expose photographic plates at depth in the sea (Fol & Sarasin 1887). The drawing is not credited. **D.** Fol's compression chamber to allow observations of specimens under the microscope over extended periods of time (Fol 1876). The drawing is not credited. **E.**

Fol's sounding device, a 'bathometer', relying on pressure induced flow of mercury from a lower chamber to an upper chamber to record the maximum depth of exposure in seawater; the image is from his re-description of the device (Fol 1877i). The drawing is by Louis Poyet. **D.** Fol's design of a closing net and a line of closing nets to simultaneously sample the plankton of discrete depth strata (Fol 1891b).
The drawing is by Louis Poyet.

Conclusions

Hermann Fol is a sterling example of the polyvalence of the 19th century naturalist whose diversity of interests contrasts so sharply with the extreme specialization of today's scientists. Trained as physician, he was at first devoted to the study of the developmental biology of marine invertebrates, then marine protists, followed by human embryology, then bacteriology, rabies, and finally studies of light penetration in seawater. With regard to the last topic, his curiosity led him to experience for himself low light conditions using a diving suit, and he concluded that avoiding a predator required only moving a short distance to become invisible (Fol 1890). Fol even wrote on economic matters, proposing a taxation scheme to increase the fertility rate of France by fixing taxation rates as a function of the number of dependents of a taxpayer (Fol 1891c).

One might say that he was of an era when 'one could know everything'. For example, the biographies of the British naturalist Robert Young (1773-1829), and the American naturalist Joseph Leidy (1823-1891) are actually both entitled 'The Last Man Who Knew Everything' (Warren 1998; Robinson 2006). However, what is notable is that naturalists in the time of Fol can be said to have been interested in everything, and entered new fields without hesitation. However, while Fol was talented, and with wide-ranging interests, unfortunately, he was also contentious. His personality was apparently a factor in his leaving Haeckel's group in the University of Jena, his loss of his position at the University of Geneva, his eviction from the Villefranche laboratory, and perhaps a factor in his disappearance.

Fol was very well-known in his time but when he disappeared at age 47, in 1892 he left behind no students nor a network of collaborators. He nearly invariably published alone. What he did leave behind was a number of people that he had accused of various errors or misrepresentations, and among them were figures of authority well into the 20th century. The anonymity of Fol today is likely due, on one hand, to the fact that he worked on a very wide variety of topics, producing a substantial body of work only in developmental biology, and on the other hand, because of his attacks over perceived slights, he left behind few people who worked in the domains he studied, inclined to acknowledge his contributions.

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Archival resources: Correspondence of Henri de Lacaze-Duthiers

Hermann Fol letters

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