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History of the research group "Formations squelettiques" at the Paris-7 University (1968–2008)☆

Histoire de l'équipe de recherche « Formations squelettiques » à l'Université Paris-7 (1968–2008)

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ABSTRACT

The research group known as "Formations squelettiques" team, specialized in the study of mineralized tissues of vertebrates, has been active for 40 years, starting in 1968. In this paper, we review the history of this group from its most remote roots – the original chair of Comparative Anatomy at the Faculty of Sciences in Paris – and explain its specialization in the study of bone histology during the second half of the 20th century. Many techniques were developed in the lab over these decades, as well as important partnerships among researchers that ultimately resulted in a lively community of paleohistologists and new generations of scientists involved in the development of this discipline.

RÉSUMÉ

Le groupe de recherche intitulé équipe « Formations squelettiques », spécialisé dans l'étude des tissus minéralisés des vertébrés, a été actif pendant 40 ans, depuis 1968. Dans cet article, nous retraçons l'histoire de ce groupe depuis ses plus lointaines origines – la chaire originelle d'anatomie comparée de la faculte des sciences de Paris – et expliquons sa spécialisation dans l'histologie osseuse au cours de la deuxième moitié du XX^e siècle. De nombreuses techniques ont été développées au laboratoire au cours des dernières décennies, ainsi que d'importants partenariats entre chercheurs qui ont abouti à la création d'une active communauté de paléohistologistes et à de nouvelles générations de scientifiques impliqués dans le développement de cette discipline.

☆ This paper is dedicated to the memory of Professor Yves François (1914–2000), initiator of the research group "Formations squelettiques".

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Introduction

L'équipe de recherche « Formations squelettiques » est un regroupement d'enseignants–chercheurs et de chercheurs qui ont développé leurs activités sur une bonne quarantaine d'années, soit de 1968 à 2008. Leurs travaux scientifiques concernent essentiellement l'étude comparative des tissus squelettiques des Vertébrés, dans des perspectives fonctionnelles et évolutionnistes.

Un peu d'histoire

Avant la Révolution, les scientifiques dépendent pratiquement du mécénat aristocratique et royal. A Paris, outre l'Académie des sciences (1666), les deux seuls établissements scientifiques structurés sont le Collège royal (créé en 1530) et le Jardin du roi (créé en 1639), qui deviendront respectivement Collège de France (sous la Restauration) et Muséum national d'histoire naturelle en 1793. Pour ce qui concerne les sciences de la nature, c'est surtout ce dernier qui va féconder l'université de Paris, aussi bien dans le domaine de la recherche que dans celui de l'enseignement supérieur au début du XIX[e] siècle. Pour les sciences animales, ce sont Georges Cuvier et Étienne Geoffroy St-Hilaire, à l'époque professeurs au Muséum, qui vont initier la chaire universitaire de zoologie et d'anatomie comparée.

Après plusieurs décennies et diverses appellations, ces deux chaires étaient devenues « zoologie » et « anatomie et physiologie comparées » à la veille de la deuxième guerre mondiale. Cette dernière chaire échoit à M. Prenant (1893–1983) en 1937. Cours, travaux pratiques et recherches scientifiques se font à la Sorbonne jusqu'au début des années 1960, où la faculté des sciences s'installe à la Halle aux Vins, dans des locaux neufs et adaptés à ses missions : enseignement supérieur et recherche fondamentale.

L'anatomie comparée des années 1950

La chaire dirigée par Marcel Prenant est constituée du laboratoire d'anatomie et d'histologie comparées. L'un des grands mérites de M. Prenant est d'avoir développé un enseignement des techniques histologiques. Dans son laboratoire, la recherche scientifique n'est pas organisée en équipe autour d'une thématique scientifique précise. Chaque chercheur a son sujet de recherche sur un modèle animal qui « lui appartient » ; son outil principal reste l'histologie topographique avec ses applications histochimiques pour décrire l'organisation générale de l'animal, son développement et/ou ses particularités biologiques. Les "invertébrés" ont occupé une place de choix dans les thèses soutenues pendant ces années. Toutefois, les Vertébrés n'étaient pas absents des préoccupations du laboratoire d'anatomie et histologie comparées. C'est dans le laboratoire de M. Prenant, et plus particulièrement dans ce noyau fécond de chercheurs spécialisés sur l'anatomie des actinoptérygiens, que s'enracine l'équipe « Formations squelettiques ». En 1965, Marcel Prenant prend sa retraite et son laboratoire est divisé en deux entités : le laboratoire d'anatomie comparée, avec comme directeur Charles Devillers (1914–1998), et le laboratoire de cytologie, sous la direction de René Couteaux (1909–1999).

Avec la création d'un nombre assez conséquent de postes universitaires d'enseignants–chercheurs, les laboratoires parisiens ont recruté de jeunes assistants motivés aussi bien par l'enseignement supérieur que par la recherche scientifique ; heureux temps où le recrutement se faisait directement après obtention de certificats « approfondis », d'un DES, d'une thèse de 3[e] cycle ou encore d'une agrégation ! Ces jeunes enseignants ayant reçu une solide formation en zoologie et anatomie comparée, le terrain était prêt pour une restructuration de la recherche et une nouvelle aventure scientifique : des chercheurs solitaires des années 50, avec des sujets de recherche disparates mais réunis autour d'une même technique, l'histologie, on passe à des équipes de chercheurs concentrés sur une thématique scientifique qui devient le fil conducteur des programmes de recherche.

Naissance et premiers pas de l'équipe

Avec les remous de mai–juin 1968, la faculté des sciences de Paris disparaît au profit de la création de deux universités : Paris-6 (Pierre-et-Marie-Curie) et Paris-7 (Denis-Diderot). Dans le laboratoire d'anatomie comparée, cinq équipes se constituent, chacune autour d'un chef d'équipe. L'équipe des formations squelettiques s'organise autour d'Yves François (professeur) et Armand de Ricqlès (maître-assistant) et recrute plusieurs assistants et des personnels techniques.

Les tissus squelettiques de vertébrés étant fortement minéralisés, l'utilisation de la microtomie à la paraffine nécessitant la disparition du composant minéral, l'os perd ainsi ce qui fait sa spécificité. Il faut donc se tourner vers les techniques pétrographiques et les adapter aux tissus osseux et dentaires. Les résines polymérisables se substituent à la paraffine, la tronçonneuse à disque diamanté associée à la polisseuse remplace le classique microtome de Minot. Enfin, des générateurs de rayons X adaptés aux faibles épaisseurs des lames minces de tissus minéralisés permettent des études qualitatives et quantitatives de la composante minérale (Boivin et Baud, 1984). Grâce à ces techniques, les chercheurs accèdent au riche domaine des fossiles, qui offrent alors toute une dimension historique de l'évolution des tissus squelettiques sur plus de 500 millions d'années (Chinsamy et al., 1995 ; de Ricqlès, 1977, 2007 ; Meunier, 2011 ; Steyer et al., 2004. . .). Par ailleurs, la quantification de la dynamique osseuse et la chronologie de sa croissance sont analysées grâce au marquage vital (de Margerie et al., 2004 ; Meunier, 1972, 1974 ; Sire et al., 1993 ; Trébaol et al., 1991).

Développement et vie de l'équipe

Pour assurer son dynamisme et sa vitalité, une équipe de recherche a besoin de moyens financiers à la hauteur de ses ambitions et doit former de jeunes chercheurs. Pour attirer les étudiants vers la recherche sur les tissus minéralisés, les membres de l'équipe se sont investis dans la création et dans la participation aux enseignements du DEA

« Structures et fonctions dans l'évolution des vertébrés », à partir de 1981.

Pour développer les recherches, il faut des moyens financiers supérieurs à ceux octroyés par l'université. Dans cette période de fin des années 1970/début des années 1980, la meilleure piste est d'obtenir le soutien du CNRS, qui apporte reconnaissance scientifique et moyens de travail. Mais ce dernier privilégiant des groupes conséquents, l'équipe s'associe avec celle dirigée par Françoise Jouffroy, « Locomotion animale », sise en anatomie comparée au Muséum national d'histoire naturelle, et obtient la création de l'URA 1137 en 1985.

Ontogenèse, structure et fonctions des tissus squelettiques

Le cœur de la thématique scientifique est l'étude comparative des tissus squelettiques, chez les Vertébrés, dans une perspective évolutionniste. Dans un premier temps, les travaux portent sur le squelette des actinoptérygiens aux reptiles ectothermes (actuels et fossiles) : ontogenèse, différenciation, croissance, vieillissement, fonction, histoire. Puis, Mammifères et Oiseaux sont venus enrichir le spectre de modèles biologiques. L'étude comparée des tissus squelettiques (surtout osseux) est au carrefour de nombreuses applications thématiques (Fig. 1) qui dynamisent l'équipe et qui ouvrent la voie à de multiples collaborations nationales et internationales pour l'ensemble de ses membres.

Les tissus squelettiques minéralisés peuvent être considérés comme des « boîtes noires », dans la mesure où ils possèdent une certaine pérennité dans les organismes. Le décryptage de l'intimité structurale de ces tissus conduit à des interprétations fonctionnelles du squelette et, plus largement, des organismes. Les résultats obtenus sur les organismes actuels sont même étendus, dans la mesure du possible aux fossiles, dès lors que les tissus sont bien conservés. On passe ainsi d'une anatomie comparée statique à une anatomie comparée fonctionnelle et évolutionniste, le tout dans un cadre darwinien.

Enfin, il faut signaler une initiative originale et qui a contribué au rayonnement de l'équipe : la création du Groupe d'étude pratique de squelettochronologie (GEPS) en décembre 1977. Cette structure voulait répondre à une forte demande de la communauté scientifique. Sur une période de 25 ans, ce sont plusieurs dizaines de chercheurs, chevronnés ou débutants, en provenance des divers pays (Canada, États-Unis, Pérou, Côte d'Ivoire, Mali, Afrique du Sud, Tunisie, Maroc, Espagne, Portugal, Pologne, Grande-Bretagne, Grèce...), mais aussi de France, qui sont venus travailler dans le cadre du GEPS pour apprendre les techniques de squelettochronologie. Cette activité scientifique fructueuse a conduit à l'organisation de « tables rondes » (Société zoologique de France, 1980), de colloques (Colloque de Bondy in 1991 ; Baglinière et al., 1992) et à la participation à différents ouvrages de synthèse spécialisés (Castanet et al., 1993 ; de Ricqlès et al., 1991 ; Francillon-Vieillot et al., 1990 ; Zylberberg et al., 1992).

On ne peut donner ici qu'un bref aperçu des principaux résultats scientifiques de l'équipe. On notera la découverte et l'explication du « double contreplaqué torsadé » de l'écaille des Sarcopterygiens actuels (*Latimeria*) et fossiles, qui demeure un modèle biophysique fascinant. De nouveaux types de tissus minéralisés, qui ne sont, ni de l'os, ni de la dentine, ont été découverts chez divers vertébrés non tétrapodes et amphibiens. Diverses interactions épidermo-dermiques et transformations cellulaires métaplasiques ont été analysées sur des modèles variés chez les ostéichthyens. Des études au microscope électronique à transmission de sections ultrafines déminéralisées de matériels d'âge Méso- et Paléozoique ont apporté la démonstration de la persistance des matrices, y compris de collagène de type 1. Le grand développement des études squelettochronologiques a apporté une foule de données sur les traits d'histoire de vie chez de nombreuses espèces de vertébrés primitivement aquatiques, amphibiens et reptiles, y compris la découverte de cycles annuels doubles chez des espèces ou populations vivant dans des conditions écologiques particulières. La découverte de polyptères en Amérique du Sud, grâce à la paléohistologie, constitue un bon exemple de son utilité jusqu'en paléobiogéographie.

Enfin, l'investissement à long terme de l'équipe dans la paléohistologie des Archosauriens, avec la mise en évidence de vitesses de croissance élevées chez les dinosaures, a joué un rôle majeur dans « la renaissance des dinosaures » intervenue à partir de la décennie 1970 et en fin de compte dans la question de l'origine dinosaurienne des oiseaux. Un recensement bibliographique complet des travaux publiés par l'équipe est en cours.

En conclusion, quel avenir?

En 2008, différents membres « fondateurs » de l'équipe « Formations squelettiques » ayant pris leur retraite, la structure de recherche s'est dissoute, et les membres restants se sont scindés en deux groupes : J. Cubo, A. Quilhac, A. de Ricqlès et L. Zylberberg à l'université Paris-6 ; V. de Buffrénil, M. Laurin et F. Meunier au Muséum national d'histoire naturelle. Les savoir-faire développés au cours des quatre décennies d'existence scientifique de l'équipe ne sont pas perdus. En plus des acquis scientifiques livrés à la communauté internationale des chercheurs, ils persistent et se développent sous la responsabilité de quelques jeunes scientifiques ayant fait leur apprentissage dans l'équipe « mère ». Les développements actuels des techniques non destructives, de la modélisation 3D associée à la tomographie (Meunier et al., 2015 ; Sanchez et al., 2010) ou au synchrotron (Sanchez et al., 2012), ouvrent de nouvelles perspectives spectaculaires de dynamisation de l'anatomie et de la micro-anatomie des tissus squelettiques. Matériels vivants et fossiles, pouvant être investis avec ces méthodologies non destructives, restent deux supports de choix aptes à livrer de nouvelles données scientifiques précieuses dans le cadre d'approches structurales et fonctionnelles comparatives. Donc de beaux jours en perspective pour les nouveaux héritiers de Georges Cuvier et Étienne Geoffroy St-Hilaire, sous la responsabilité de Michel Laurin, (au Muséum national d'histoire naturelle), de Jorge Cubo (à l'université Paris-6), de leurs plus jeunes collègues parisiens (Sidney Delgado, Damien Germain, Alexandra Houssaye et Alexandra Quilhac), mais aussi dans d'autres laboratoires, en France et ailleurs.

1. Introduction

The research group known as "Formations squelettiques" team was composed of University professors and of full-time research scientists (CNRS) who have dedicated their research to the study of vertebrate mineralized tissues for more than 40 years, starting in 1968.

To tell the story of this research group without proper historical and scientific background would be meaningless, because scientists are influenced by these two factors. On one hand, they work within their own time in connection with other scientists spread among various laboratories of numerous countries all over the world. On the other hand, they set their activities within a knowledge derived from the works of their predecessors over several generations, sometimes very remote in time (Schmitt, 2006).

Without attempting to provide a historical survey of the "mother discipline" from which the team comes, namely Comparative Anatomy, it is useful to offer some historical landmarks.

2. A short historical review of Comparative Anatomy at the Paris University

Without going back to Aristotle, nor attempting a detailed historical review, it seems nevertheless useful to recall some steps in the long history of comparative anatomy (Schmitt, 2006), a rich and fascinating scientific domain of which we are heirs and followers.

Before the French Revolution, scientists had to rely almost exclusively on the sponsorship of the King and aristocracy. Apart from the Academy of Sciences (founded in 1666), two well-structured scientific institutions were the Collège Royal (King's College, established in 1530) and the Jardin du Roi (King's Garden, established in 1639), which would evolve respectively into the Collège de France (named as such during the Restauration in 1815–1830) and the Museum National d'Histoire Naturelle (National Museum of Natural History, in 1793). It was mostly the second institution that gave the impetus to the Paris University in natural sciences, in research as well as in teaching, during the beginning of the 19th century; the University (La Sorbonne) then quickly took its scientific destiny into its own hands.

With the Revolution, the situation of scientists quickly changed as science became more and more institutionalized during the first half of the 19th century. Let us go back to those early post-revolutionary years: the Opening of the Science Faculty of the Paris University took place in 1811. Because the teaching and scientific skills were located at the Museum and at the Collège de France, the authorities thus appealed to the Professors of those institutions to provide the lectures. Georges Cuvier, then already a famous anatomist and paleontologist at the Museum, was appointed vice-rector of the Faculty by the Academy of Sciences. He created the chair in "Comparative anatomy and physiology", first held by his friend and collaborator Étienne Geoffroy Saint-Hilaire (Le Guyader, 1998). At the beginning, because the Faculté des sciences had no dedicated building, the lectures were given in the Museum's lecture halls in the Jardin des Plantes. The Faculty of Sciences settled in its own buildings at the Sorbonne in 1821–1822, but there were no research laboratories in the Faculty until 1855.

After several decades and name changes caused by the development of natural history and biological sciences, the original chair of the early 19th century was split into two in 1847. The first of these two resulting chairs, entitled "Zoology, Anatomy, and Comparative Physiology", first held by Henri Milne Edwards, mostly focused on the anatomy and physiology of metazoans, and resulted in the creation of the still active Marine Biological Station in Roscoff (Brittany). Many prominent zoologists held the chair, including Yves Delage, Charles Pérez, and Georges Teissier, who made a significant contribution to the development of the concept of allometry.[1]

The second chair, entitled "Anatomy and Comparative Physiology", focused more on vertebrates, and was held by many followers of Georges Cuvier and Étienne Geoffroy Saint-Hilaire for Comparative Anatomy. Among them were Henri-Marie Ducrotay de Blainville, Isidore Geoffroy Saint-Hilaire (Étienne's son), Louis Pierre Gratiolet, Paul Gervais, Henri de Lacaze-Duthiers, George Pruvot, and Paul M.J. Wintrebert. Special mention should be made of Paul Gervais (1816–1879) who, through his numerous works on the hard tissues of extant and extinct vertebrates, turned out to have paved the way that we followed a century later (e.g. de Ricqlès et al., 2009; Meunier and Herbin, 2014; Taquet, 2001), and to Paul Wintrebert (1867–1966), who famously coined the term "cytoskeleton" in 1931, and changed the name of the chair to "Comparative Anatomy and Histology", thus starting the tradition of histological preparation and teaching that would later shape the origin of our group.

Lectures, practical classrooms and research took place at La Sorbonne up to the early 1960s, when the Faculté des Sciences was relocated to the brand new Jussieu campus, which was better adapted to its duties of university teaching and basic research. The Laboratory of Comparative Anatomy and Histology was among the first to move from the old Sorbonne to the new facilities in 1961.

3. The Comparative Anatomy and Histology lab in the 1950s

Let us go back to the Chair of Comparative Anatomy and Histology: headed by Marcel Prenant since 1937, it led the Laboratory of Comparative Anatomy and Histology set on two floors (levels 2 and 3) at 7, quai Saint-Bernard (Building

[1] Teissier used the allometry equation in his studies on the growth of insects (Teissier, 1931) and reached an agreement with Julian Huxley to develop a common terminology on relative growth: they coined the terms allometry and isometry in two papers published simultaneously in English and in French (see a review in Gayon, 2000). Beyond the terminological issues, a conceptual disagreement existed between them: for Julian Huxley, the intercept of the allometry equation is only a statistical parameter, which depends on the measurement units, whereas for Georges Teissier this parameter may have a biological significance (Gayon, 2000). According to the results obtained by Katz (1980), Teissier was right: the intercept of the allometric equation describing the relative growth of two parts of an organism may correspond to the relative number of cell division centers of these parts.

A) of the new campus, and of a third level (on the first floor) devoted to practical classrooms, teaching, and an extensive collection of anatomical and zoological specimens used for teaching, and organized in part as a pedagogical Museum of Zoology.

One of the great contributions of M. Prenant is to have developed, after a first try by P. Wintrebert and M. Parat before the war (Prenant, 1966), an intensive teaching program of histological techniques, following a path set by his father, Auguste Prenant (1861–1927), at the Faculty of Medicine at the beginning of the 20th century. During the second half of the 20th century, this specialized practical cursus in histology was taken by a large number of scientists.

In Marcel Prenant's laboratory, research was not organized in research groups or teams devoted to a common research goal. Each student, or scientist, had his own research subject on an animal model (some of which were vertebrates), that "belonged" to him (or her). Its main tool for research remained topographical histology with its histochemical extensions, to describe the animal's general organization, its development and/or its biological peculiarities, sometimes associated with various experimental approaches. As Professor Prenant put it during his valetudinary lecture: "In my Laboratory, I have been watchful that the research goals remained based, in priority, on the use of histological techniques [...]. Histology is merely a means, but put in service of diversified problems and models depending of the scientists' orientation, histology is also a rallying point, a way of thinking, and a common language." (Prenant, 1980, p. 324). The only link among scientists, as far as research was involved, actually remained the use of histology techniques, through what would now be called a technical platform. The close links that Marcel Prenant kept with the Marine Biological station in Roscoff (Devillers, 1966; Teissier, 1966), of which he had been the director for several years, allowed marine animals to hold a large place in the theses defended during those years.

Nevertheless, vertebrates were not absent from the research activities of the Laboratory of Comparative Anatomy and Histology, as demonstrated in two noteworthy theses defended respectively by Charles Devillers (1947) on the development of the dermal bones of the skull, and by Yves François (1958) on the development of vertebrae and fins, both on teleostean models (Meunier, 2000). The contributions of Devillers to the great Traité de Zoologie (Devillers, 1954a,b, 1958), as well as numerous pedagogical handbooks published by both authors for the Paris students (notably seven illustrated booklets on Agnathans, Chondrichthyans, Osteichthyans, Amphibians, Reptiles, Birds, and Mammals), firmly established the vertebrate comparative anatomy developed at the Sciences faculty within the long lineage of heirs of Cuvier and Geoffroy Saint-Hilaire. It was in Marcel Prenant's laboratory, and more especially within the fertile milieu of actinopterygian comparative and developmental anatomy, that the "Équipe Formations squelettiques" found its roots.

In 1966, Marcel Prenant retired and his laboratory was split into two entities (Prenant, 1966): the Laboratory of Comparative Anatomy (second floor) with Professor Charles Devillers as Director, and the Laboratory of Cytology (third floor) under the Directorship of Professor René Couteaux, who worked on the "motor plate" or neuromuscular junction. Strengthened by the tradition left by former generations of great teachers, the lectures on Comparative Anatomy and Zoology given in the Paris Faculté des Sciences by competent teachers shaped new generations of post-war students. Those high-level lectures stimulated some of them to begin doctoral studies in histology.

Thanks to the creation, during the 1960s, of a fair amount of positions for teaching and research, as the University trained numerous students from the post-war "baby boom" generation, the Parisian laboratories recruited young assistant professors, well motivated for teaching and scientific research. These were happy days when recruitment could take place after a Master's degree or roughly equivalent titles!

Because those younger teachers had received a strong training in Zoology and Comparative Anatomy, the time was ripe for a restructuring of research and new scientific endeavors. Gone were the solitary scientists of the fifties with individual and disparate research subjects, only united by the same techniques of histology: now came the time of research teams focused on a scientific subject that became the target of research programs. Paraffin histological techniques were no longer the ultimate tool; they remained useful, inescapable, but became extensively associated with new, specialized tools, especially in our field of skeletal hard tissues (see below).

4. Birth and first steps of the team

Following the turmoil of the May–June 1968 events that led to the "Law of orientation of higher education" (known as Loi Edgar Faure), the Science Faculty of the Paris University was dismantled and replaced by two new pluridisciplinary Universities: Paris-6 (Pierre-et-Marie-Curie) and Paris-7 (Denis-Diderot), oddly intermingled on the Jussieu Campus, which had expanded following the final departure of the last "pinardiers" (wine traders: the Jussieu campus was built on the former "Halle aux vins", Paris' gross wine market facilities, and is sometimes still known under this nickname).

In the Laboratory of Comparative Anatomy, five research teams were organized around their respective scientific leaders:

- developmental biology (C. Devillers, 1914–1998);
- vertebrate skeletal tissues (Y. François, 1914–2000);
- nervous system (R. Bauchot, b. 1929);
- sclerotization processes among Invertebrates (J. Vovelle, 1933–2009);
- ontogeny and destruction processes of the Molluscan shells (M. Chétail, b. 1926).

All the University staff (teachers, researchers, and technicians) were requested to choose between one of the new Universities. Like most of the staff in the aforementioned five research teams, the team led by Yves François chose University Paris-7 and got the name of "Formations squelettiques". It remained in Building A, second floor (Laboratoire d'anatomie comparée), with some extra-technical rooms on the eighth floor. However, all teaching facilities on the first floor were used by Paris-6, and the teaching for Paris-7 had to be performed elsewhere; in the end, lectures and practical classrooms were hosted in an "Animal Biology" teaching facility set far away on the Campus, at the third floor of towers 23–33. Similarly, former collections and libraries were split through a time-consuming and expensive process. Nevertheless, a constant will animated the teachers and researchers: to maintain a close link in their activities between research and teaching.

The team "Formations squelettiques" was organized by Yves François (Professor) and Armand de Ricqlès (Assistant), with the recruitment of "new assistants" François Meunier and Jacqueline Géraudie in 1967, and Jacques Castanet and Hélène Francillon in 1969. The team was completed by two technicians: Mrs. Paulette Koechlin (administration, secretary) and Yvette Rupaud (histology, animal facilities). Some years later, in 1981, Françoise Allizard (CNRS) brought to the group her masterful practice of ultrathin sectioning for the TEM. In 1977–1979, the team increased its staff with the arrival of Dr. Louise Zylberberg (CNRS) and two doctoral students: Vivian de Buffrénil for a thesis on varanid squamate histology, and Jean-Yves Sire for a thesis on the scales of Cichlid teleosts. de Buffrénil subsequently got a position in the Paris Museum, and Sire in the CNRS, and both remained with the team for their postdoctoral research (Figs. 1 and 2).

Given that vertebrate skeletal hard tissues are strongly mineralized, the use of classical paraffin microtomy obviously requires removing the mineral component, hence the tissues lose their specific component in the process. Accordingly, a good part of their biological information is lost. One has thus to turn to petrographic techniques and adapt them to study bone and dental tissues.

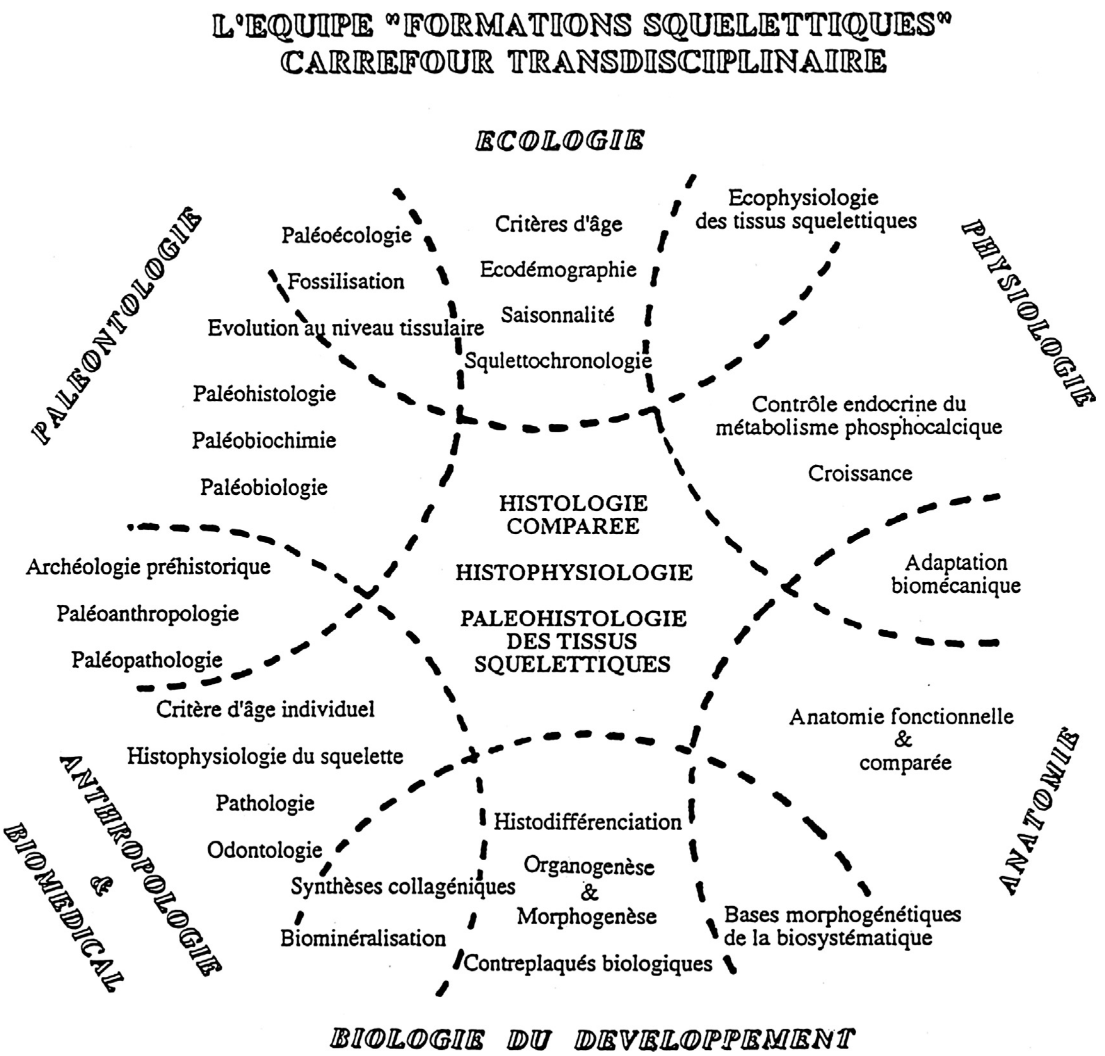

Fig. 1. Reproduction of the summary diagram used by the team in the 1989–1992 report to the CNRS to exemplify the position of vertebrate skeletal tissues at the center of a wide interdisciplinary field.

Fig. 1. Reproduction de la figure utilisée dans le rapport d'activité 1989–1992 de l'équipe au CNRS, pour illustrer la position des tissus squelettiques des vertébrés au centre d'un vaste domaine interdisciplinaire.

Fig. 2. (Color online.) Some members of the team “Formations squelettiques” in 1979. From left to right, back row: Louise Zylberberg, Hélène Vieillot, François Meunier, Yves François; front row: Jean-Yves Sire, Armand de Ricqlès.
Fig. 2. (Couleur en ligne.) Quelques membres de l’équipe « Formations squelettiques » en 1979. De gauche à droite, deuxième rang : Louise Zylberberg, Hélène Vieillot, François Meunier, Yves François ; premier rang : Jean-Yves Sire, Armand de Ricqlès.

Those adaptations, first performed for the study of human (and more generally mammalian) hard tissues, were extended to other vertebrate groups. Polymerisable plastics replaced paraffin, and thin circular blades with diamond powder and polishing machines replaced the classic Minot’s microtome. Finally, new “soft” X-ray generators, adapted to the characteristics of microscopical thin sections (100 μm or less) allow qualitative and quantitative studies of the mineral components *in situ* (Boivin and Baud, 1984). Those techniques, which quickly became part of the routine, also allowed the scientists of the team “Formations squelettiques” to explore the rich field of fossilized hard tissues which, under favorable taphonomic conditions, allow us to study the evolution of tissues in deep time (over 500 million years; e.g. Chinsamy et al., 1995; de Ricqlès, 1977, 2007; Meunier, 2011; Steyer et al., 2004).

Quantification of growth dynamics and chronology were experimentally analyzed by the team on extant models thanks to vital dyes (e.g. de Margerie et al., 2004; Meunier, 1972, 1974; Sire et al., 1993; Trébaol et al., 1991). Three doctoral theses on this topic were defended in 1982 (J. Géraudie, J. Castanet, F. Meunier), following in the footsteps of A. de Ricqlès, who had defended his thesis in 1973. In 1982, the team leader Yves François retired, and Armand de Ricqlès took over.

During the 1980s and 1990s, some doctoral students joined the team before being employed to work on other research topics or in other teaching structures. Some of the youngest ones are now the heirs of this long tradition in comparative anatomy and histology of the vertebrate skeleton.

5. Growth and life of the team

In order to thrive in the University environment, the team had to raise sufficient funding for its research and to train new doctoral students. To attract students, the team took part in the creation and daily operations of a new graduate program starting at the Master’s degree level, the DEA “Structures and Functions in Vertebrates Evolution”, which opened in 1981.

We employed a few doctoral students from this program, notably Marina Alcobendas, Virginie Levrat and Frédérique Lecomte, who strengthened the group for several years. At the same time, we strengthened already strong links with laboratories of the Muséum National d’Histoire Naturelle, notably those of paleontology (Professor J.-P. Lehman) and comparative anatomy (Professor J. Anthony), especially with a group working on tetrapod locomotion, which was strongly involved within the DEA “Structures and Functions”, co-organized by the Museum and Paris-7 University. This DEA later gave birth to the Master’s degree program “Systematics, Evolution, and Paleontology” (still operational), through which a few more students later contributed to several projects of the team between 2000 and 2008.

To fund our research, extramural financial support was needed, especially given that the University had seen its resources dwindle, and at best stabilized following the first oil crisis (1974). During the late 1970s/early 1980s, the best option for university research teams was to seek financial support from the CNRS, which would also enhance scientific visibility. Even though the CNRS normally supports fairly large research groups, we were recognized as a “Jeune équipe” (“young team”) in 1982, with Armand de Ricqlès as director. It was a major victory and the beginning of our long-lasting association with the CNRS. This was confirmed in 1985 with the creation of the URA (associated research unit) 1137 which, in order to reach its “critical mass”, included both our research team and the team “Animal Locomotion” led by Dr. Françoise Jouffroy in the Laboratory of Comparative Anatomy of the Museum. A long-lasting

Fig. 3. (Color online.) Members of the "Formations squelettiques" (FS) and "Locomotion" (L) research teams worked together in the organization committee of the 7th International Congress of Vertebrate Morphology held in Paris in July 2007. From left to right: Sophie Sanchez (FS), Vincent Bels (L), Jean Sébastien Steyer, Rémi Hackert (L), Jacques Castanet (FS), Marc Herbin (L), Annick Abourachid (L), Jorge Cubo (FS), and Emmanuel de Margerie (FS).

Fig. 3. (Couleur en ligne.) Les membres des équipes de recherche « Formations squelettiques » (FS) et « Locomotion » (L) travaillèrent ensemble dans le comité d'organisation du 7th *International Congress of Vertebrate Morphology*, qui eut lieu à Paris en juillet 2007. De gauche à droite : Sophie Sanchez (FS), Vincent Bels (L), Jean. Sébastien Steyer, Rémi Hackert (L), Jacques Castanet (FS), Marc Herbin (L), Annick Abourachid (L), Jorge Cubo (FS) et Emmanuel de Margerie (FS).

cooperation between the two teams followed, requiring diplomatic skills and flexibility in the administration of available funding, but above all allowing fertile discussions on our research themes and their evolution within the research and teaching structures (Fig. 3). Within the framework of the URA, we had the opportunity to recruit two new able technicians: Mrs Jacquie Bourguignon and Marie-Madeleine Loth who took the positions of P. Koechlin and Y. Rupaud after their retirements.

6. Ontogenesis, structures and functions of the skeletal tissues

The heart of our research topic is the comparative study of skeletal tissues among vertebrates, set in an explicit evolutionary framework. The main focus was first put on extant and extinct ectothermic vertebrates, mostly actinopterygians and reptiles, with emphasis on ontogeny, differentiation, growth, maturation, function, and evolution. Later on, we added mammals and birds to our biological models, using the opportunities offered by collaborative projects or the arrival of new doctoral students. The comparative study of vertebrate hard tissues (mainly bone) became a crossroad, the center of a transdisciplinary web spreading towards numerous other topics (Fig. 1) that stimulated the team and paved the way to numerous national and international collaborations. This created close links with Professor Melvin J. Glimcher (1925–2014) of Harvard Children's Hospital, Boston, who came several times to work with the team and contributed much to our efforts to decipher the intimate relationships between the organic and mineral components of fossil and extant hard tissues (Cohen-Solal et al., 1987). Other long-term collaborators include Professors J.R. Horner (Museum of the Rockies, Bozeman University, Mt.) and K. Padian (University of California, Berkeley), who worked with us on the paleohistology of archosaurs and related taxa (Horner et al., 1999).

We used both classical histological and cytological techniques with light (Francillon, 1974, 1977) and electron transmission microscopy (Quilhac et al., 2014; Sire, 1988; Sire and Géraudie, 1983, 1984; Sire and Huysseune, 1993; Zylberberg, 2004; Zylberberg and Meunier, 1996), topographic and histochemical colorations (Géraudie, 1974), experimental embryology (Géraudie, 1981), raising animals at the laboratory and monitoring in the wild. We have developed various techniques: thin sections, vital dyes (de Margerie et al., 2004; Francillon and Castanet, 1985), qualitative and quantitative micro X-rays (Alcobendas and Castanet, 1985; Meunier, 1984), ultrathin sections of extant and fossil non-demineralized tissues (Rimblot-Baly et al., 1995; Zylberberg and Laurin, 2011), MEB (Géraudie and Singer, 1981), electron microscope (Zylberberg and Meunier, 1984)...

Mineralized hard tissues can be somewhat viewed as "black boxes" as far as they are persistent in the organisms. Deciphering the "message" recorded in those tissues yields functional clues about the skeleton and the organisms. The results gained on extant organisms (where experimental data can be recorded) can be extended,

Fig. 4. (Color online.) Attendees of the international symposium “Perspectives on vertebrate evolution: topics and problems”, held at the Collège de France (Paris) in June 2010. This symposium was organized by Jorge Cubo and Michel Laurin to celebrate the retirement of Professor Armand de Ricqlès.
Fig. 4. (Couleur en ligne.) Participants au congrès international « Perspectives sur l’évolution des vertébrés : thèmes et problèmes » au Collège de France (Paris) en juin 2010. Ce colloque a été organisé par Jorge Cubo et Michel Laurin en hommage au professeur Armand de Ricqlès.
Photo: Patrick Imbert (Collège de France).

mutatis mutandis, to extinct vertebrates, whenever preservation of the tissue fine structure is sufficiently good (de Buffrénil et al., 1987, 1990; de Ricqlès, 2000; Horner et al., 1999; Meunier and Laurin, 2012). Within a Darwinian-evolutionary framework, we moved from a “traditional approach” in comparative anatomy and histology, set within the synthetic theory, to research endeavors set within a cladistic framework beginning in the early 1970s.

The creation of the “Groupe d’étude pratique de squelettochronologie” (GEPS; group for the pratical study of skeletochronology) in December 1977 enhanced the visibility of the team. This organization sought to meet a strong demand for the understanding of growth dynamics and age structure of populations from the scientific community, especially ecologists. This is explained in the original catalog presenting this technical support structure:

> “Because they are hard, vertebrate skeletal tissues behave in various ways as biological recorders. The most familiar use of this tissular peculiarity is scalimetry, used to assess age of fishes (but this method is only available, of course, among scale-covered bony fishes). [. . .] More and more workers belonging to various scientific fields – Ecology, Demography, Prehistoric research and Archeology, Rythmology – are now becoming aware of the advantages that could be gained, for their particular studies, by making full practical use of the information recorded in the microscopic structure of bone, dentine, and cementum. Considering such information allows research into new directions. One of the most important and promising prospect in this field, but not the only one, is of course to evaluate individual age thanks to skeletal microstructure. [. . .] Skeletochronology uses various hard tissues that are found among all vertebrates (bone, dentine, cementum. . .). Some of those hard tissues, among many vertebrates (and not only among poikilotherms with indefinite growth) are laid down in successive layers of varying aspect. Already available descriptive and experimental evidence now offers enough theoretical background, and instances of technical processing, to allow a widespread practical use: not only can individual age be reliably assessed, but other data like speed of growth, age of sexual maturity, and longevity, can be gained from skeletochronological surveys”. Such inferences are illustrated by several papers of the team (de Buffrénil et al., 1994; Castanet et al., 1996; Meunier et al., 1997. . .).

Over a period of 25 years, several dozen scientists, experienced to beginners, from various countries (Canada, USA, Peru, Ivory Coast, Mali, South Africa, Tunisia, Morocco, Spain, Portugal, Poland, England, Greece) as well as from France, came to work with us to learn and use skeletochronological techniques. This fruitful scientific activity

Fig. 5. (Color online.) Attendees of the first International Symposium on Paleohistology, held at the Institut Català de Paleontologia (ICP) in Barcelona, in July 2011. Conveners: Meike Köhler and Jorge Cubo.

Fig. 5. (Couleur en ligne.) Participants au premier congrès « International Symposium on Paleohistology » à l'Institut catalan de paléontologie (ICP) à Barcelone, en juillet 2011. *Conveners* : Meike Köhler et Jorge Cubo.

Photo: ICP.

led to the organization of "roundtables" (Société zoologique de France, 1980), of symposia (Colloque de Bondy in 1991; see Baglinière et al., 1992) and to our contribution to several textbooks and specialized books and reviews, some of them likely to remain as references of the "state of the art" about the skeletal tissues of vertebrates at the end of the 20th century (Castanet et al., 1993; de Ricqlès et al., 1991; Francillon-Vieillot et al., 1990; Zylberberg et al., 1992). In the foreword of Volume 7 of "Bone" series of which he was the Editor, Prof. Brian K. Hall, the noted Canadian embryologist, expressed this opinion of our chapter (Castanet et al., 1993): "... Chapter 9 completes a series of superb chapters produced for this series by the French workers in the Équipe de Recherche 'Formations squelettiques' of the Université Paris-7. In this chapter they provide a masterly synthesis of the use of growth marks preserved in bone to age individual organisms, the discipline of skeletochronology...".

It is not possible here to record all the interesting results obtained by the team over the decades. The extensive works on the dermal skeleton of vertebrates allowed us to discover important new data. The peculiar "double twisted plywood" structures in the scales of Sarcopterygians, including extant *Latimeria* and Dipnoans, was deciphered and still offers fascinating models for further biophysical analyses. New mineralized tissues types, with either collagenous or non-collagenous matrices, which are neither dentine nor bone, were discovered and described in various actinopterygians and amphibians.

The implication of extracellular material of epidermal origin, as well as the metaplastic conversion of melanophore cells into bone forming cells, have been demonstrated in several models of osteichthyan scales.

TE microscopy of demineralized ultrathin sections of Mesozoic and Paleozoic skeletal tissues demonstrated the continuous occurrence of non-collagenic and collagenic matrices in very old fossils, including the fibrillar pattern and cross striation of Type 1 collagen. The extensive development of skeletochronology allowed us to decipher important life history traits in a large number of actinopterygians, amphibians, and reptiles, sometimes including histological evidence of sexual dimorphism during growth. Especially noteworthy was the demonstration of "double yearly growth cycles" in teleosts and amphibians living under peculiar ecological conditions. Cases of "Island gigantism" linked to the selection of "K growth strategies" among reptiles have been also deciphered. The discovery of Polypterid remains in South America thanks to palaeohistology exemplifies its usefulness even in paleobiogeography.

The decade-long involvement of the team in comparative paleohistology of archosaurs, with evidence for high growth rates in many dinosaurs, played a major role in the trend towards the “dinosaur renaissance” starting in the 1970s, and ultimately in the issue of the dinosaurian origin of birds. A complete bibliographical census of the team’s publications will be attempted elsewhere.

7. As a conclusion: what about the future?

In 2008, most of the “founding members” of the team had retired (some of them already for several years), the research team disappeared, and the remaining members split into two groups: J. Cubo, A. Quilhac, A. de Ricqlès and L. Zylberberg at the Paris-6 University, and V. de Buffrénil, M. Laurin and F. Meunier at the Muséum National d’Histoire Naturelle.

Nevertheless, the “know how” developed during the four decades of the research team has not been lost. Apart from the published scientific results, a generation of scientists trained by the “Formations Squelettiques” team has been recruited in Parisian institutions in recent years: Alexandra Quilhac (Quilhac et al., 2014), Sidney Delgado (Delgado et al., 2008), Damien Germain (Germain and Laurin, 2005) and Alexandra Houssaye (Houssaye, 2014). We also had the opportunity to recruit a new able technician in 2005: Mrs Hayat Lamrous.

The research group headed by Dr. J.-Y. Sire at the Paris-6 University can be viewed as a direct offshoot of the team, now with emphasis on the study of dental tissues with morphological, developmental, and molecular approaches (Delgado et al., 2008; Sire et al., 2007).

The current development of “non-destructive” techniques of 3D modelingn, linked with tomography (Sanchez et al., 2010; Meunier et al., 2015) or the “synchrotron light” (Sanchez et al., 2012), opens new prospects for dynamic studies of the anatomy and microanatomy of skeletal tissues. Extant or fossil material may be investigated through these non-destructive techniques and can still yield new data on the evolution, structure and function of vertebrates.

Michel Laurin and Jorge Cubo, educated respectively at the University of Toronto and the University of Barcelona, joined the research team in the late 1990s. Both were interested on analyzing bone osteohistological data using phylogenetic comparative methods (i.e. statistical methods that incorporate phylogeny). They and their PhD students produced paleobiological models to estimate the lifestyle (Germain and Laurin, 2005; Canoville and Laurin, 2010) and bone growth rate (Cubo et al., 2012; Legendre et al., 2013) of extinct tetrapods using bone histology. Michel Laurin, now head of the research team “Phylogeny and the

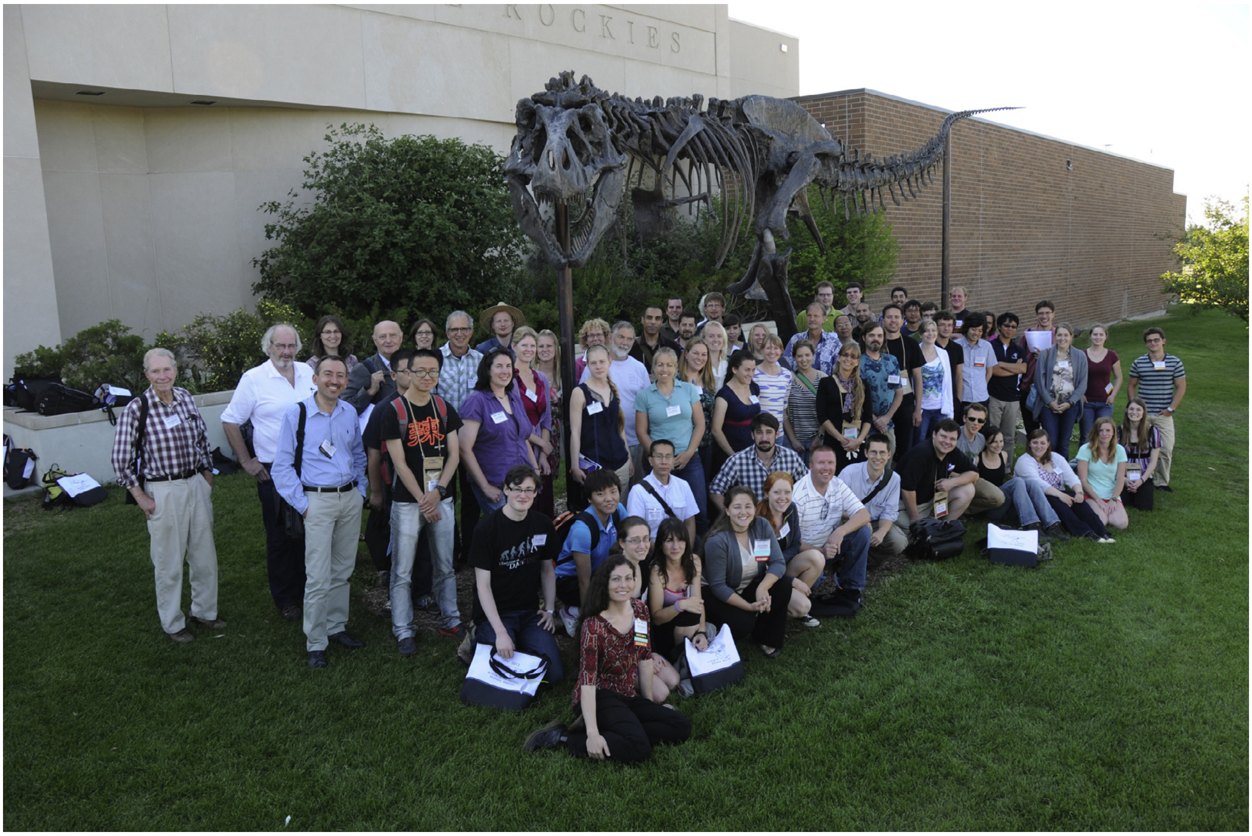

Fig. 6. (Color online.) Attendees of the second International Symposium on Paleohistology, held at the Museum of the Rockies in Bozeman, in July 2013. Conveners: John Horner and Holly Woodward.

Fig. 6. (Couleur en ligne.) Participants au deuxième congrès « International Symposium on Paleohistology », au Museum of the Rockies à Bozeman, en juillet 2013. *Conveners* : John Horner et Holly Woodward.

Photo: Martin Rollefson.

Fig. 7. (Color online.) Some members and collaborators of the current paleohistology research groups in Paris. Grande Galerie de l'Évolution, Muséum national d'histoire naturelle (MNHN), Paris, January 2015. From left to right: Lucas Legendre, Jorge Cubo, Jacques Castanet, Alexandra Houssaye, Armand de Ricqlès, Sidney Delgado, Vivian de Buffrénil, François Meunier, Jean-Yves Sire, and Michel Laurin. Behind them, the famous painting "Les explorateurs" by Raoul Dufy (1939).

Fig. 7. (Couleur en ligne.) Quelques membres et collaborateurs des groupes de recherche actifs en paléohistologie à Paris. Grande Galerie de l'Évolution, Muséum national d'histoire naturelle (MNHN), Paris, janvier 2015. De gauche à droite : Lucas Legendre, Jorge Cubo, Jacques Castanet, Alexandra Houssaye, Armand de Ricqlès, Sidney Delgado, Vivian de Buffrénil, François Meunier, Jean-Yves Sire et Michel Laurin. Derrière eux, le fameux tableau « Les explorateurs » de Raoul Dufy (1939).

Photo: Lilian Cazes (Muséum national d'histoire naturelle [MNHN]).

diversification of Metazoa" at the Museum National d'Histoire Naturelle, and Jorge Cubo, who leads the Paleohistology research group at the University Paris-6, organized the symposium "Perspectives on vertebrate evolution: topics and problems" (Fig. 4) to celebrate the retirement of Armand de Ricqlès (Cubo and Laurin, 2011; Laurin, 2011). Coffee break discussions at this symposium were at the origin of the creation of the biennial International Symposia of Paleohistology. The first two meetings, organized in Barcelona (Spain) in 2011 (Fig. 5) and Bozeman (Montana, USA) in 2013 (Fig. 6), were very successful both in terms of number of participants and quality of presentations. The third one is scheduled for July 2015 in Bonn (Germany). In a retrospective view, the research team "Formations squelettiques" can be viewed as a "nucleation point" at the origin of these symposia.

After the forthcoming retirement of the last long-term members of the research team "Formations squelettiques" (Vivian de Buffrénil in 2016 and Jean-Yves Sire in 2018), the community of Parisian comparative hard tissues histology will make a new start. Members of that generation of French bone histologists to which this special issue of *C. R. Palevol* is dedicated meet regularly with the younger generation and provide valuable input for emerging projects. Some of them have obtained emeritus status in their respective institutions and remain scientifically active (Louise Zylberberg: Emeritus CNRS researcher; Armand de Ricqlès: Honorary Professor at the Collège de France; François J. Meunier: Emeritus Professor at the Museum national d'histoire naturelle). The future looks bright for the new heirs of Georges Cuvier and Étienne Geoffroy Saint-Hilaire, under the leadership of Michel Laurin, at the Paris Museum, Jorge Cubo at the Paris-6 University, their younger Parisian colleagues Sidney Delgado, Damien Germain, Alexandra Houssaye et Alexandra Quilhac, and also in other laboratories in France and elsewhere (Fig. 7).

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