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Essay in Development

Louis Sébastien Tredern de Lézérec (1780-18?), a forgotten pioneer of chick embryology

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ABSTRACT Tredern's thesis on chick embryo development was submitted in Jena (Germany) in 1808 and seems to have been completely overlooked by historians of embryology during the 20th century. However, K.E. von Baer and C. Pander were much interested in that thesis in 1816-1817, when they resumed work on the chick embryo. Tredern, who was born in France in 1780, had then left Germany and abandoned his studies, but von Baer tried to find trace of him throughout his life, wanting to pay homage to his pioneer work. Von Baer published a short biographical notice (1874), which was later extended by Stieda (1901). The accuracy of Tredern's observations and the reasons that could have justified von Baer's interest are discussed. Tredern went back to Paris in 1811 to submit a second medical thesis, the value of which is also considered. It is also shown that, in the teaching of embryology, 18th century preformation concepts were still vivid, remaining in French textbooks of the period 1800-1830. This situation strongly contrasts with the new epigenetic views that were developed by the German scientists with whom Tredern had performed his studies.

KEY WORDS: *Von Baer, chick embryo, history of embryology, ovist preformation, Tredern*

Introduction

Two years ago, the second centenary of Karl Ernst von Baer (1792-1876) was celebrated. Von Baer is now considered the founder of modern embryology, with the publication (1828b, 1837) of the two volumes of his treatise on animal development, *Über Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion* (Babkov, 1992; Kohl, 1992).

Von Baer himself published his autobiography in 1865 but at present, the most comprehensive book available on his life and his works was written in Russian, then translated into German (Raikov, 1968).

Von Baer was born on February 17, 1792 in Piep, in Estonia, at that time a province of the Russian Empire, in a family of landholders that came from Western Germany in the 17th century. He was a pupil at Reval (now Tallinn) "cathedral school" from 1807 to 1810; then he studied medicine in Dorpat (now Tartu) University from 1810 to 1814. The University of Dorpat was closed at the beginning of the 18th century after the Russians conquered the country and was reopened by Czar Alexander I in 1802, although teaching was done in German. In 1814, after he had submitted a thesis on the endemic diseases of Estonians, von Baer left for Austria and Germany. He first stayed in Vienna, then settled in Würzburg to work with Döllinger in 1815-1816. Döllinger was both a physiologist and an anatomist and he wanted to base a better analysis of morphology on embryology. He planned to have a young scientist resume the study of chicken embryology, but the applicant had to be able to meet the high expenses which were involved in this kind of research (purchase and surveillance of artificial incubators, purchase of several hundred hen eggs). Von Baer himself was absorbed by his search for stable employment during the next few months, but he wrote to one of his former college friends, Christian Pander, the son of a wealthy tradesman in Riga, and proposed that he come to Würzburg and undertake a thesis on early chick development. This matter had not been reinvestigated since the famous studies by Caspar Friedrich Wolff (1759, 1768), half a century before. Wolff's work had been trying to rejuvenate and defend the concept of epigenetic development, as opposed to preformationist theories that were supported by Albert von Haller and Charles Bonnet. The controversy between Wolff and Haller is known to have lasted several years and it has been extensively analysed (Roe, 1981). Preformationist views offered a long resistance but were finally abandoned in Germany at the end of the 18th century, and they were totally rejected by *Naturphilosophie* (Lenoir, 1984).

In Würzburg, Pander worked relentlessly for one year on the first five days of egg incubation. He used a total of 2,000 eggs. In a series of incubated eggs, one was opened every quarter of an hour. Pander's thesis (in Latin) was completed in 1817 (Pander, 1817a), and a modified German version was printed in the same year, illustrated by remarkable plates which were engraved by d'Alton (Pander, 1817b). It has long been known that Pander's work laid the foundations for the theory of germ layers in bird egg blastoderm. Von Baer modified and completed this theory a few years later.

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In the same year (1817), von Baer obtained his first position in Königsberg, where he was appointed as an "ordinary professor" in 1822. As soon as 1819, he had taken up the study of overall embryonic chicken development that Pander dropped after completing his thesis. He carried on these studies for several years (1819-1823 and 1826-1827) and finally published the fundamental work mentioned at the beginning (Von Baer, 1828b, 1837).

In Würzburg, when he and Pander were looking for previous books devoted to chick development, von Baer had found a thesis submitted in Jena a few years earlier, in 1808, by Ludwig Sebastian Tredern, termed as a "Russian from Estonia" on the head page. Although himself from Estonia, von Baer did not know that author's name. Puzzled, he was informed that Tredern had left for Germany after he had obtained his doctor's degree, but he did not find any trace of him in Estonia either.

Von Baer was filled with admiration for such short thesis, illustrated by a plate of very precise line drawings. He wrote: "The work schedule is so extraordinary that, if someone wanted to take it through to its conclusion, he would need to be immortal!.." About ten observations, with bibliographical references, show that the author is thoroughly acquainted with the literature on the subject. Explained in very few words, these observations are so accurate and so reliable that, by these fragments, we are compelled to consider the author of that dissertation as one of the most talented men in fine anatomy research. In 1808, after 40 years during which no significant work on chick development appeared, it was Tredern who started that new series of studies. For the same reason, he could not have received significant guidelines, because there was nobody who could have given them to him. Blumenbach himself could only encourage him. That makes the author more remarkable because, even without him, the Baltic provinces of Russia, more than any other country, can boast of their recent contribution to important studies on the history of development, especially if we consider immigrants (Von Baer, 1836a). Thus wanting to pay homage to the man he considered an outstanding pioneer, von Baer never lost hope of finding his trace again. He therefore searched for witnesses who might have met Tredern by publishing a first appeal in a German Baltic newspaper (Von Baer, 1836a), which brought about quick results (Von Baer, 1836b). The same process was used again thirty years later in a German magazine (Von Baer, 1867). Several people who had known Tredern in Estonia and in Germany, actually wrote to von Baer following those articles. However, the exact origin of Tredern remained to be established. Von Baer, who retired in 1867, had to wait until 1873 when he was informed by his French colleague Armand de Quatrefages, that Tredern had been born in France in 1780 and more precisely in a noble family in Brittany. During the French Revolution, he emigrated to Russia with his father in 1796. Later on, he left for Germany to study there, before returning to France. So von Baer (1874) was able to publish a short biography of Tredern. When he died (1876), his documents, manuscripts, archives were exploited by Ludwig Stieda, who himself published a more detailed biography of Tredern (1901), making use of documents that von Baer had left aside. Stieda added the Latin original and the German translation of Tredern's thesis next to his article, which is a considerable help, though the translation contains a few inaccuracies.

Stieda ended Tredern's biography with a series of questions, following up the scarcity of documents available to reconstruct Tredern's life and career. Among those questions were: why did Tredern abruptly abandon his program of embryological studies in 1809? Why was he induced to move towards medical practice after he had submitted a second thesis in Paris in 1811? Why did he give up publishing the whole of his observations? What has become of his documents, particularly of the remarkable drawings of which the witnesses spoke? What was the origin of his very early vocation for biology during the Revolutionary period, without a known master except for his father, who was not a biologist? Why should Tredern not have been able to carry on a scientific career in Paris? Those questions were repeated by Vialleton (1902) who did not make any suggestions as to the possible answers. Nearly one century later, we are compelled to note that the documents which might allow us to find the answers to those questions still remain unknown. However, for at least one question, I shall consider a possible answer.

First I shall expose briefly the biographical data that is known from von Baer's and Stieda's inquiries, dealing with Tredern's family origin and education. Then I shall analyse the original aspects of his research work and the reasons why von Baer, until the end of his life, looked for the circumstances under which Tredern had been living and carrying out his scientific work. Finally, I shall consider some aspects of the teaching of embryology in France from 1800-1830, in contrast with the new ideas on animal development that arose in Germany under the influence of *Naturphilosophie*, and I will make a hypothesis about their possible relationship with Tredern's career.

L.S.M. de Tredern de Lézérec: a biographical summary

Louis Sébastien Marie de Tredern de Lézérec was born in Brest (Brittany) on September 24, 1780. His father Jean Louis, born in Quimper in 1742, was then a lieutenant in the French Royal Navy and he became a captain during the American War of Independence, in which he was severely wounded. Appointed "Inspecteur des Classes" in 1785, he became the director of the Royal Marine Academy in Brest (Levot, 1857). During the French Revolution, he participated in the battle of Quiberon (1795) with his brother, who was killed there, when the Republican army crushed the Royalist insurgents whom the British Navy had landed in Brittany. Following this defeat, captain Tredern and his son Louis Sébastien emigrated to Saint Petersburg in Russia. Czar Paul I proposed a military position to the father, who refused it, so that he would not have to fight against his countrymen, should the occasion arise. On the other hand, the Czar accepted that the son (aged 17) was trained in the Imperial Navy. And that was how in October 1797 Louis Sebastien Tredern became a midshipman on board the Pimen in Reval harbour (now Tallinn) in Estonia. There he remained for 4 years while his father, a mathematician and an engineer, probably earned his living as a teacher in the well-known Nicolle French boarding school. Witnesses later remembered an eccentric marine officer, who kept brooding hens on board, a pastime that was of course regarded as useless! Tredern's vocation for embryology had thus been very precocious. Moreover, he used to dissect various animals (cats, dogs, rats), which also brings evidence of his early interest in comparative anatomy.

In 1801, captain Tredern wanted to leave Saint-Petersburg. Louis-Sebastien told the Czar he wanted to resign from his position to accompany his father. Both left in August. The father went back to France, given amnesty by Napoleon, and died in Quimper in 1807. The son remained in Germany to undertake university studies. He registered at Würzburg University on October 30, 1804 with the title of "candidate" in medicine, which implies previous

studies that might have been carried out between 1801 and 1804, although we do not know where Tredern was living during those three years. In Würzburg, Döllinger had been appointed professor of physiology and anatomy in 1803. Some years later, replying to von Baer's question, he supposed that von Baer might easily find Tredern again, since the student called himself a Russian from Estonia. Tredern's stay in Würzburg ended during the summer 1807; he then moved to Göttingen where he met Johann Friedrich Blumenbach, to whom he presented the results of his studies on chick development and the many drawings he had produced to illustrate them. Blumenbach advised him to use only part of his results for submission of his thesis and to schedule a later comprehensive publication. However, Tredern still applied himself to improving some particular aspects. While taking advantage of the rich University Library of Göttingen to consult the former works on chick embryology of which he was unaware, he completed the study of incubated embryos during the winter and the next spring. In all, testimonies on his stay in Göttingen mention relentless work.

We still ignore why Tredern submitted his thesis to Jena University on April 4, 1808, since he had written it in Göttingen. Von Baer (1874) neither mentioned Tredern's return to the latter city, nor his second stay in Göttingen until March 1809, which were analysed by Stieda (1901), basing his work on a detailed testimony by Stender, who had become a notary in Libau (now Liepàja, in Latvia) and who had written to von Baer in 1836 to inform him about his memories as a youth of his friend Tredern. After his thesis, Tredern had resumed his observations on bird development and was still working steadily. For unexplained reasons that Stender did not know he left Göttingen again in March 1809 and his trace is found only two years later in Paris.

Tredern came back to France in order to submit a new thesis that would give him the right to practise medicine in his native land. He was exempted from the first four examinations and admitted to take the fifth one on July 19, 1811. The thesis was submitted one month later (August 20, 1811). It bears on the organization of hospitals and shows an exact knowledge of the hospitals in Würzburg and Bamberg. From that date onwards, Tredern started a medical career of which nearly nothing is known. In 1873 von Baer obtained from Quatrefages information according to which Tredern was recruited as a ship's doctor. He thereafter founded a hospital on Guadeloupe island, remained unmarried and died at an unknown date (Von Baer, 1874).

Tredern's thesis on avian egg development

Tredern's first thesis was entitled *Dissertatio Inauguralis Medica Sistens Ovi Avium Historiae et Incubationis Prodromum* (preliminary contribution to the history of the avian egg and its incubation). It is presented as a summary of a much more complete work, which would be published later. It is very short: in all only 16 pages and an engraved plate including 32 separate figures. Of those 16 pages, five are devoted to the introduction and a detailed research program bearing on a comprehensive study of the "natural history of egg", egg abnormalities ("with excess" and "with defects"), egg chemistry, incubation conditions, development of the various organ systems of the embryo the detailed study of which remains to be carried out (osteology, myology, angiology, neurology, splanchnology). The next 7 pages include a more precise and detailed study of the formation of various organs without a logical order between the sequential chapters. The author deals with the ligament of albumen, the beak, the beak protuberance, the yolk peduncle, the intestinal duct, the limbs. Bibliographical references about each theme are indicated at the end of each section. The figure legends fill the last 4 pages.

This work constitutes only a small part of the observations that Tredern had accumulated over several years. But he was working as a self-taught man. He does not tell us what gave him the idea of focusing on embryonic development after having performed practical studies on comparative anatomy of Vertebrates, and especially of birds.

As mentioned above, it is known that Tredern already bred brooding hens on his ship in Reval harbour (Von Baer, 1867). Tredern was thus about 20 years old when he performed his first embryological studies. According to the introduction of his thesis, he became aware in Göttingen only in 1807 that many authors had already published detailed observations on these topics and that he could not present all of his own as new ones. Blumenbach advised him to choose only part of them for the thesis and to write a bibliographical analysis. He says he did not listen to such wise advice. From the report of his results it can be concluded that on the one hand he based some of his observations on those of his predecessors, correcting them and their contradictions if necessary, and on the other hand he developed the analysis of those which were really new. Thanks to the excellent library of Göttingen, he was actually able to determine the bibliography for each theme chosen. During a few months he carried out additional observations on several ill-known points, with the help of the State councillor Zacharias who provided him with a number of fertilized eggs, in spite of the winter season.

To construct his thesis, Tredern seems to have finally drawn up two principles:

1. To establish a chronology of the development of any given organ as precise as possible. Later, he replaced the brooding hens by incubators made of tin or earth vessels which were filled with white sand and contained the eggs, were heated with an alcohol or oil lamp and were equipped with a thermometer to check the sand temperature: such procedures are testified by an eyewitness (Stieda, 1901). Such technique remained the only one available for a long time, and Pander also used it for his own thesis (1817a).
2. To describe as accurately as possible the phenomena that were poorly studied by his predecessors: development of the face, the beak and the limbs. In contrast, Tredern does not dwell much on gut formation that had been studied in detail by C.F. Wolff during his controversy with Haller. To improve his observations, Tredern said he only used magnifying glasses but no microscope: however, the line drawings that he published are life-sized, which makes the younger stages difficult to read. But the eyewitnesses had been greatly impressed by the quality of the original drawings. To evaluate their quality, I have selected the description of wing and leg development, and that of beak formation, comparing them to the standard normal stages of chick development (Hamburger and Hamilton, 1951).

Development of limbs

To begin with, Tredern points out that he takes up the question at the very stage where Wolff left it, since the latter was only interested in the very first primordium of wings and legs. He also stresses the differences that appear among the different authors who studied the chronology of limb formation. Tredern actually saw limb-buds forming on days 3 and 4 but he noted digit formation only from day 6 onwards. On the whole, the evolution of the footplate

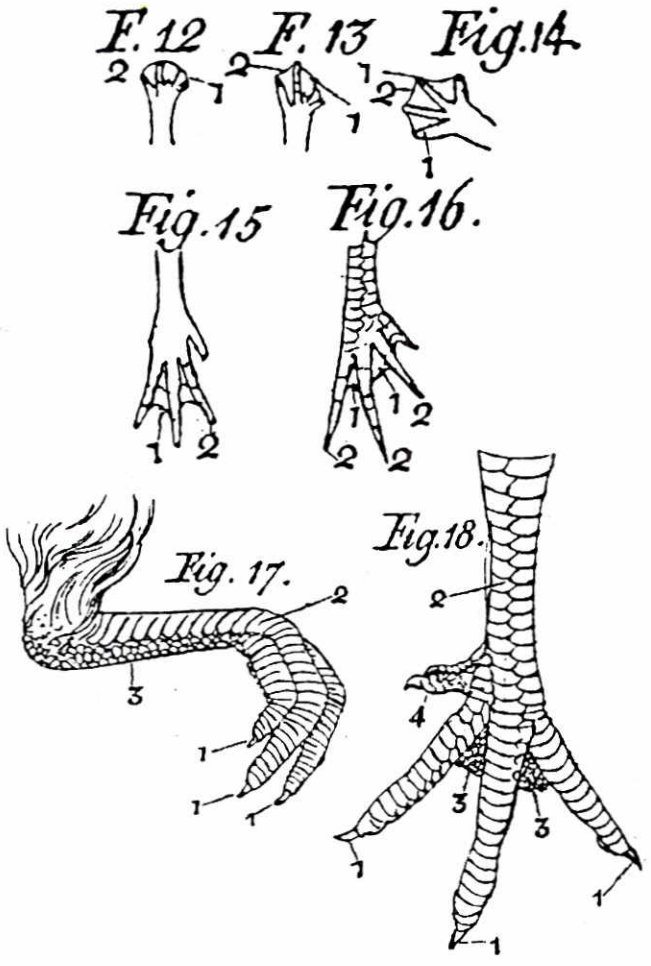


Fig. 1. Tredern's drawings describing hind limb formation, from day 8 (F. 12) to day 21 (F.18).

and the lengthening of digits are described correctly, but with a 1-2 day delay. The regression of interdigital membranes is well observed in the chick, even though in the goose embryo, the web is seen to stay on. Tredern precisely observes the appearance of scales on day 12, then he describes the corresponding pattern formation on the following days. Formation of claws is observed on days 11-12 (with a 24-48 hour delay), but their curving is not immediately detected. The quality of Tredern's observations is proved by the accuracy of his drawings (Fig. 1). It may be acknowledged that Tredern gave the first description of interdigital membrane regression in the chick embryo. However, Tredern's observations were not mentioned in von Baer's book (1828b), whose description of digit formation shows that von Baer himself did not understand the regression of interdigital membranes that Tredern had correctly described.

Development of the beak

In that case too, the chronology of events still remained confused. Tredern establishes in opposition to the opinion of former authors, that the beak itself does not appear prior to the 5th day. He observes that mandibular processes are formed first, as early as day 3, and he follows their convergence forward. In the same way, he describes the formation of maxillary processes that, he believes, occur somewhat later.

Evolution of the face and changes in the morphology of the nostrils above the beak are followed and drawn accurately, as are the successive steps of beak morphogenesis (Fig. 2). The formation of the "egg-tooth" on the beak that is used to break the eggshell at hatching is described from day 9 on. Vialleton (1902) admired the novelty of those observations, which would only be resumed and detailed at the end of the 19th century. Here too, it is surprising that von Baer (1828b) did not quote Tredern's observations and drawings since a) Tredern's thesis had been quoted by Pander (1817a), and b) much later von Baer was very enthusiastic about the quality of those investigations on beak formation (Von Baer, 1874). However, von Baer (1828b) actually mentioned very few authors and, at that time, the figure of Tredern was still an enigma for him.

In his analysis of egg incubation, Tredern also paid attention to physiological processes with regard to the behavior and origin of egg and embryonic membranes, the origin and role of fluids (amniotic fluid) during development, the appearance of venous blood circulation. Von Baer himself paid much attention to those developmental aspects of higher Vertebrates. In that case, he mentioned Tredern's interpretation of albumen structure but only in the second part of his book (Von Baer, 1837), which anyhow had been partly written several years earlier.

In his first appeal to *Das Inland* (Von Baer, 1836a), von Baer wrote that he was searching for Tredern again after getting back to his homeland in 1835. From the preceding overview of Tredern's thesis, it is understandable why such careful observations should have been of great interest to von Baer, who was also impressed by Tredern's line drawings and their accuracy. Today this might seem more difficult to admit considering how small some of those drawings are. But we know that von Baer, whose interpretative diagrams in the 1828 treatise are often excellent (Figs. 3 and 4), was not necessarily so naturally talented for drawings. The superb plates that were engraved by d'Alton to illustrate Pander's work (1817b) show a professional technique. There is no possible comparison between them and Tredern's drawings, the accuracy of which nevertheless results in admiration in spite of their small size. Moreover, the extent of the research program that was worked out by Tredern caught von Baer's attention because of its ambition. Many years would actually have been necessary to carry out such a program.

Thus we can understand better the reasons why von Baer throughout his life and in spite of the above-mentioned oversights, tried to find a trace of Tredern: he considered him a forerunner of his own ambitions of the comprehensive study of Vertebrate development. He was anxious to pay homage to him because of the scope of his views and of the precocious talent he had shown.

Though he had later forsaken embryological studies to the advantage of other aspects of zoology and natural history, von Baer never stopped evoking Tredern's short career and its interruption. Only near the end of his life he summarized what he learned about it, which shows how persevering von Baer was and how true he remained to his early feelings.

Tredern's second medical thesis

We do not know why Tredern suddenly decided to leave Göttingen in March 1809 after having spent the winter working

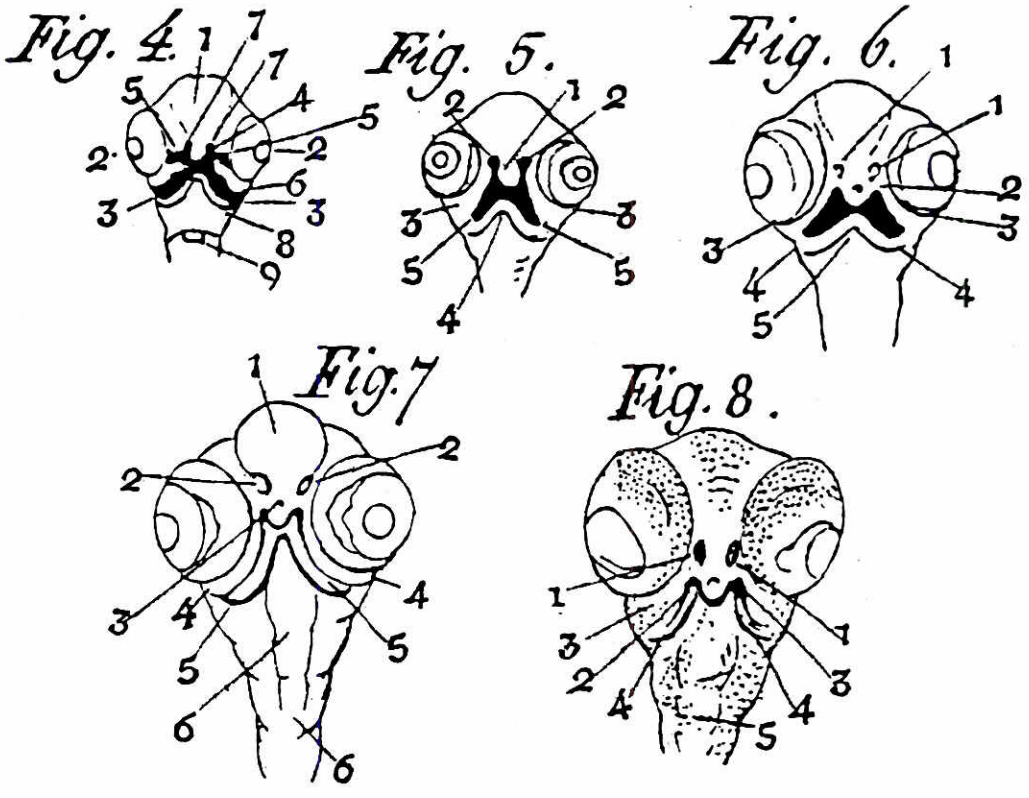


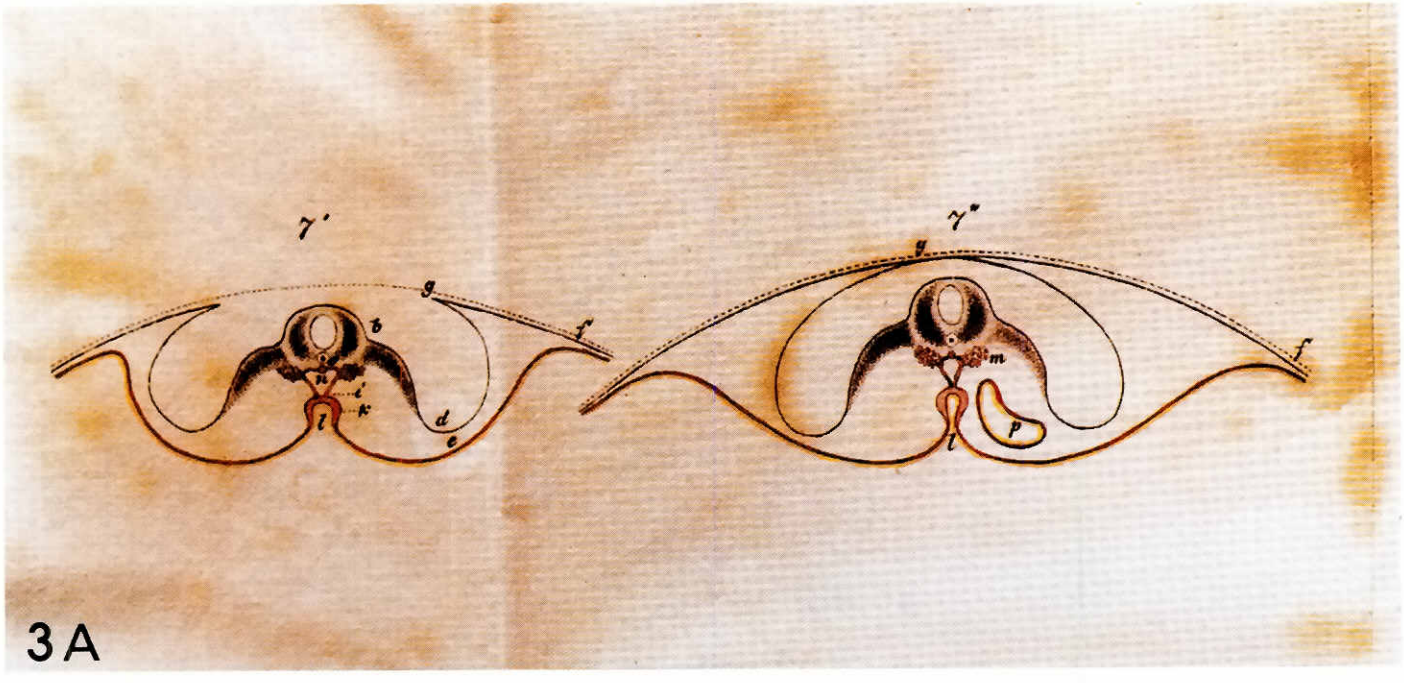
Fig. 2. Tredern's drawings illustrating beak formation from day 6 (F.4) to day 13 (F.8).

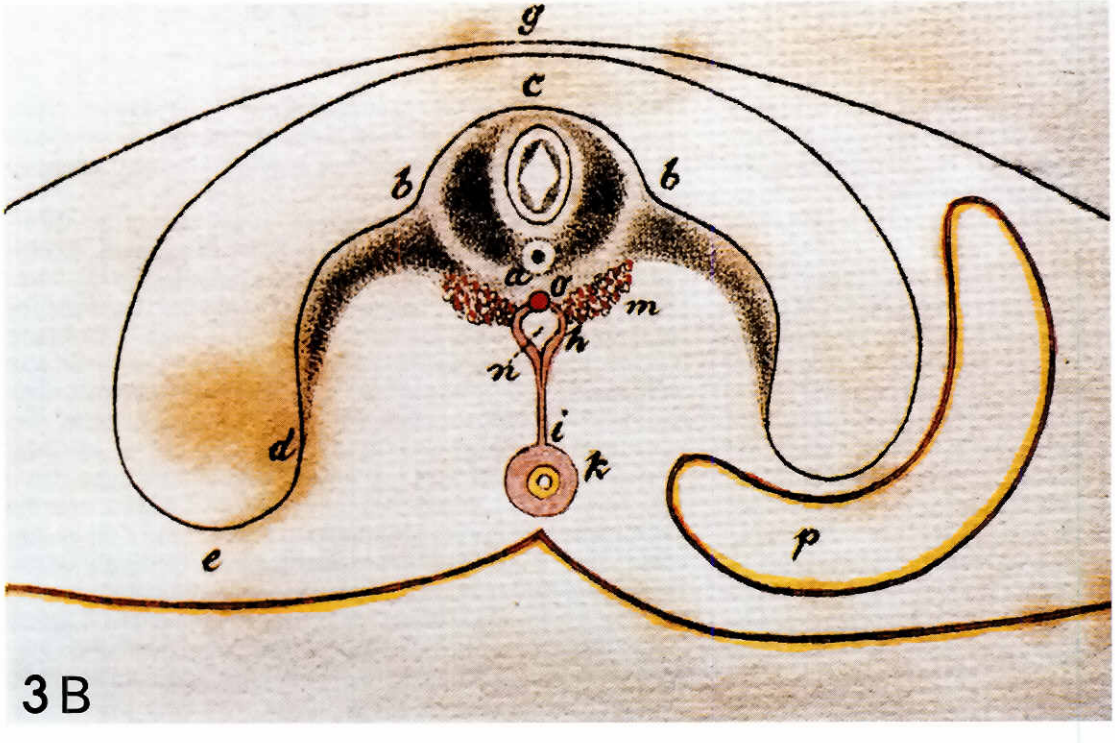
zealously on bird embryos again (Stieda, 1901, pp. 28-31). Neither do we know whether he still stayed in Germany, which seems likely since he displayed a good knowledge of German hospitals (Würzburg, Bamberg, Halle) in the second medical thesis that he submitted in Paris in 1811. In any case, we do not know the exact time of his return to France.

Tredern's second thesis, written in French, was entitled *Propositions sur les Bases Fondamentales d'après lesquelles les Hôpitaux Doivent Être Construits* (Propositions on the grounds according to which hospitals should be built). It was submitted on August 20, 1811 to the Faculty of Medicine of Paris. Von Baer was not able to consult a copy of that thesis, a short report of which was sent to him by Quatrefages. Neither did Stieda consult the thesis itself. But Vialleton (1902) refers to the very favourable comments on that work made by one of his colleagues. The second thesis, like the first one, must still be considered as a summary, since the author mentions in a dedication that it only represents "several propositions separated from a more substantial work". Those propositions are numbered I to XXII and tackle the practical problems arising from modernization of hospitals, so that they conform to their objective, i.e. curing patients.

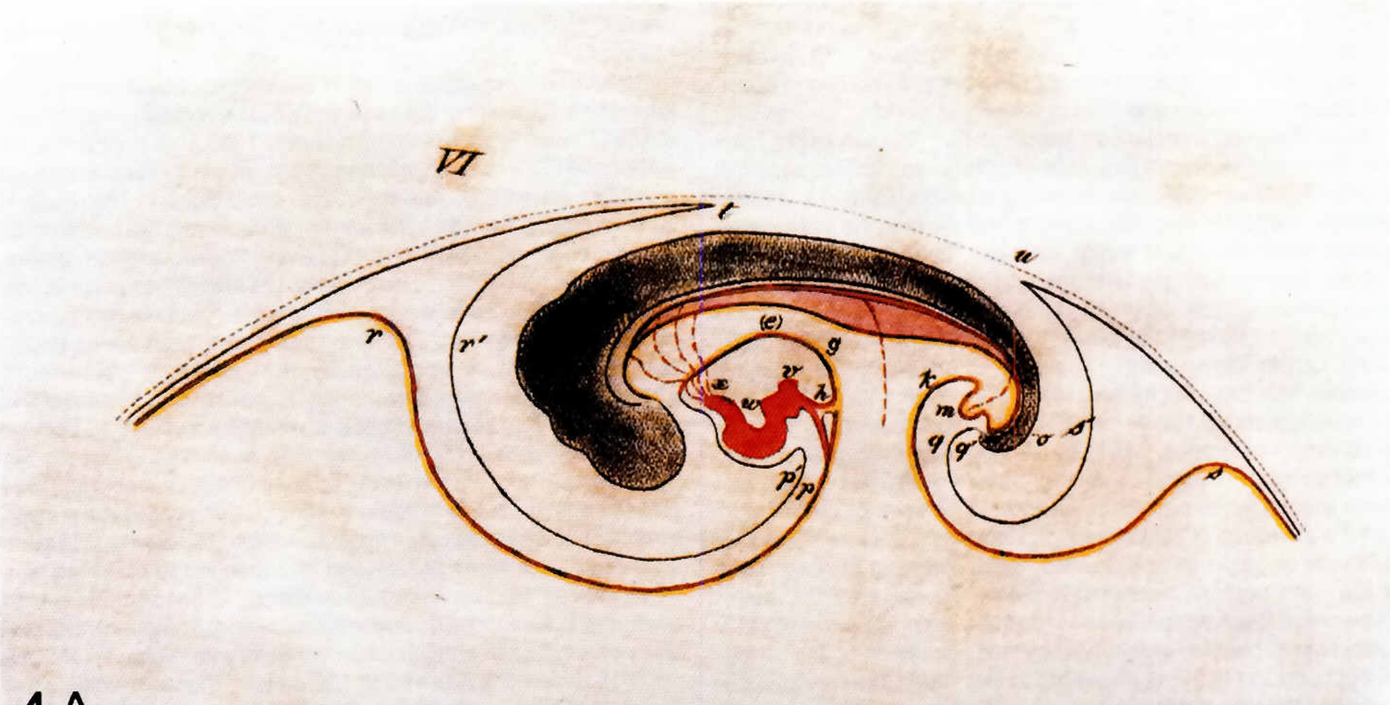
First of all, hygiene is required and Tredern suggests a number of measures for improving it. He proposes that the various categories of patients be separated in different rooms, and that the convalescents be separated from the patients. He also advises construction of separate buildings and cites the Plymouth hospital as an example. Several paragraphs are devoted to the heating and airing of rooms and even the colour of the inner walls: green is recommended for eye diseases. The role of local climate – temperature and dampness – is considered in detail to prescribe desirable fittings. Many of those proposals were obviously ahead of their time, or had been tested only locally. Tredern mentions many European hospitals (Germany, Great Britain, France, Netherlands, Spain), which he knew either directly or from available books. His own personal experience appears to be more extensive about German hospitals.

According to testimonies whose origin cannot be determined, Tredern put his ideas into practice in a remote colony, Guadeloupe island, where he founded a hospital. So far, it has been impossible to find the documents from which Quatrefages obtained that information except the certificates of birth and baptism that he communicated to von Baer. The latter was convinced only very late in life that Tredern was born of French parents. The family name sounded German or English to him. In a letter dated June 8 and 12, 1873 (Von Baer, 1873), von Baer acknowledges receipt of two letters from Quatrefages dated May 14 and 21 – which indicated Tredern's origins and the official report on the medical thesis in Paris –, and a third letter dated June 4 including informations about Tredern's death. Those three letters from Quatrefages are unfortunately missing from the "Baers Nachlassen" which Stieda later left as a legacy to the University Library of Giessen (Germany), neither do they appear in the archives of the von Baer Museum in Tartu (Estonia). At the time of those letters, von Baer lived there, having retired in 1867. On the other hand, Tredern's name does not appear in the official rosters of army medical officers and ship's doctors of French colonies from 1815 to 1835 *(Annales Maritimes et Coloniales, Partie Officielle)*. It is therefore possible that Tredern served as a doctor, not in the French Navy, but in the merchant navy, before settling in Guadeloupe. But no mention of his death has been found in the registers of deaths there. The origin of the information obtained by Quatrefages in 1873 thus cannot be checked at the present time, due to the missing letters in which he gave it to von Baer.





Figs. 3 (left) and 4 (right). Selected diagrammatic figures from Plate II (folded) in von Baer's book (1828b). *Sagittal or transverse sections through embryos at day 3* **(Fig. 4A, VI)**, *day 4* **(Fig. 3A, 7' and 7")** *and day 5* **(Figs. 3B and 4B, VIII)**. *The "serous sheet" (now ectoderm) is drawn in black, the "mucous sheet" (now endoderm) is drawn in yellow, the "blood sheet" (now mesoderm) is drawn in red, as are the arteries and the vitelline vessels, while the body veins are drawn in blue. Vitelline membrane is a broken line* **(Fig. 3A)**. *Abbreviations are different for cross and sagittal sections, respectively. Cross sections* **(Fig. 3)**: *a, vertebral column; bc, dorsal plate; bd, ventral plate; deg, amnion; e, serous sheet; hin, mesentery; m, Wolff's body; o, aorta; p, bladder (allantois). Sagittal sections* **(Fig. 4)**: *a and b, anterior and posterior ends of the vertebral column; c, anterior end of the dorsal plate; d, anterior end of the digestive tract; e, respiratory system; f, stomach; g, anterior gut; h, biliary canal; i, liver; k, posterior part of the digestive tract; l, rectum; m, bladder (allantois); n, caeca; o, posterior end of the digestive tract; p, blood and mucous sheets; p', serous sheet; p'r'tus'q', amnion; rtus, serosa or "Pander's false amnion"; r, anterior margin of the chorioamniotic fold, not yet invaginated into the serous sheet (r') of the head cap (anterior part of the amniotic fold t); ss'u, posterior amniotic fold; vw, heart chambers; x, aortic bulb; y, aorta; z, mesenteric artery; α mesenteric vein; ß, umbilical vein; γ, venous trunk. Photographs by F. Pelata, Bibliothèque Interuniversitaire of Toulouse.*



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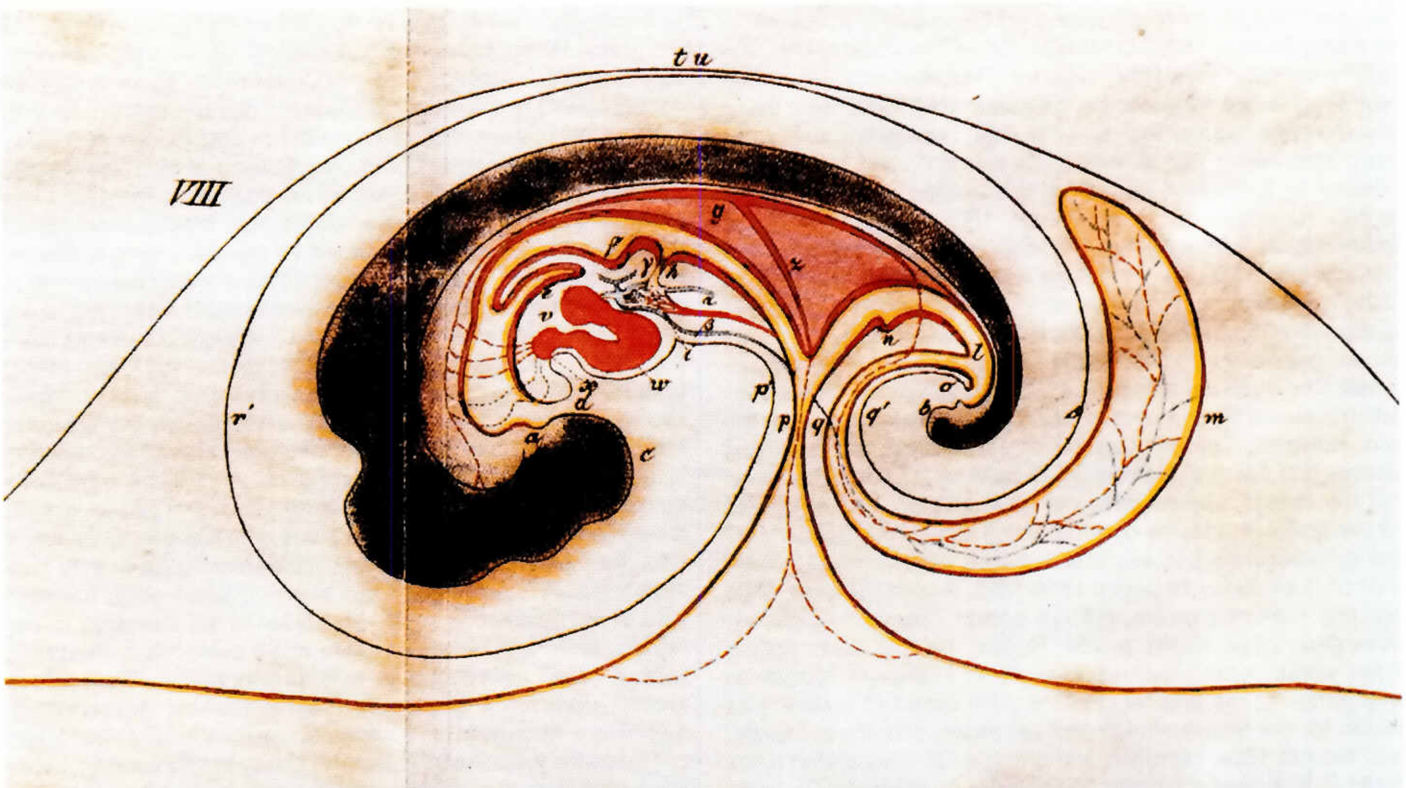

4B

On the teaching of embryology in France during the early decades of the 19th century

At the end of Tredern's biography, Stieda (1901) asks a last question: "Why was he not able to succeed, like his famous compatriot Cuvier? The latter too came to Paris with German training, like Tredern, and he acquired a brilliant position in scientific society in France and later in the whole world".

Such flattering comparison assumes that Tredern might have had the same wide-ranging scientific mind as Cuvier, which of course remains hypothetical. However, it seems justified to wonder whether Tredern's scientific training and the way he considered embryonic development would not have impeded his integration into the French scientific and medical environment at that time, since preformationist opinions prevailed there, not only under the First Empire (1804-1815) but still under the Restoration (1815-1830). Cuvier had actually been a young student in Stuttgart at the Caroline Academy, but he left it at the age of eighteen in 1788, and he never subscribed to the new but much too hypothetical ideas of his German comrades, which gave rise to the *Naturphilosophie*. Cuvier's high reputation as a comparative anatomist quickly became international, but was linked to the defence of creationism and the dismissal of evolutionist conceptions that were illustrated in France by Lamarck and Geoffroy Saint-Hilaire at the beginning of the 19th century, and developed in Germany by the many followers of the *Naturphilosophie* (Lenoir, 1984; Appel, 1987). A conservative position of embryology was also taken up in France, as opposed to the ideas prevailing in Germany. We can actually compare the observations made by Tredern, a follower of C.F. Wolff, the supporter of epigenesis and an opponent to preformationism, with the conceptions that were taught at the Faculty of Medicine in Paris during the same period. However, in his thesis Tredern does not mention the old controversy between Wolff and Haller (see Roe, 1981 for a detailed analysis of that controversy). But we know that preformationist ideas were being rejected by German biologists at that time. The first one who broke away from Haller was Blumenbach, accompanied by Reil and followed by Kielmeyer, during the last twenty years of the 18th century (Duchesneau, 1982; Lenoir, 1982). Epigenesis as an embryological concept then seems to go without saying when Tredern describes the embryonic development of the chick in 1808. It appears to be obvious when he describes the details of beak and limb formation, as I previously mentioned. Beak primordia appear gradually and their final morphology is progressively acquired. The digits develop from a digital plate without any demarcation between the prospective toes, then the scales appear on the skin. However, Tredern says he only made use of magnifying glasses and not of a microscope, to perform his observations. Is that the reason why he does not take up a position in the old controversy? Or does he consider that it is definitely out of date? The epigenetist attitude was later adopted by his followers Pander and von Baer during the period 1816-1828, though von Baer, while rejecting preformationism, did not accept simplistic epigenetic views (Von Baer, 1828b, p. 156; Raikov, 1968, p. 124). Facing those works, what was being taught in France in relation to embryology at the beginning of the 19th century? A book was written for the reform of high and secondary schools in France, published in 1804, reprinted and enlarged (2 volumes) in 1807 *Traité Élémentaire d'Histoire Naturelle* by André-Marie-Constant Duméril, professor of Anatomy and Physiology at the School of Medicine in Paris. The book is dedicated to Georges Cuvier. In those first two editions, on pages 4-5 and 6 respectively, it is stated: «Plants and animals, when increasing their size, only develop. Whatever their smallness, by careful examination, we can see them already wholly formed, with their different parts which only unroll». That is a preformationist definition of embryonic development.

The same viewpoint is adopted in a very famous teaching book for medical students of the same period. The first edition appeared in 1801. It was reissued nine times until 1833 and, prior to the 5th edition (1811), it had already been translated in several European countries (Germany, Great Britain, Italy, Spain). The book is entitled *Nouveaux Élémens de Physiologie* and was written by Anthelme Richerand (1779-1840), a well-known surgeon, professor at the Faculty of Medicine of Paris. The first edition (one volume only) was dedicated to the chemist Antoine-François de Fourcroy (1755-1809), who had just been appointed permanent undersecretary for public education by the Consulate government. Fourcroy was to organize a number of educational institutions in France, including several schools of medicine and law. As early as 1802, the second issue of Richerand's book was enlarged (two volumes) and so were the following ones that appeared from 1804 (3rd edition) to 1825 (9th edition). Minor modifications were made in each successive edition. The tenth edition (1833) was still further enlarged (3 volumes) and greater changes are to be found in it. Nevertheless, human reproductive biology is considered from an unchanging standpoint throughout that period. Anatomy and physiology of generation and gestation are dealt with in chapter X of the 1801-1820 editions (from 80 to 108 pages), then in chapter XII of the 1833 edition (130 pages). The influence of the 18th century physiologists and preformation supporters (Haller, Spallanzani, Bonnet) is still powerful, as shown by references to those authors and by approval of their views. About the origin of the embryo and the fetus, Richerand remains a follower of ovist preformation. However, he rejects the theory of preformation by *emboîtement* (encasement) of the embryos since the day of Creation, considered to be metaphysical and fantastic. But, though remaining cautious and conscious of the uncertainties of that time, he still writes in 1814 in the 6th edition of his book, on page 406: «The foetuses pre-exist in the female ovary, though they have not stayed there since the creation of the world, as was the feeling of Bonnet and all those who, like this metaphysician, adopted the system of germ *emboîtement*; but the eggs which contain those germs are formed from the peculiar action of the ovary which secretes them [.....]. That egg, a product of the elaboration of the blood that is brought to ovaries by spermatic *(sic)* vessels, contains the lineaments of the new being». The same text was already present in the first edition (1801) and was to be reproduced without any changes in the 1817 and 1820 editions. Further on, a reference to Bonnet's opinion is clearly given about organ formation (1st edition, p. 518; 8th edition, Vol. 2 p. 439). "All our parts form together at the same time, they all are *cooevales*, as Charles Bonnet said; they only appear visible earlier or later, due to their different ability to reflect light. If we admitted a successive order in the formation of our organs, brain and nervous system might exist before the heart, without being visible due to their transparency". The various ancient theories of generation (semen mixture, animalculism, ovism) are discussed in a separate paragraph. But Richerand considers the more likely theory to be "the system of ovarists, which is in highest favour at the present time" (8th ed., Vol. 2, p. 431). The role of the male semen, following Spallanzani's experiments (1785), is considered to be that of an egg activator. Heredity of characters

from the father is explained by a modifying effect of sperm fluid acting on the periphery of the embryo, still gelatinous, since the core of the egg forms the basic organs which were pre-formed in the unfertilized germ. We must await the 10th edition (1833) to find greater changes and significant additions. Richerand cites the experiments which had been performed by Prevost and Dumas (1824a,b,c), who had first repeated Spallanzani's work on frog egg fertilization. Richerand states that those authors did indeed see the mammalian ovum expelled from the Graafian follicle and does not refer to the discovery of that mammalian "egg" by von Baer (1827, 1828a), though the corresponding articles had been translated into French by Breschet as early as 1829. The treatise on Vertebrate development, the first volume of which had been published by von Baer in 1828 and also partly translated by Breschet (1829), is neither mentioned in Richerand's book. Now, if we refer to Prevost and Dumas's article on the mammalian egg (1824c), we see that those authors did not assert that they had seen the ovum in the Graafian follicle, but that it should be present in it, since they had twice observed a small opaque body which might give rise to the transparent "ovules, whose diameter is 1 to 1.5 mm *(sic)*, that are found in the oviducts".

In the tenth edition (1833) of Richerand's book, preformation of the fetuses in the ovary is only considered as one of the assumptions on embryo origin. The system of the "ovarists" is still exposed, to be linked to animalculism that Richerand considers to have been rejuvenated by Prevost and Dumas: they admit that, introduced into the ovum, the spermatic animalcule transforms into the foundations of the new individual whose nervous system derives from it. However, under Serres's influence, Richerand now considers it likely that "the living germ, though amorphous from its origin, successively goes through all the forms and the steps of organization and life", which means that it shows the general appearance of a worm, an insect, a fish, a reptile, before it acquires the organization that characterizes the species to which it belongs. The same views had been expressed by Meckel (1811). The theory sounds fully recapitulative and was already strongly criticized by von Baer. Nevertheless, from those ideas, it can be considered that the concept of epigenetic development is about to replace the old preformation system in the author's mind. Richerand still insists on the lack of precise knowledge available to check the various contradictory hypotheses that he cites. It must be remembered, as emphasized by Roe (1981, p. 150), that the German biologists of the beginning of the 19th century "never really disproved preformation in any significant experimental way; most simply rejected it out of hand". And Oken (1809-11) declared: "The theory of preformation contradicts the laws of natural development". It is known that Oken very much appreciated Tredern's thesis at that time, which is easy to understand since, as we have shown, Tredern's new observations brought arguments in support of Oken's philosophical statements. But those who, like Richerand, were waiting for more experimental evidence and were not ready to change the old views for the new ones only on philosophical grounds, preferred to stay in the comfortable bed of preformation, rather than hazarding a teleological causality of epigenetic development. But since they did not accept any longer the *emboîtement* theory, they still had to explain how the organization of the future embryo could be preformed by secretory activities into the ovary, which is another kind of epigenesis! It seems that such a great problem was not tackled during the transition period of 1800-1830.

At the same time another textbook of comparative physiology was published, whose first volume mainly dealt with reproduction and development of living creatures (Bourdon, 1830). Bourdon was then a member of the French Royal Academy of Medicine and had been one of Cuvier's former collaborators. In his book, he analyses and discusses the various systems that were conceived from antiquity to the 18th century to account for the origin of embryos. His criticism is more detailed than Richerand's analysis. Nevertheless, Bourdon finally comes round to the concept of germ pre-existence. He even believes that the *emboîtement* theory is basically plausible when it is admitted that embryonic organization primarily lies in the ovum. The successive emergence of the various organs during Vertebrate development may only be a misleading appearance, hiding the presence of transparent preformed rudiments, as thought by Haller and Bonnet. This is consistent with Richerand's position.

So, Richerand's opinions on embryonic development clearly remained unchanged for 30 years, in spite of the new observations made by the German-speaking embryologists. In 1833, Richerand still writes as if von Baer's conceptual revolution on Vertebrate development (1828b) did not occur, and it is very difficult to believe that he was not aware of it. Similarly, he attributes to Prevost and Dumas the first discovery of the mammalian ovum, and does not cite von Baer's work. This attitude strongly contrasts with that of other French scientists, who very soon published summaries of von Baer's other articles in the *Annales des Sciences Naturelles* from 1828 onwards. Gilbert Breschet (1783-1845), also known as a Germanist, was a professor of Anatomy, Physiology and Surgery in Paris, and a member of several European academies. He published a French translation of von Baer's articles on the discovery of the mammalian ovum and of the first part of the treatise on animal development one or two years after they appeared, in the *Répertoire Général d'Anatomie et de Physiologie Pathologique*. "Keenly aware of what was being done in foreign countries", he also translated articles by several other German authors (Gillispie, 1970-1980).

Anyhow, being clearly omitted in a well-known treatise of physiology for medical students, the new ideas still had to be imposed in higher education. Cuvier's conservative attitude, though largely dominating the official scientific circles, should not be exaggerated as explaining the behavior of most of his French fellow physicians. Actually, von Baer greatly admired Cuvier, whose zoological classification he adapted to characterize the fundamental types of animal development. Von Baer nevertheless supported epigenesis very soon, following the German professors of whom he had been a student.

In France, during the first decades of the 19th century, epigenetic concepts were introduced in the Museum d'Histoire Naturelle and the Faculty of Sciences of Paris by Etienne Geoffroy Saint-Hilaire, followed by the physician Etienne Serres. But, as emphasized by Fischer (1993), those comparative anatomists (to whom Cuvier was opposed) remained unconcerned about scientific embryology, because it did not fit the general system that they had constructed to explain the whole organismic world. Scientific embryology had to wait to be recognized as an autonomous discipline: Victor Coste (1807-1873) was appointed to the first Chair of Comparative Embryology that was established for him in the Collège de France, only in 1844.

Conclusion

It may be likely that Tredern finally chose to practise medicine so that he could better earn his living. On the other hand, he may

have given up his embryological research program because of a sudden discouragement. But we are entitled to think that, had he tried to carry on that program in Paris, he would have found it hard to impose the new concepts of embryology in a scientific environment that was still impregnated with officially-taught preformationist ideas.

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