Experimental Embryology in France (1887-1936)

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I. The "founding fathers" of experimental embryology

From the point of view of the biological historian, experimental embryology was born in the 1880s through the largely simultaneous work of Hermann Fol and Stanislas Warinsky in Switzerland, of Wilhelm Roux in Germany and of Laurent Chabry in France (Oppenheimer, 1967; Churchill, 1973; Fischer, 1986; Horder *et al.*, 1986). Of the three countries, it was Germany that produced the greatest number of embryologists specialized in the new discipline. This can be easily understood when we consider that it was also in "Germany" that embryology gained scientific status in 1817, thanks to the research of Christian Pander (Balan, 1979), followed by that of Ernst Von Baer, Johannes Müller, Heinrich Rathke, etc.: that is, there was in that country a tradition of embryology and a political awareness of the need to support "basic research" that caused developmental science, in its early experimental phase, to be essentially German. From W. Roux to H. Spemann, who was awarded the Nobel Prize in 1935, there are numerous names of distinction in this field.

The French contribution was more modest in the early days of experimental embryology, which has also been given the names of developmental mechanics (*Entwicklungsmechanik*) (Roux, 1884; Churchill, 1975), biomechanics (Delage, 1895), developmental physiology (Caullery, 1939) and causal embryology (Brachet, 1921). And this contribution, despite its modest proportions, was nevertheless marked by research that contributed to furthering our knowledge of embryology. Three names illustrate this period: L. Chabry, Y. Delage and E. Bataillon.

This study will be limited to the period between the years 1887 and 1936 – 1887 being the year that L. Chabry defended the thesis that became the seminal text for experimental embryology in France, and 1936 being the date that corresponds to the thesis of E. Wolff, who was, together with L. Gallien, the founder of a school of embryology that generally set the pattern for "developmental biology" as we know it in France today.

The monstrous ascidians

Laurent Chabry (1855-1893) had all the qualities necessary for a great career in science (Pouchet, 1893; Fischer and Smith, 1984; Fischer, 1990). And yet he was refused important teaching positions because he had been an adherent of, and participant in, the "revolutionary collectivism" movement of J. Guesde, who was not much in favor with the politicians of the time. This explains why Chabry had to abandon experimental science and the national laboratory system and turn instead to making dental protheses in a private office.

The evolution of Chabry's scientific work followed a perfectly logical pattern. As a medical student in Paris, he was particularly interested in the courses on physiological and animal mechanics taught by E.J. Marey at the Collège de France, towards the end of the 1870s (J. Marey, 1868, 1872 and 1878, in Fischer, 1990). In

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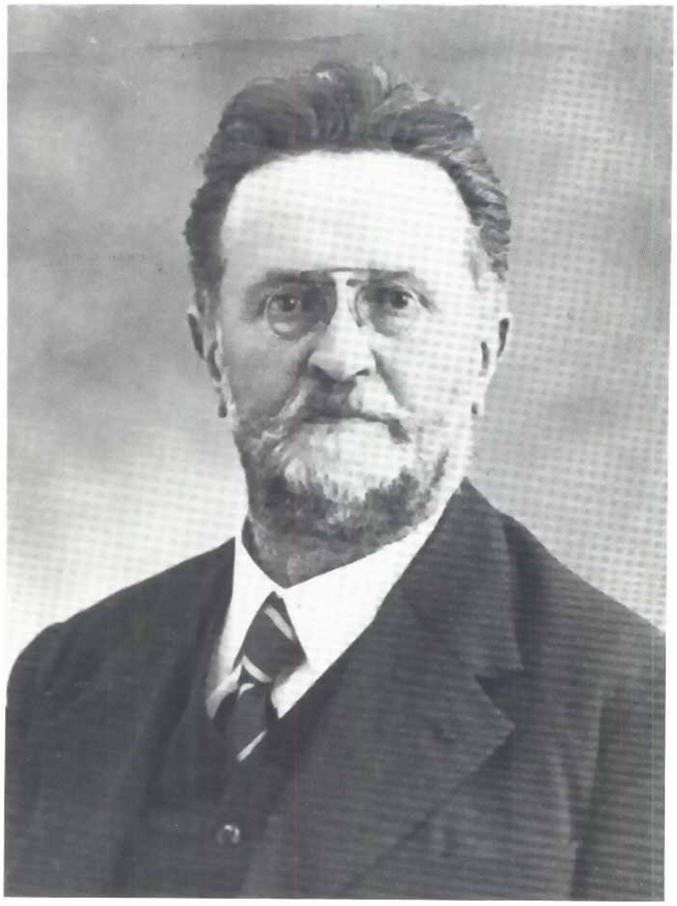

Fig. 1. Professor Eugène Bataillon *(1864-1953)*

1881, Chabry defended his medical dissertation, entitled *Contribution à l'étude du mouvement des côtes et du sternum* (Contribution to the Study of Movement of the Rib Cage and the Sternum). This thesis was a work steeped in the methodology developed by Marey. Chabry continued his study of animal mechanics and authored papers entitled *"Mecanisme du saut"* (The mechanics of jumping) (1883), *"Sur le mécanisme de la natation des poissons"* (The mechanics of swimming in fish) (1883) and *"Sur la longueur des membres des animaux sauteurs"* (The length of members in jumping animals)(1885)

It was the impulse given by the "convinced positivist", Georges Pouchet, director of the laboratory of marine zoology at Concarneau (Pettit, 1902) that propelled Chabry, an associate director of that laboratory, towards cellular mechanics. The originality of Chabry's 1887 thesis, *Embryologie normale et tératologique des Ascidies* (Normal and Teratological Embryology of Ascidians) lies not only in his scientific method, but also in his ability to manufacture the instruments indispensable for carrying out new experiments.

Here again we may recall how Chabry was influenced by Marey, who wrote: "The experimenter must know at every instant how to modify the instruments that he uses and often how to manufacture them himself" (1878). Chabry's thesis is concerned primarily with the teratology of tunicates produced by experimental techniques, and only secondarily with normal ascidian embryology.

Chabry observed the different stages of segmentation in *Ascidia aspersa* using material regularly dragged up from the sea bed. Several successive catches provided specimens whose eggs all showed abnormal segmentation. Such "monstrous segmentation" had already been observed (*Quatrefages*). But the history of biology abounds with such cases judged to be of "no interest" within a particular sociocultural context, even though they often do turn out to be of very considerable interest. Such was the case with the abnormal eggs of *Ascidia aspersa*.

In fact, Chabry had no other suitable material ready at hand and he therefore studied these eggs while waiting for a fresh, normal batch. He noted the strict relationship existing between faulty or abnormal segmentation, cell death and the production of monstrous larvae. In his own words, here was an "absolutely new subject". He observed that the death (*sphacèle*) of a blastomere at stage II produced a half-embryo. Death at a later stage (IV) resulted in organic agenesis that was specific for the particular blastomere affected. Thus, lack of the left superior blastomere at stage IV led to larval forms from which the otoliths were missing. After these findings, Chabry wrote: "From here it is easy to reach the conclusion (which I believe to be valid only for Ascidians and animals whose blastomeres differentiate early) that each blastomere contains certain potential parts which, if destroyed, are irremediably lost and that different parts of the animal are preformed in the different regions of the egg" (Chabry, 1887).

This remark, the result of simple observation, raised important questions which were debated not only at that time, but also much later. These were the problems of mosaic eggs and of their "preformist" corollary (a notion which, incidentally, bears no relationship to that of the pre-existence of germs, as certain historians continue to believe) (Roger, 1971; Maienschein 1986; Rey, 1989). This preformism, or predetermination, was to receive its methodology from Weismann and micromerist theory.

Subsequently, Chabry thought he could, by means of a pinprick, produce a trauma harmful enough to destroy a blastomere and thus reproduce certain natural abnormalities that he could then study in detail. At this point, Chabry's technical skill came into play. In order to perform these experiments, he conceived an apparatus which was a modification of the one he had built to observe normal egg development in Ascidia – a capillary specimen holder. This device was fitted with a fine glass needle drawn out over a flame. One of the tips of this needle was placed on a red-hot surface (platinum knife of a thermocautery) and then quickly removed. This operation concocted by Chabry produced a microcapillary. In this way, he invented the microforge and the micromanipulator, two instruments of great value to Chabry (and to embryologists in general), making it possible to destroy one or more blastomeres of a segmenting egg and follow its development after the operation.

According to Chabry, experimentation would always be possible provided the teratological effect to be studied – the result of a chain of causally-related phenomena – arose from a simple initial event. If several such events were involved, then experimentation would be difficult. Further, Chabry remarked, "experimental teratology, since it concerns normal eggs, enables the chain of anatomical events to be studied, but tells us nothing of the initial cause" (1887). Here was food for discussion, with its implications of hereditary malformations (i.e. mutations) contained in the eggs before division or external agression, whose prime cause remains elusive. There was also a warning substance or a physical act as the cause of an effect, for clearly the causes leading a normal and an abnormal egg to produce a given monstrosity cannot be identical. The problem of substances or physical actions and their teratogenic specificity on the egg and the embryo remained the subject of animated discussion in causal embryology in the years that followed.

Be that as it may, Chabry was able to reproduce natural half-embryos experimentally be destroying one of the blastomeres at stage II. Similarly he produced embryos lacking otoliths, thus showing that the otolith was localized in the lower right blastomere at stage IV. He discovered the regulatory ability of the left blastomere at stage II to give rise to pigment spot originating, as he showed experimentally, from the division of the right blastomere (localized in the lower right blastomere at stage IV). The destruction of 3 blastomeres at stage IV produced quarter-embryos, etc.

These facts contained sufficient matter to construct a preformist theory and defend autogenic predetermination. However, Chabry did not venture along this path. He was reluctant to theorize and plunged deeper into his experimental or normal observations of ascidian monsters. However, he refused to generalize findings: "The technique of cellular trauma should not always lead to the same results; although some people may find decisive proof in my experiments that the animal is preformed in the egg and that each part of the animal is preformed in part of the egg, I am anxious to avoid such a conclusion, which is far too absolute" (1887).

Such prudence proved to be justified, for although E.G. Conklin confirmed Chabry's experimental results in 1905 (Conklin, 1905), A. Dalcq, in 1932-1938 showed by means of an experimental technique (merogony), invented by Delage, that the ascidian egg can regulate "under certain conditions" (Dalcq, 1932, 1941). It is in fact a spatial and temporal relation that determines the isotropy or anisotropy of the egg. This is what leads the proponents of preformation (neo-preformation or neo-evolution, terms employed by biologists at the end of the 19th century), like those proponents of a theory of epigenesis (neo-epigenesis), or even those who, more rationally, wished to reconcile the two theories to see in the ascidian egg examples of alternatives to support their argumentation.

Epigenesis or preformation

In any case, in taking up theoretical positions, scientific facts are not always sufficient. Chabry, who made the experimental demonstration of neo-preformation, was against generalizing this theory because of the political ideology that he espoused. According to this ideology, men are equal and free, and social constraints must be combatted, together with the inequality of classes: whereas neo-preformation is a theory that imposes a biological constraint on the individual. Chabry was exposing the shortcomings of a biological theory that ran counter to his political and social theory; therefore, there could be no grounds for intellectual agreement between his ideology and scientific demonstration. On the other hand, A. Weismann, who came from a Protestant family that defended the family line and the "heredity" of social class, was predisposed to elaborating a theory of preformation (Huard *et al.*, 1949).

Neo-preformation and neo-epigenesis held an important place in biology debates at the turn of the century. While we cannot, within the scope of this article, present all the different positions giving rise to these debates, nor all the consequences they eventually had, we cannot avoid mentioning the theoretical currents developing in France during this period marking the beginnings of causal embryology.

In France, what we especially find is a neo-epigenetic tendency among the embryologists who expressed their choice of theory. From Y. Delage and E. Rabaud to P. Wintrebert, scientists combat neo-preformation on the grounds that they reject all systems that hold that the characteristics of the living being are predetermined in particles at the time of genesis – systems like that of A. Weismann, with his "*ides*" and "*idantes*", that of de Vries with his "pangenes", or the chromosomic theory of heredity espoused by T.H. Morgan. It was on the basis of some deeply-held conviction, having more of sentiment than of science, that embryologists (or biologists) became neo-epigenesists and neo-Lamarckian, since the one is generally accompanied by the other, and were opposed to neo-preformationism and neo-Darwinism. And if Delage preferred P. Kropotkine and his theory of "*entr'aide*" (mutual assistance) as an evolutionary factor, rather than Darwinian selection and Morganism, and if the inverse tendency is much more pronounced in the English-speaking countries, it is because both groups, though observing identical phenomena, each interpret the results in ways that satisfy their ways of thinking and their wish to explain the living organism within different cultural frameworks. Sea urchin or ascidian embryos do not change; when subjected to identical experimental procedures, they respond in similar ways; only the interpretations of the observers and experimenters change when confronted with the same biological object.

A new science

In 1887, Yves Delage (1854-1920), one of the committee that examined Chabry's thesis defended that year, was working on problems of physiology and particularly on the function of "semi-circular canals" and "otocysts".

In 1891, when Bataillon defended his thesis, Delage – president of Bataillon's examining committee – published an *Essai sur la théorie du rêve* (Essay on the Theory of Dreams) (1891), after having carried out numerous studies on the embryology of sponges at Roscoff. He continued these studies while formulating a number of precise theoretical ideas which first saw the light of day in 1895 in an article entitled, "*Une science nouvelle: la biomécanique*" (1895), and which were developed in his work on heredity (1895). In the same year he launched *l'Année Biologique* and published a manifesto in favor of the change in orientation of biological research in France in order to catch up with Anglo-Saxon work in the fields of embryology and cell physiology.

In Delage's opinion, embryologists (including himself) had spent their time describing embryos and comparing stages of development. This descriptive and comparative embryology, concerned with the "hows" of ontogenesis, was in his view "more or less well understood". On the other hand, the "whys" remained "obscure" (note that this "why" corresponds to the immediate cause of phenomena and not to the "ultimate reason why"). For instance, we may know everything about the form, the histology, the time of appearance of the different types of cells during ontogenesis, but we do not know why one cell becomes a neuron, another a muscle cell and yet another a glandular element. Of course it is necessary to possess a complete description of phenomena before being able to provide an interpretation of them, and it is obviously easier to describe than to explain. Delage, perhaps weary of having described so much fine structure, decided to devote himself to explanation.

Thinking of micromerist theories, and certainly of Weismann, he pointed out that the most popular theories of the 1890s were those that emphasized the explanation of phenomena by a nuclear predetermination of characters. However, Delage considered that this kind of theory was doomed as a result, first, of experimental evidence proving the egg to be isotropic (H. Driesch, Pflüger, etc.) and, second, of the phenomenon of regeneration. Thus, "positive data" proved that the egg does not contain predestined germ.

The egg is a cell with a "determined physico-chemical constitution". Confidently, Delage affirmed that the notion of heredity explained nothing and that, instead, one should search for directing forces that will lead to histological differentiation. Such factors are the "tropisms" and the "tactisms" of W. Pfeffer (1888) and W. Roux (1894). Apparently, Delage overlooked Chabry (1887), who termed "attraction" what Delage (1895) called "cytotaxis", Roux "cytotropism" and Herbst "chemotaxis" (see Fischer *et al.*, 1984). Although Roux was guilty of a semantic error, the expressions used by these authors, as well as their methodological implications, were to take on considerable importance in later years.

According to Delage, mesodermal cells enter into contact either with endoderm or ectoderm by cytotaxis or chemotaxis rather than as a result of the evolution of "gemmules" that no one has ever seen, or of some hereditary metaphysical tendency" (Delage, 1895).

If on top of this we add the exogastrulation obtained by Driesch (1893) after placing sea-urchin eggs in water at 30° C, or the formation of pseudoarthrose during fractures, it was not surprising to find "functional excitation", formulated by Roux, evoked to explain these phenomena; the physiological explanation resides in "automorphosis" and "autoregulation" in which organs, tissues or cells "develop in the direction in which they work and adapt continually to their function".

The aim of this new science founded by Roux was the study of "positive factors of ontogenesis" (simple mechanical, physical, chemical or physiological effects), which would explain developmental phenomena. It should be pointed out that the results of Chabry, Driesch, Herbst, Roux and O. Hertwig had already served to open the route along which Delage embarked in 1898 with the publication of his note on "Embryos lacking a maternal nucleus".

By microsurgery, Delage separated sea-urchin eggs into two parts, only one of which possessed a nucleus. After fertilization of each fragment, Delage obtained divisions, and occasionally larval forms, from the part without a nucleus (as little as 1/37th of the egg – 1899). This experiment was based on those of Hertwig (1890) and Boveri (1889). The latter, using foreign (hybrid) sperm, fertilized portions of cytoplasm obtained by shaking virgin eggs in a glass tube. However, this method did not allow nucleated and non-nucleated fragments to be distinguished – as did the technique of Delage (or so he affirmed). In any event, this "merogony" (Delage's term) was in contradiction with the "merotomy" experiments of Balbiani (1892a). "Merotomy" consisted in cutting an infusorian into two halves: the nucleated part regenerated, while the anucleate half degenerated. This type of experiment, repeated by other workers (Klebs, 1887; Nussbaum, 1886; Verworn, 1891), led to the affirmation that the nucleus governs vital functions (Delage, 1899a, b; Balbiani, 1892 a, b, c).

Delage's experiments on "merogony" – particularly those (1899) that convinced him that "merogonial" larvae possess a double complement of chromosomes (and not the simple set provided by the nucleus of the sperm) – comforted him in his "organicist" theory. In this way he was able to conclude that the nucleus of the ovule is not required for fertilization and, as a corollary, that fertilization is not exclusively defined by the union of female nucleus with a male nucleus.

An experiment demonstrating the "uselessness" of the female nucleus was a real godsend for Delage. In the light of these results, he proposed a new, somewhat "*animalculistic*" definition of fertilization without entirely rejecting the ancient definition: "The union of spermatic nucleus and any given mass of ovulary cytoplasm and the transfer to this ovulary cytoplasm of a special energetic plasma contained in the spermocentre" (Delage, 1899b).

It would be inappropriate here to go into a detailed discussion of the validity of the experimental results. However, it is interesting to consider the extrapolation made from them by other biologists to support or reject their hypotheses. It is well known that biologists have always been ready to twist their interpretation of facts in the way that best suits their personal views of the living organism or the concept they wish to impose.

Although Delage affirmed the importance of the cytoplasm, he did not believe that it had the monopoly of directing phenomena (as others believed of the nucleus), but that the vital forces were governed by the nucleus and cytoplasm together (protoplasm).

After these experiments, it was only natural that Delage should turn his attention to parthenogenesis. Merogony is the union of two sexual elements, whereas parthenogenesis concerns only the development of a "larva" from a mature ovule (or the beginning of a division of the egg – abortive parthenogenesis). The interest aroused by parthenogenesis at this time was primarily due to the fact that Loeb had just published (1899) his first results concerning parthenogenetic sea-urchin larvae, obtained by chemical treatment of unfertilized eggs.

It is unnecessary to go into the numerous experimental studies on parthenogenesis performed by Delage or the ecstatic gratitude showered upon him by a handful of feminists for having "at last delivered women from the shameful bondage that obliges them to resort to men in order to become mothers" (Delage *et al.*, 1913; Delage, 1913). More noteworthy is his theory of parthenogenesis (1913), with its concept of "colloidal morphogenesis" (parthenogenetic agents were thought to bring about coagulation and liquefaction of elements contained in the "protoplasm", thus triggering the ontogenetic pathways). This theory was in opposition to that of "chemical morphogenesis" of Loeb, but possessed similarities to the notion of "electric morphogenesis" of Lillie. It was far removed from Bataillon's theory of "organic and heteroplastic catalysis".

According to Delage, it was not worth paying attention to parthenogenetic agents, for the "effective cause" was the "reaction of the egg". This idea was also to be developed by Bataillon. At the International Zoology Congress in Graz (Austria) (August 15-20, 1910), Delage read a long paper on "Experimental Parthenogenesis" in which he related the success of Bataillon in provoking traumatic parthenogenesis in a vertebrate. He qualified this experiment as "extraordinary" (Delage, 1912).

The golden age of biology

"L'âge d'or de la biologie" was the term used by Eugène Bataillon (1864-1953) (Fig. 1), to qualify that period at the beginning of the century that marked experimental biology by the success of ex-

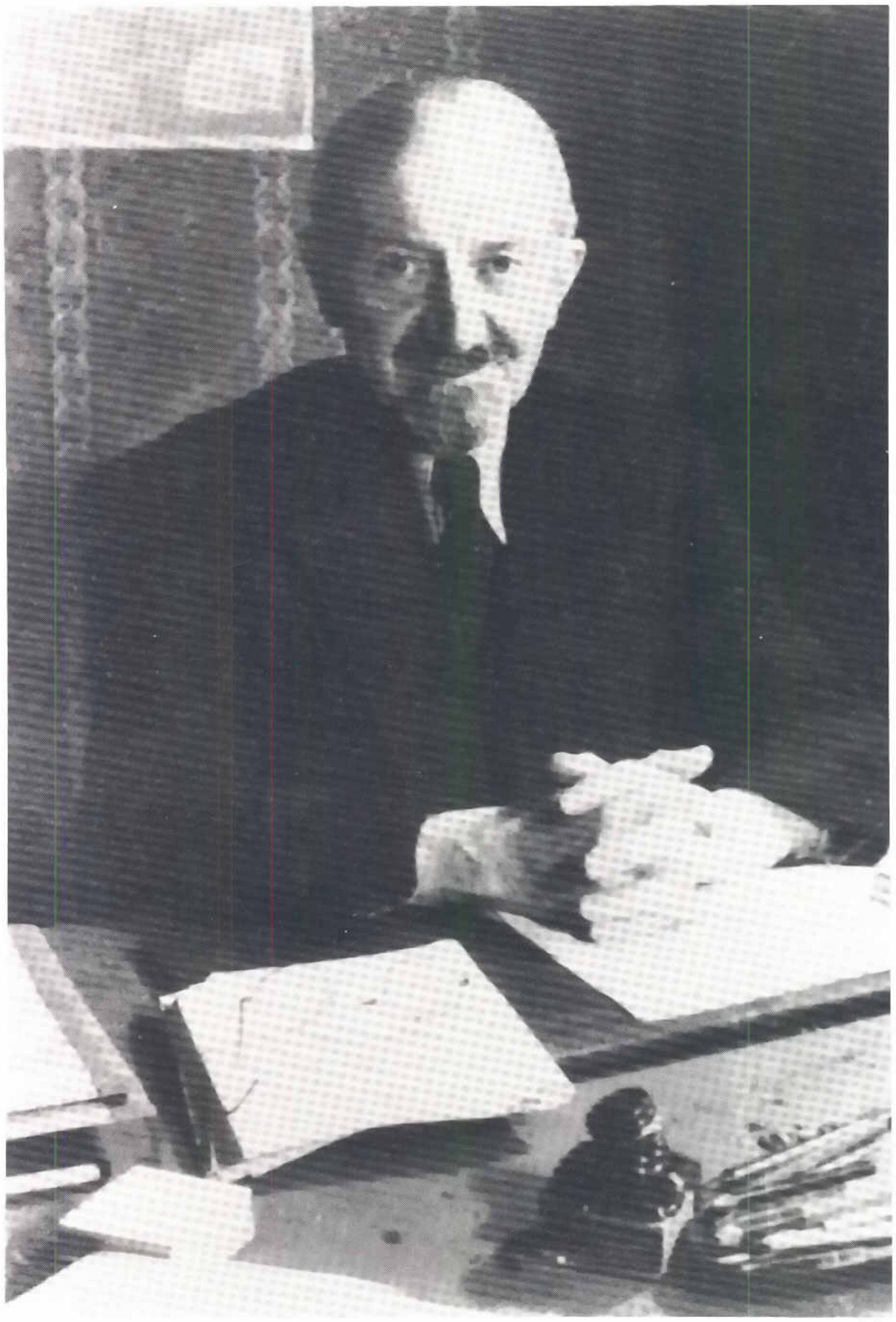

Fig. 2. Professor Paul Ancel *(1873-1961)*

perimental parthenogenesis in a vertebrate. J. Loeb's successful experiments with parthenogenesis in sea urchins influenced all subsequent research carried out on experimental parthenogenesis. Both Delage and Bataillon were greatly influenced by this type of research.

Before becoming interested in experimental parthenogenesis, Bataillon had studied the physiology and metamorphosis of anurans, with particular reference to the phenomena of histolysis and respiration which control the anatomical modifications of the tadpole. Concluding that the physiological determinism of metamorphosis amounts to little more than a collection of asphyxic phenomena (1891), he also demonstrated the importance of respiration in the ontogenesis of fish and amphibians. In fact, Bataillon, by attributing to a physiological function – respiration – a determining role both in metamorphosis and in the extension of the blastoderm (1896), was performing chemical embryology before this term existed.

In 1894, A. Giard called the attention of physiologists to "anhydrobiosis", in other words, latent life. As he was interested in this problem, Bataillon was led by the results of a great number of experiments to generalize the action of osmotic pressure as a factor responsible for certain biological events (1901).

An elevation of osmotic pressure can, in certain organisms, bring segmentation to a temporary halt in eggs that do not normally display diapause. For a given concentration of NaCl, CaCl2 or sucrose, the effects are the same. Eggs that have been in contact with salt water will, when placed in normal water, give rise to similar abnormalities of segmentation, and an excess of osmotic pressure will produce double or multiple formations from lamprey eggs. Bataillon confirmed in vertebrates the results that Loeb (in 1892) had obtained by similar means in sea-urchin eggs. In Bataillon's view at this time, osmotic pressure was also responsible for the parthenogenetic development of eggs.

In order to confirm the results of Loeb in invertebrates, as well as the experiments of O. Hertwig (1890), Morgan (1899) and Giard (1900), Bataillon attempted to obtain parthenogenesis in fish and amphibians and, in so doing, to discover the common denominator governing all these results. His experiments produced only abortive parthenogenesis. Nevertheless, he was able to demonstrate that his generalization concerning the effect of osmotic pressure was correct. In this way, he refuted the notion of specific chemical or ionic effects. Lithium (Morgan), salt (Hertwig) or sugar are no more specific as stimulators of ontogenesis than magnesium (Loeb) (Bataillon, 1901a, b, 1904).

In this context, the work of Kulagin (1898) should not be forgotten. He obtained segmentation in unfertilized frog eggs that had previously been treated with anti-diphtheria serum (Bataillon, 1900). Bataillon pointed out that the osmotic pressure of anti-diptheria (or normal) bovine serum is the same as that of 0.9% sodium chloride and carried out the following experiment: three series of unfertilized frog eggs from the same batch were treated for three hours with a 1% solution of NaCl, a 10% solution of cane sugar or bovine serum. Each lot, put back into running water, divided irregularly after several hours.

Not unnaturally, Bataillon underlined the role of osmotic pressure in this phenomenon. However, this notion could not explain everything: the "why" of development remained unanswered, and Bataillon was obliged to turn to the neo-vitalism of the german embryologist, H. Driesch, with whose principles he was in total agreement: "It is a principle of correlation that dominates the emergence of forms" (Driesch, 1899).

In other words, research into the mechanics of development should be devoted entirely to the more concrete "how" (*wie*), "without", as Bataillon wrote, "compromising itself in a vain research for the why (*warum*)".

Bataillon abandoned his studies on osmotic pressure, which resulted only in abortive parthenogenesis and turned to "heterogeneous hybridizations" (1910). In these experiments, he noted that certain hybridizations (♀ *Bufo calamita* x ♂ *Triturus alpestris*) resulted in a beginning of development of the eggs. In his "scientific testament", he wrote concerning these findings the following sentence, remarkably instructive for whoever wishes to grasp the logic of his thoughts and to understand the scientific work that was to follow: "One Sunday in March 1910, I sat hypnotized in front of my microscope, contemplating an impressive picture: a preparation of eggs of the toad *Bufo calamita* impregnated with sperm from the newt *Triturus alpestris*. The eggs were riddled with these strange male elements whose voluminous heads appeared on the slides like so many surgeon's stylets" (Bataillon, 1955).

It was at this precise moment that the idea suddenly came to him that "a slight traumatism such as a prick from a sharp glass or metal needle could be as effective as heat or hypertonicity". This insight was no doubt partly the result of Chabry's teaching Bataillon his techniques during the years they spent together, which had given him an aptitude for "tinkering about". As soon as the idea had struck him, Bataillon admitted that "at once" he prepared "glass stylets", and put eggs from a ripe female on several watch glasses. The result was beyond all expectations: he obtained 90% abortive development, about 10% rudimentary embryos, but also a few cases of swimming larvae. However, he believed that the latter derived from eggs that had been contaminated by sperm. He repeated his experiments and, all doubts gone, published his note on April 18, 1910. At last he had managed to obtain in vertebrates what Loeb had obtained ten years or so earlier in invertebrates.

However, the theoretical interpretation was not simple. At the end of 1910, re-reading the latest volume of *l'Année Biologique*, he came across a note by Guyer: "Unfertilized frog eggs injected with blood" (1907). Although parthenogenesis was not foremeost in Guyer's mind, Bataillon thought over the problem and saw in his imagination the blood that had contaminated the eggs during his early experiments on traumatic parthenogenesis. Wishing to repeat (1911) on the frog the experiments of Loeb in which unfertilized sea-urchin eggs were activated by low concentrations of cyanide, Bataillon discovered that high concentrations (0.5%-1%) of this chemical dissolved the coat that covered the eggs. Quite fortuitously, Bataillon now had in his possession a technique that was to enable him to carry out the crucial experiment: eggs from whose coat had been removed were divided into three lots. The first was impregnated with horse serum, the second with leucocytes, the third with erythrocytes, each group of eggs being subjected to the traumatic effect of the injection. With the serum, no regular cleavage was obtained; with the red blood cells about 1% regular cleavage was obtained; with leucocytes, the proportion of cleavage and gastrulae rose to 75%. Bataillon completed these results by cytological studies and concluded that parthenogenesis took place in two steps: activation by the pinprick and regulation by introduction of the nucleus: it was an exact replica of normal fertilization (see bibliography in Fischer *et al.*, 1984).

Chabry, Delage and Bataillon can be considered a group. There are a great number of affinities in their theories apart from their rejection of preformation. They may be considered the first representatives of this new biology whose strong point is experimental embryology.

Although Chabry was not allowed to develop a school through teaching, in compensation Delage and Bataillon did become professors who were able to form a generation of researchers. Delage, who taught at the Faculty of Science at the University of Paris, became in 1901 the director of the marine laboratory of Roscoff, which he baptized as his "Biological Station". The teaching career of Bataillon was spent at the Dijon Faculty of Science, and also at that of Montpellier.

II. Embryology and embryologists: from the Collège de France to a series of portraits

This, then, is the group of "founding fathers" of experimental embryology in France. There are other groups that we could identify on the basis of their similar scientific interests or the institutions they belonged to. V. Coste, G. Balbiani, F. Henneguy, and E. Fauré-Frémiet all held the Chair of Embryology at the Collège de France.

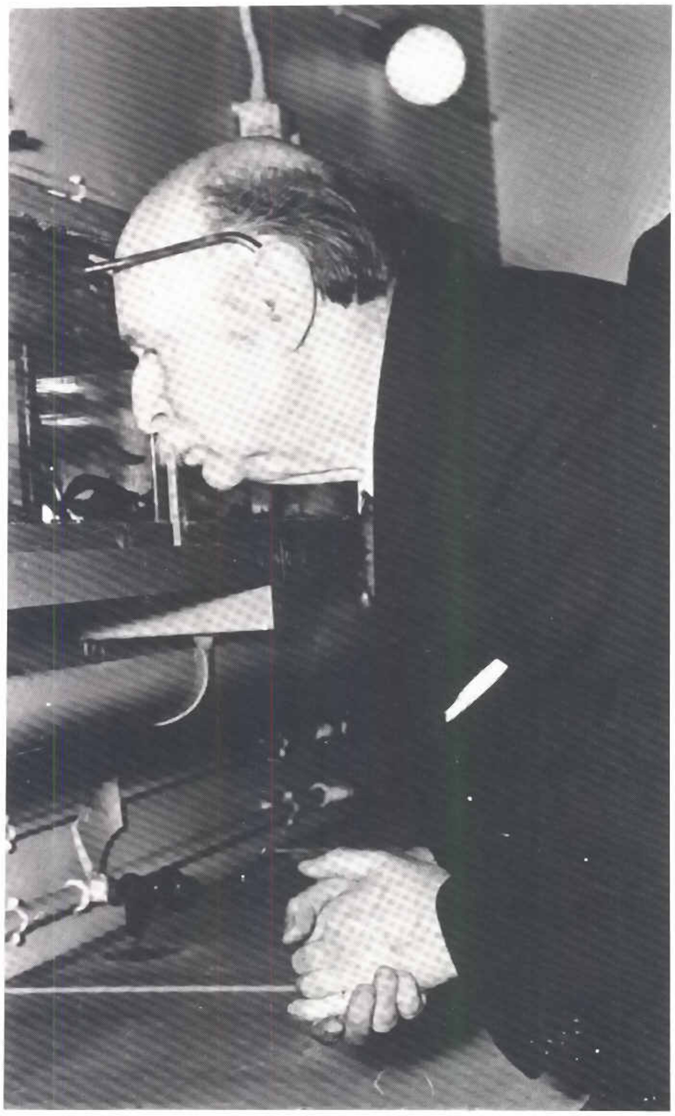

Fig. 3. Jean Rostand *(1894-1977) looking at Pleurodeles in L. Gallien's laboratory*

P. Bouin, P. Ancel, R. Courrier and E. Wolff formed another group belonging to the Nancy/Strasbourg school of anatomy, histology and embryology. There was also a group of people belonging to the University, composed of names such as A. Giard, M. Caullery, A. Michel, E. Rabaud, M. Abeloos, P. Wintrebert, etc. And there were those who taught at the Schools of Medicine, such as L. Bard, M. Aron, A. Prenant, etc. In addition to these groups, there were those who worked alone, such as J. Rostand or Dr. J. Balazuc, whom we cite here from memory, since his thesis, *La tératologie des coléoptères et expériences de transplantation chez Tenebrio molitor (L.)* dates back to 1948. This remarkable work, in the line of entomological teratology and embryology of P. Cappe de Baillon (1927), was never followed up. And we could complete the list with the histologists, the specialists in marine invertebrates, for in addition to the experimentalists, there were those whose work was descriptive and who proceeded from simple observation without any experimentation. The work of this type of researcher is not without interest for the experimentalists, since it provides the basis for analyzing the results of experiments. A thorough knowledge of normal development is essential to understanding the "mechanisms" that experimentation brings to light. The historian who attempts to analyze experimental embryology from 1887 to 1936 will find that the field is vast, and indeed far too vast to be able to discuss within the scope of this article all the factors that contributed to the development of embryology in France.

The Chair of Embryology at the Collège de France

On August 4, 1844, a royal decree was issued creating the Chair of Comparative Embryogeny at the Collège de France for Victor Coste (1807-1873) (Fauré-Frémiet, 1929a), who was named for the Chair on September 2, 1844. It is to Coste that we owe the introduction into France of scientific embryology: he is the one who made the break with abstract, speculative embryology developed within the framework of transcendental anatomy – closely related to the German *Naturphilosophie* or philosophy of nature – of the school of E.R.A. Serres and E. Geoffroy Saint-Hilaire.

Gérard Balbiani (1823-1899) (Henneguy, 1900) became Coste's successor in 1874, after having been the "head of histological research" at the physiology laboratory of the Museum of C. Bernard. To him we are especially indebted for his research entitled "On sexual phenomena in infusorians" (1861) and "Research on germ constitution in the animal egg, before fertilization" (1864). For this work he was twice awarded the Montyon Physiology Prize, which at that time was a very distinguished award in the world of science (Egli, 1970). His *Lessons on the generation of vertebrates* (1879) were edited by his pupil, F. Henneguy and became a fundamental work for embryologists of that period. The name of Balbiani is also associated with experiments in merotomy and with *Archives d'Anatomie microscopique,* which he founded together with L. Ranvier in 1897.

In 1900, F. Henneguy (1850-1928) (Fauré-Frémiet, 1929b), succeeded to the Chair of his professor, Balbiani. Like Balbiani, he had spent a period of time at the laboratory of the Museum of C. Bernard, and had developed a passion for cytology, which was becoming the leading discipline in biology thanks to the work of E. Strasburger (1875) and W. Flemming (1879-1882) on cell division. If embryologists know of Henneguy especially for his studies on the embryogeny of the trout (1889), he is above all, like Balbiani, a cytologist and protozoologist: indeed, he recalled in 1901, "M. Balbiani and I were the first, in France, to study karyokinesis (i.e. mitosis) in animals...".

Embryologists in the early 1880s were concerned with the structure and functioning of the cell. This interest should be considered a logical outcome of the studies of comparative embryology that took the egg as their starting point. The embryologist scrutinizes the constitution of the cell (its protoplasm, its nucleus) as the original element of the organism and as part of a pluricellular whole, but also as a specific unit, as a living being that nourishes itself and is reproduced (unicellular organisms). This new generation of embryologists of the 1880s also represents a break with the comparative biologists of the period from 1860-1870, who, accustomed to "the Darwinian effect", used embryology with the aim of discovering the phylogenetic origins of living beings. Now, phylogenetic problems would no longer be the final aim of embryological studies. Thus, Henneguy agreed with A. Kölliker (1882), who wrote: "The right thing for embryology to do is follow its own path and, leaving aside phylogenetic hypotheses, work to discover the laws governing the formation of organs..." (Kölliker, 1882).

Henneguy, who was a contemporary of "biomechanics", was by no means an inconditional believer in experimentation, for without denying the important role that it played in contributing to the progress of embryological knowledge, he was also convinced of the importance of the role played by mere observation. "After a number of years," he remarked, "embryogeny has entered upon the experimental pathway, and certain biologists who are attracted by the new methods seem only to attach importance to results obtained by experimentation, and to consider simple observation as impotent for solving most problems in embryology. Without sharing this view, I consider that experimentation can yield great services to embryogenists as a method of control..." (Henneguy, 1901).

As a cytologist, Henneguy rejected the "micromerist" theory of Weismann. Like Delage and the French movement that rejected the neo-preformation theory, he remained convinced of the firm basis of the laws of hybridity: to be against the micromerist theories of heredity and against Morganic genetics did not mean a rejection of Mendelism.

Having left numerous embryological works on sexual cells and on organogenesis, Henneguy also distinguished himself with his research on protozoology and on histology, disciplines that contributed to his embryological research.

Recalling the teachings of Henneguy at the Collège de France, his former pupil and son-in-law E. Fauré-Frémiet wrote: "It is by delving deeply into his teachings, in which both the scientific and moral seem to interlock, that one comprehends how important the influence was of this professor on those who had the opportunity of approaching him" (Fauré-Frémiet, 1928).

Fauré-Frémiet's view of himself was as follows: "Born into a family of artists, where my parents were my first teachers, it was perhaps through learning to see the form of beings and of objects, and through understanding the moving unity of a melodic pattern, that I was led towards the study of the living being (Fauré-frémiet, 1928). Emmanuel Fauré-Frémiet (1883-1971) (Willmer, 1972), whose intellectual sensitivity had led him to see the logic of a continuity between art and science, was designated the next successor to the Chair of Comparative Embryogeny at the Collège de France, so dear to the scientific interests of Henneguy. He also began work at the embryogeny laboratory of the Collège de France in 1911, at first as a lab assistant, and later as sub-director and as assistant professor, before being named to the Chair in 1928.

For Fauré-Frémiet, embryology is simply a chapter in the developmental sciences, which must resort to various biological disciplines. Research in embryology must be simultaneously descriptive and morphological, experimental and physiological. The idea of development is in his mind inseparable from the idea of the organism or the living being (Fauré-Frémiet, 1925). He further felt that his studies (*The Kinetics of Development, Cell Multiplication and Growth* (1925) on protozoans and on sexual cells, which were particulary useful models for understanding the mechanics of development, were the result of this intellectual achievement, and gave a new meaning to embryology.

Balbiani, Henneguy and Fauré-Frémiet represent the line of embryologists that approached developmental science through cytology and protozoology. The "protozoological" tendency is the one that, in France, led to the establishment of genetics as a science in the 1940's, and it is therefore logical that B. Ephrussi learned from Fauré-Frémiet and published together with him from 1925 to 1928 (Willmer, 1972; Burian *et al., 1988*).

As Fauré Frémiet's successor in 1955, E. Wolff broke with the tradition of cytologists and protozoologists by introducing into the Collège de France a new tradition – that of the Nancy/Strasbourg school of morphology and embryology. The Chair of Comparative Embryogeny was also to change names and become the Chair of Experimental Embryology (1955) (Wolff, 1955).

The Strasbourg school of embryology: P. Bouin, P. Ancel and E. Wolff

Because of the Prussian occupation, on March 19, 1872 the Medical School of Strasbourg was moved to Nancy, which had managed to avoid the occupation (Maubeuge, 1973). This was the date that the Nancy School of Morphology was founded (Legait, 1975), with Charles Morel and his pupil, Mathias Duval, with Edmond Lallement whose successor to the Chair of Anatomy, Adolphe Nicolas, who founded the Association of Anatomists (1899), was to have Paul Ancel (1873-1961) as a pupil. Ancel (Wolff, 1962) would hold the Chair from 1907 to 1919. Morel's Chair of Histology was eventually held by Léon Baraban and then Auguste Prenant, author of the voluminous *Eléments d'embryologie de l'homme et des vertébrés* (1891). Later on, Pol Bouin (1897) worked under Prenant, who directed his thesis, and Bouin later became Prenant's successor, in 1908.

After he had begun his curriculum in Nancy, Robert Courrier (1895-1986) (Jost, 1986), following the liberation of Alsace, went on to Strasbourg, whose University revived and built a new Medical School. Bouin left Nancy and founded in Strasbourg the Institute of Histology (1919), and was later followed in the Alsacian capital by Max Aron and Jacques Benoit. It was at this Institute that Courrier pursued his studies under Bouin and began his scientific career in sexual endocrinology.

Similarly, Ancel left Nancy to teach embryology at the new Medical School at Strasbourg (Chair of Embryology, November 22, 1919). Among his earliest collaborators were P. Vintemberger, S. Lallemand (his daughter) and, a bit later, E. Wolff.

In Nancy, Bouin and Ancel collaborated together on research in sexual histophysiology, which was to lead them to the eventual discovery that the interstitial tissue of the testicle corresponded to the only testicular endocrine gland secreting the male hormone: their work forms the basis of sexual endocrinology. In this regard, an unsigned typescript dated January 17, 1940 has been preserved in the dossier/file on P. Bouin in the archives of the Paris Academy of Sciences, showing that P. Bouin and P. Ancel were nominated for the Nobel Prize.

Whereas Bouin was engaged in carrying out research in sexual histology, histophysiology and endocrinology in Strasbourg, Ancel (Fig. 2) for his part was on the point of developing new lines of research in experimental embryology, especially from 1924 on. Ancel was not the first to introduce experimental embryology in France, but he was the one who gave it a new direction.

1924 was the year of his first publications, in collaboration with P. Vintemberger, concerning the action of X rays on embryonic development. Although this was not the first time that Ancel worked with radio-biology – since he had, in 1907, published together with

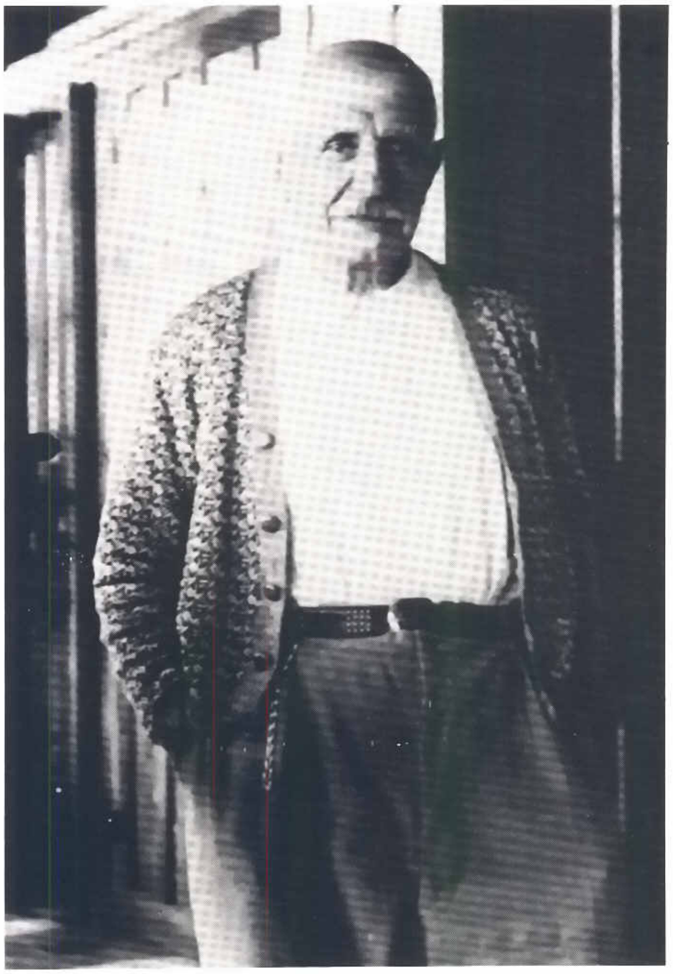

Fig. 4. Professor Maurice Caullery *(1868-1958), in the marine laboratory of Wimereux (destroyed during World War II) in 1938*

Bouin a work on *"Rayons X et glandes génitales"* (X Rays and the Gonads) – it was the first time that he had used this technique in embryology: according to E. Wolff, "it was with P. Vintemberger that he established the principal laws concerning the effect of X rays on the cell. He settled the question of the erstwhile stimulative action of these rays by showing, on amphibian eggs and bird blastoderms, that cells undergoing mitosis are not more sensitive than interphasic cells, but that the latter manifest their lesions during the course of mitosis.... Another very general law concerns the cumulative effect of doses over the course of successive irradiations." He further showed that embryonic cells are radiosensitive during the morphogenetic phases: all differentiation processes cease in these cells, whereas cells that have not yet begun morphogenesis at the moment of irradiation can, in the future, carry out their differentiation (1924, 1925, 1928). In addition, Ancel and S. Lallemand were able to document the phenomena of "radiophylaxis" in germinating plants (1928).

In 1932, Ancel and Vintemberger began carrying out research on the bilateral symmetry of the fertilized brown frog egg – research that was still being conducted in 1938. Concerning this work, J. Rostand (1966) stressed that this bilateral symmetry corresponded to a "fundamental event in development: the egg had a top and a bottom and must now have a right and a left". Meanwhile, Ancel welcomed E. Wolff as his assistant in the laboratory, and proposed that Wolff "try to induce localized lesions on the chick embryo". Wolff began his research in February 1932, and then perfected, together with Ancel (Ancel and Wolff, 1933, 1934), the technique of localized X ray irradiation "on a territory of precise size and shape on a blastoderm". Their aim was to identify and describe the precise organ-forming areas of the chick embryo, "following the model that Vogt had established for the amphibian embryo". Their results were not long in coming, and in 1933 Wolff started publishing a series of ten notes on omphalocephalic chick embryos, on the topography of presumptive liver primordia, on the experimental creation of double-hearted monsters, etc. and a report entitled *Recherches sur la structure d'Omphalocéphales obtenus expérimentalement* (Studies on Structures of Experimentally Obtained Omphalocephalic Chickens). In 1936, he defended his thesis entitled, *Les bases de la tératogenêse expérimentale des Vertébrés amniotes, d'après les résultats de méthodes directes* (The bases of experimental teratogenesis in amniote vertebrates, as shown in results obtained from direct methods). Moreover, it was also in 1936 that Wolff opened up in France a line of research on sexual differentiation, as a result of the discoveries made in sexual endocrinology and the success of chemists, biochemists and the chemical industry in extracting and making pure preparations from synthetic sex hormones (steroid hormones, 1935-1936) (Girard, 1933; Butenandt, 1936; Collin, 1938; Wolff, 1946). Thus, in 1936, Wolff began establishing the bases of his future school.

Portraits of embryologists

"Y. Delage had a considerable influence on me; he was enthusiastic and preached by example." With this statement, written in 1922, P. Wintrebert acknowledged his intellectual filiation and affinity with the ideas of the French neo-Lamarckians in creating "Lamarckian chemistry", from which he developed his theory of the heredity of acquired characteristics. Paul Wintrebert (1867-1966)(Grassé, 1966), who began his scientific career in medicine, quickly turned to the biological sciences, and studied under Alfred Giard, to whom he owed his training. Wintrebert succeeded Georges Pruvot to the Chair of Comparative Anatomy and Physiology at the Paris Faculty of Science in 1923 (on June 9, 1923, this Chair was to be rebaptized the Chair of Comparative Anatomy and Histology). Under Pruvot, who had been the successor of Lacaze-Duthiers at the marine sciences laboratory in Banyuls, Wintrebert cultivated a life-long attachment to this important marine biology facility.

We owe to Wintrebert the discovery, in April 1906, of the presence of *Discoglossus pictus* (Oth.) in Banyuls. This anuran amphibian was to become a favorite material among embryologists. However, it was not until the years between 1928 and 1931 that Wintrebert carried out his extensive research on the embryology of the painted frog. One year prior to the work of Ancel and Vintemberger, Wintrebert had used the technique of staining to study the patterns of bilateral symmetry in the egg of *Discoglossus*. The technique initiated by W. Vogt in 1925, which he perfected at the same time as Weissenberg by using Bismarck brown, also enabled him to define the fate maps of *Discoglossus*. But Wintrebert's conclusions have not survived, nor has the majority of his embryological research. A staunch believer in epigenesis, which for him was "the only real mode of development", he adapted his observations to his theoretical ideology. Contrary to the tendency among many embryologists, who reached a compromise between preformation and epigenesis, Wintrebert refused to go along with this theoretic dualism: "Epigenesis reveals, in amphibians, the existence of an initiater center and an organizer center, which are, in the literal sense, germinal locations, but which differ essentially from those of the preformists in that they they do not contain organ-forming substances and are not predestined. They fulfill the inductor functions in the embryo. The latter must not be confused with the ulterior capacity of the cells of these centers and of their fields of induction to differentiate the primordia induced by the organizer center" (1933).

Because his early training was in the field of comparative anatomy, Wintrebert was to remain throughout his scientific career drawn more towards the study of function than to the study of structure (*la fonction fait l'organe*): "Indeed, it is only by analyzing the most intimate processes of functions, rather than by doing violence to living beings or imagining how they might be pre-organized, that we will discover the secrets of life and evolution" (1962).

At the age of 95 to 98, Wintrebert published a trilogy in which he explains and develops his position on life and the living being: 1) *Le vivant créateur de son évolution* (The living being is the creator of his own evolution) (1962); 2) *Le développement du vivant par lui même* (The self-development of the living being) (1963); and 3) *L'existence délivrée de l'existentialisme* (Existence delivered from existentialism) (1965). Among all his contemporary scientists, only P.P. Grassé, due to a certain affinity of theoretical ideas, manifested any interest in the work of Wintrebert (Grassé, 1973).

Wintrebert and Rabaud, who studied under Camille Dareste (Fischer, 1987a, 1989) and to whom we owe the first experimental production of monsters and the discovery of the duality of the cardiac primordium in the chick embryo, are today considered of only marginal interest because their ideas are not recognized by the scientific community. From the point of view of the biological historian, these men held important institutional positions and attained these positions thanks to decisions made by their peers; they went along with a certain mode of thinking, and therefore belonged to a scientific trend that at one time had possibilities. They were part of the "scientific scene" of a given period, and in this sense are worthy of our attention. The *"logique du vivant"* was not the same for everyone.

How many people are familiar today with the name of L. Bard? And yet this associate professor of the Lyon Medical School, who was a specialist in tumors, discussed in 1886 on "Cell specificity and histogenesis in the embryo": he proposed the theory of the *arbre histogénique*, which views all the cell lines involved in making up the future being as already predetermined in the egg cell. The cells are not differentiated at the beginning of embryogenesis but are, however, rigorously determined. Cell division is nothing more than the process of distributing the different categories of cell. In this theory, the anisotropy of the egg is absolute. We owe to Bard the clear development of the thesis of cell lines using a "genealogical tree of ontogenesis" (Bard, 1886) three years before De Vries (1889), to whom this concept is generally attributed. Bard's theory is close to the micromerist theories of De Vries and Weismann, and therefore to neo-preformation. Bard's idea logically could not avoid triggering the criticism of Delage, because it did not correspond to the scientific ideals of the French biologists of the period.

For his part, A. Michel, in the opening lesson of his course on General and experimental morphology taught at the Sorbonne in 1902, came out in favour of epigenesis and preached "the ideal of a mechanistic future" (Michel, 1902).

In describing his re-encounter with Jean Rostand (Fig. 3), Bataillon recalled their first conversation: "There we were at the beginning of the century, in that golden age of biology with its long list of famous researchers: Morgan and his famous team, those great experimenters whose names are Loeb, Delage and Brachet; Wilson, Spemann and that impressive cortege of embryologists that shed light on the mechanics of early development. From the amphibian to the sea urchin, from *Drosophila* to man, from heredity and sex to the transformist hypothesis, our thoughts touched on all the great enigmas of Life" (Bataillon, 1953).

Jean Rostand (1894-1977) (Dubois, 1977; Tétry, 1983; Fischer, 1987b) shares certain similarities with Delage and Bataillon. With Delage, because he was attracted from youth to the great problems of biology, and as the inventor of merogony is responsible for having awakened the French scientific community to the importance of developing the study of this new biology. With Bataillon, because he undertook research that completed that of the discoverer of traumatic parthenogenesis.

Similar to Delage in his desire to make biology accessible to the layman, Rostand published, during the period we are concerned with here, a number of works on biology designed for the general reader, among which his *Les chromosomes, artisans de l'hérédité et du sexe* (Chromosomes: the artisans of heredity and sex) (1928) was especially singled out for special praise by Bataillon.

During the 1920s, Rostand published many notes on biology and embryology concerning insects, such as the habitat of pedogenic larva of the Miastor genus (1922), half fly larvae obtained by egg ligature (1927). The latter experiments were modeled on Spemann's work on egg ligature in urodeles and the regulation of the egg.

The fascinating experiment of Bataillon, as Rostand called it, revealed two steps in the mechanism of traumatic parthenogenesis: activation and regulation. Bataillon was especially interested in the problem of activation, whereas Rostand worked on the problem of regulation. It was through his study of the second step that Rostand began his work on the problem of traumatic parthenogenesis. Traumatic parthenogenesis by dry sperm (1924), or by sperm treated with sodium fluoride, glycerine, alcohol, acetone (1926) wherein certain positive results seemed to "plead in favor of the presence in the sperm of fertilizing catalysts (1926). In 1928, he published his results on the *"catalyseur-noyau"* (catalyzing nucleus) in traumatic parthenogenesis.

Within this same vein, he made test hybrids among different species of amphibians of the same or different genus, and he discovered the favorable influence of cooling on the development of these "hybrid" eggs (gynogenesis) (1933-1934). It was as a result of these observations that he was drawn to the technique of gynogenesis: the diploidizing effect of cold was to be the most remarkable result of this work.

This diploidizing effect of cold was, in the USA, demonstrated cytologically by G. Fankhauser in 1939. The results of Rostand provided the basis for the work of Fankhauser and his school on experimental polyploidy.

It was as a "peerless professor" and "mind-opener" (*"éveilleur* *d'esprit"*) that Rostand remembers the teachings of Maurice Caullery: "In my youth I went often to both of the laboratories that Professor Caullery successively directed: first, the venerable building in the Rue de l'Estrapade, where I studied for my diploma in general embryology and was one of only four candidates; later, that bright and imposing building on the Boulevard Raspail" (Rostand, 1966). The Evolution of Organized Life Laboratory was created by the city of Paris for Giard in 1888 and the Chair in 1892; the laboratory on the Boulevard Raspail was built in 1923 (Viré, 1979).

Maurice Caullery (1868-1958), the successor of Alfred Giard, cannot be defined as an embryologist, but he had such close relations with this general biology discipline that one cannot avoid mentioning his name (Fig. 4). First, because of the publication of his lectures: *Les problèmes de la sexualité* (1913) and *Les progrès récents de l'embryologie expérimentale* (1939), and then because of his prefaces to embryological works that have since become classics: the preface to *Traité d'embryologie comparée des Invertébrés* by C. Dawydoff (1928), the preface to the book by his pupil, M. Abeloos, entitled *La régéneration et les problèmes de la morphogenèse* (1932), etc. Other pupils of Caullery who made a name for themselves in biology were, for example, E. Guyénot, A. Vandel and L. Gallien.

Albert Raynaud, who studied under A. Vandel at the University of Toulouse, was recommended by the latter and by M. Caullery to Antoine Lacassagne, director of the Laboratoire Pasteur on the Rue d'Ulm in Paris (Raynaud, 1975). He entered the laboratory in October 1936, and his thesis, *Modification expérimentale de la différenciation sexuelle des embryons de souris par action des hormones androgènes et oestrogènes* (Experimental modification of sexual differentiation in mouse embryos using androgen hormones and estrogens) published in 1942, marked a period in the history of embryology concerning the problems of sexual morphogenesis.

It was in 1931, in the "Laboratoire d'évolution des êtres organisés" on the Boulevard Raspail, and at the marine laboratory in Wimereux that Louis Gallien began his scientific career. There he wrote his thesis on a parasitic Trematode worm, *Recherches expérimentales sur le dimorphisme évolutif et la biologie du Polystomun integerrimum Froel* (Experimental research on evolutionary dimorphism and biology of *Polystomum integerrimum Froel*) (1935). That same year was decisive for him: "1935 was the year that determined my final orientation. The progress made in my studies of the endocrinology and embryology of sex was, in this regard, decisive" (Gallien, 1962). The career of Gallien had been decided, and he was to become one of the major figures in French embryology.

Conclusion

Experimental embryology was born of a *theory* and a *method*. The theory was established by His in 1874 and developed by Roux during the 1880s. This was a theory that saw the entire individual as contained within the egg cell, with the successive divisions of this cell being nothing more than the distribution of the different elements that would go into forming the increasingly specialized cell lines that eventually give rise to the different tissues and organs. This is the mosaic theory, the basis of the micromerist theories with their representative particles contained within the nucleus; it is the origin of neo-preformationism.

The method was born with the introduction of experimental handling of the embryo or the blastomeres. It was, using the terminology of Fol and Warynski, the direct method. This method contrasted with the indirect method, which was then practiced by Dareste. The indirect method consisted in subjecting a whole embryo to the effect of a teratogenic agent. Fol and Warynski wished to understand the mechanism of embryonic development; Dareste wanted to engage in experimental transformation (Fischer, 1986, 1987a). Both had adopted a method that responded to the biological problem posed by them.

This direct method in embryology was applied by Roux, in Germany, on frog eggs, and by Chabry, in France, on ascidian eggs. The experimental results spoke in favor of a neo-preformation – the egg was a mosaic. But the same method applied to the sea-urchin egg produced converse results: the egg regulated. In other organisms, these new embryologists discovered eggs with regulation: these experiments nurtured the arguments in defence of neo-epigenesis. The debate between these two fundamental theories concerning generation and heredity was set off starting in the 1890s.

Scientists took up different theoretical positions not only on the basis of the experimental material used, but also on the basis of personal ideology. O. Hertwig defended neo-epigenesis; Driesch took the side of neo-epigenesis in the early 1890s, only to decide in 1896 that neo-preformation was the only theory capable of explaining the phenomena of embryogenesis. In France, the tendency is towards neo-epigenesis, whereas in the English-speaking countries, scientists lean towards neo-preformation.

In any case, embryologists, who were to be more conciliatory than geneticists after 1910, ended up adopting both theories. From Roux to Wolff and Gallien, without forgetting Dalcq, one had to admit that the only logical and rational course was to reach a reconciliation of theories. The result was that the embryologists continued, as regards theory, to lean towards epigenesis. "Thus, epigenesis triumphs in many regards... If epigenesis means that everything is not preformed, one must nevertheless remember that everything is indeed prepared".

Th. H. Morgan, who began his scientific life in experimental embryology, refused to follow the theoretical ideal of the geneticists (Morgan, 1936). If the geneticists preferred neo-preformation to neo-epigenesis, it was because they had a reductionist view of biological phenomena. On the other hand, if embryologists were able to reconcile neo-preformation and neo-epigenesis, it was because they considered that biological events could be explained only through a dualist theory. This is the essential teaching from embryology.

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