“Rediscovery” of Paul Gervais’ paleohistological collection

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ABSTRACT

Paul Gervais (1816-1879) developed an obvious interest for paleohistological researches during the latest phase of his career at the National Museum of Natural History, in Paris (Laboratory of Comparative Anatomy) and produced a collection of thin sections of extant and fossil eggshells, teeth and bone, although he did not published much on the subject. Current curatorial efforts have unveiled remains of this collection which is presented and assessed herewith.

KEY WORDS
Paleohistology,
fossil bones and teeth tissues,
history of sciences,
mammals.

MOTS CLÉS
Paléohistologie,
tissus dentaires et osseux fossiles,
histoire des sciences,
Mammifères.

RÉSUMÉ
« Redécouverte » de la collection paléohistologique de Paul Gervais.
Paul Gervais (1816-1879) a manifesté un intérêt certain pour les recherches paléohistologiques pendant la dernière partie de sa carrière, comme Professeur au Laboratoire d'Anatomie comparée au Muséum national d'Histoire naturelle, Paris, à partir de 1868. Il y a développé une collection de préparations microscopiques d'oeufs, de dents et d'os de vertébrés actuels et fossiles mais n'a que peu publié sur le sujet. Des travaux récents d'inventaire et de mise en valeur des collections d'anatomie comparée ont révélé l'existence de restes de cette collection qui sont décrits et évalués ici.

INTRODUCTION

With the current development of histological researches in vertebrate paleontology, it is becoming more and more obvious that old collections of thin sections of fossil materials have a high historical interest and patrimonial value. Above all, they may be still useful for current researches. In spite of that, however, older collections of thin sections, and more generally of histological collections, are so far rarely the subject of careful curatorial efforts in Museums, and especially in Universities (Ricqlès 2007).

Of course it is understandable that "routine" histological sections from easily obtainable laboratory animals are often considered as a consumable material which can be disposed of, or which can suffer high damage rates from the "attention" of students in the histological classrooms. However this policy cannot be accepted as soon as one is dealing with historical collections, extensive comparative collections from rare animal tissues, or collections which form the evidence of important experimental works. Histological collections from the past may not be easily duplicated. For instance, current – and welcome – nature conservancy regulations on rare or endangered species may hinder production of new extensive comparative histological collections, especially of growth series, and there are little incentives among modern biologists to start such kinds of researches anyway. This makes the preservation and curation of older histological collections of extant biological material a matter of special concern and even of urgency.

The situation is obviously even more stringent for the collections of thin sections from fossils because the general rarity or uniqueness of well preserved fossils enhances their patrimonial value. Whether they come from extant or fossil materials, in both cases the technical processes which have been used to obtain good histological sections have always been time consuming, labor-intensive and sometimes highly sophisticated. Only one large thin section may represent several hours of painstaking work for a highly skilled technician. Irrespective of any moral considerations, common sense suggests that it is a terrible waste of value, time, and energy for Science and Society at large to throw away such kind of collections, as it is too often the case when or after a researcher takes retirement, rather than preserve them for the community along sound curatorial practices, as demonstrated by the ultimate lucky fate of Professor Donald H. Enlow's collection (Ricqlès 2007).

This is all the more true now, than the current technical breakthroughs in image analysis and information processing and transmission and, by and large, generalized computerization, allow easy communication of data worldwide. It remains that histological collections should be now curated accordingly, forming "histothèques" or "histological data Banks" with access on line.

With this general framework in mind (Ricqlès 1987), we became involved in the research, inventory and preservation of older collections of thin sections of fossil vertebrates. Accordingly, some findings on the first thin sections processed from

Saharian Dinosaurs (Ricqlès 1994) and from old sections from very early jawless vertebrates (Ricqlès 1995a) have been published. Similar works on the earliest thin sections from Pterosaurs have been performed (Steel 2003).

In connection with historical researches on the earliest studies of dinosaurs bones and eggs in Southern France, one of us (Ph. Taquet) noticed in the Collections of the Laboratory of Comparative Anatomy of the Muséum national d'Histoire naturelle, Paris (MNHN) an old collection of thin sections of fossil and extant birds and reptiles eggshells, performed as early as the 1870s at the request of Professor Paul Gervais (Taquet 2001). This collection apparently contains the earliest known thin sections of dinosaurs eggshels ever processed and is of lasting interest for researches on the early history of dinosaurs discovery in France (Taquet 2001). Further investigations in the Laboratory of Comparative Anatomy performed by Drs C. Cremières, M. Herbin, Fr. Poplin and one of us (V. de Buffrenil) unveiled additional material in Paul Gervais' collections, namely a series of thin sections of fossil bones and teeth, which, as far as we know, were never described and figured in the scientific literature (Ricqlès 2006). Paul Gervais (1816-1879), a well-known comparative anatomist and palaeontologist (Laurent 1996) who published extensively on fossil mammals, remained doubtful on the general significance of evolution. Gervais' own use of his collection of thin sections appears to have been limited to a two part publication (Gervais 1875a, b).

The purpose of the present work is to offer a listing, brief description, selected illustrations and assesment of this collection. As it mostly deals with fossil mammals, we felt advisable to dedicate this survey to our good colleague and friend, Professor Louis de Bonis, who himself contributed to some paleohistological endeavors (Bonis *et al.* 1972).

MATERIAL AND METHODS

As currently preserved, Paul Gervais' collection of fossil thin sections consists of several boxes. It is obvious that the collections experienced numerous circumstances over the decades, involving box changes, successive cataloging and labeling efforts, and discarding of sections in poor condition, to make room for newer preparations (Crémière 2004.). The boxes were numbered and given general titles such as "œufs" (eggshell thin sections), "os, cartilage" (bone and cartilage thin sections) but no attempt was apparently ever made to catalog each thin section individually. One small box contains 45 slides (ground sections on standard 7.5 × 2.6 cm glass plates with round coverslip) of eggshells from extinct and extant birds and reptiles (Taquet 2001). A larger box contains almost 100 slides (thin sections) of fossil bones and teeth, similarly mounted. Only the later, still undescribed up to now, will be dealed with here. With few exceptions, the technical quality and general preservation of the sections have been found to be rather satisfactory. We stress that the collection described here may be only a part of Paul Gervais' original collections of fossil thin sections possibly still surviving in the Laboratory of Comparative Anatomy of the MNHN: some isolated thin sections apparently from the same collection have been found scattered in other boxes and further inquiries are in progress. The additional fossil thin sections found elsewhere but presumably part of the same initial collection, according to Drs C. Crémière and M. Herbin, have been also described here (they are noted N-1 to 13). Moreover, a great number of comparative thin sections of dry bone and scales from various extant vertebrate species are also preserved. They are not dealed with here and considerable further curatorial and descriptive works obviously lie ahead. Indeed several other old histological collections, including bone thin sections, were performed at the Laboratoire d'Anatomie comparée during the late 19th century, at considerable technical cost, although they have been apparently of little scientific use so far, for various reasons (Crémière 2004; Ricqlès 2006).

Each section has been first carefully cleaned from dust and examined regarding the various old numbers or labels that it may bear (Fig. 1A, B). It was then observed under a coumpound microscope in ordinary and polarized transmitted light. The original labels read (as far as possible) on each section are reported below *ne varietur*. Uncertain-

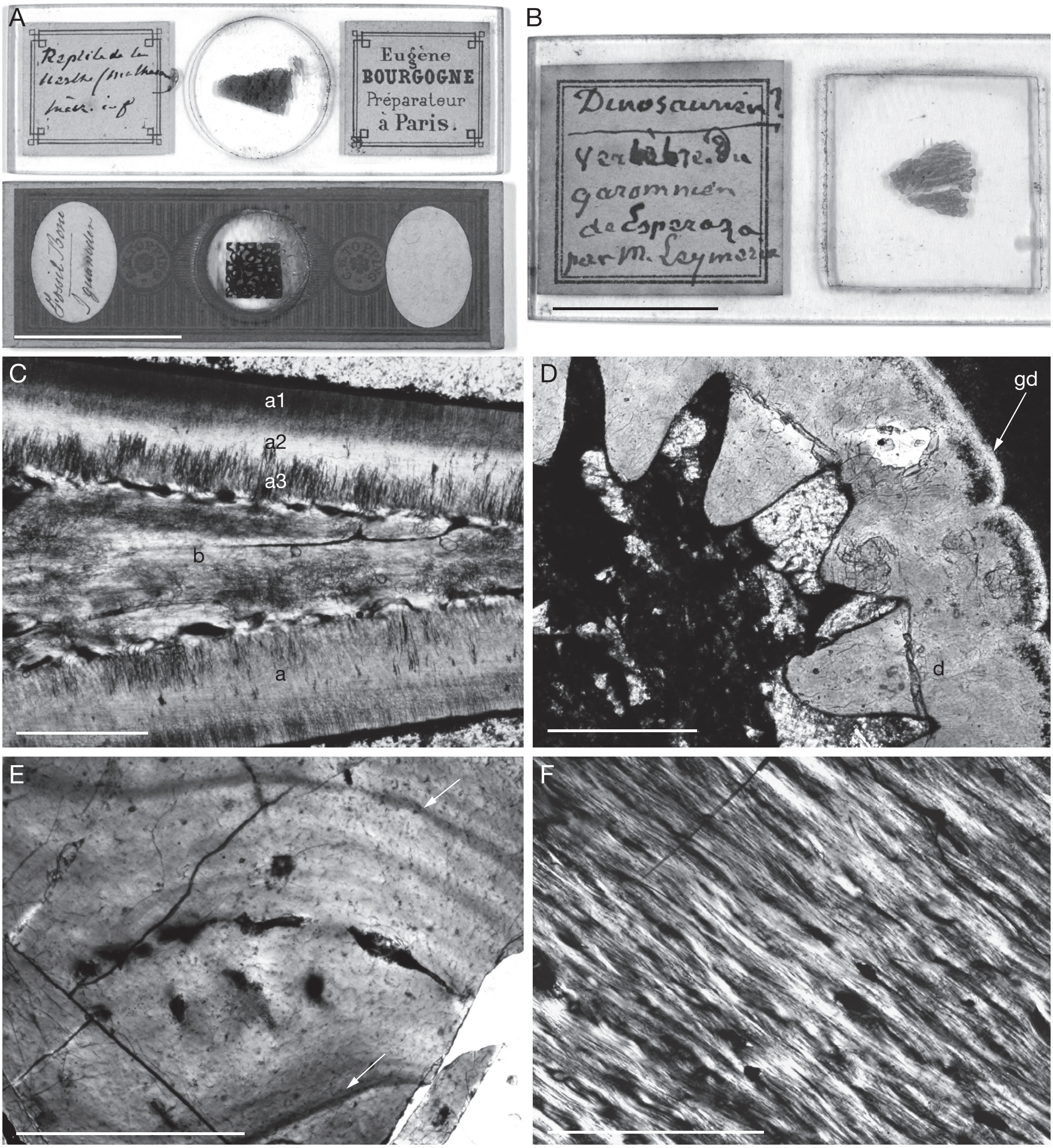

FIG. 1. — **A**, General aspect of the ground sections in Paul Gervais' collection; above: section 76 x 26 mm (a format still in use today) from a dinosaur bone (so called "reptile de la Nerthe") made in Paris by E. Bourgogne (section 27 [N-10]), below: section from an *Iguanodon* Mantell, 1809 bone made in Great Britain (section 23 [N-7]). The latter section is protected by a cover of strong paper; **B**, detail of the kind of information written on the labels. This section (section 28 [N-11]) is supposed to be from a dinosaur; **C**, tooth-like organ of *Lamna* Cuvier, 1816 (section no. 3), longitudinal section in ordinary transmitted light, ***a1-3*** and ***b*** refer to the two main tissue types observed in this section (see description in text); **D**, *Archegosaurus latirostris* Jordan, 1849 (i.e. juvenile *Archegosaurus decheni* Goldfuss, 1847) tooth (section no. 4), cross section in ordinary transmitted light, globular dentine (**gd**, dark peripheral layer) is close to the tooth surface; **E**, section of a "cranial bone" of *Labyrinthodon* Owen, 1842, a synonym of *Mastodonsaurus* Jaeger, 1828 from Wurtemberg (section no. 7), ordinary transmitted light, a few vascular canals and lignes of arrested growths (**arrows**, lines of arrested growth) can be observed; **F**, section of the "temporal scale" of *Labyrinthodon* from Stuttgart (section no. 9), polarized transmitted light (crossed nicols), the tissue is finely lamellar. Scale bars: A, 26 mm; B, 13 mm; C, 0.55 mm; D, 0.32 mm; E, 1 mm; F, 1.2 mm.

ties are quoted between parentheses with question marks, and further discussed (see *Comments*). We found unwise to add any new label or number to the sections.

Accordingly, the short descriptions below refer each section by the original labels and number(s) it bears. Irrespective of their order as found in the boxes (or elsewhere: sections "N-1 to 13"), they are described herewith *seriatim*, following a numerical sequence roughly reflecting current taxonomic order.

DESCRIPTIONS

"FISHES"

Placodermi

1. "*Coccosteus cuspidatus* du Dévonien plaque? capl." (céphalique?). Pencil number: 1186, ink label: 1938-621. Anat. comp. 1876.

2. "*Coccosteus cuspidatus* (Dévonien)? Peta". Pencil number: 1186, ink label: 1938-621. Anat. comp. 1876.

Description. The two slides may correspond to very thin scale-like materials observed *in toto* rather than to actual thin sections. In both cases, the two objects, of a few square milimeters, have an irregular shape with broken edges. They are formed by a homogeneous brownish material, monorefringent under crossed nicols. The whole surface is marked by very numerous thin undulating crests, roughly parallel to each others and, likely, also to the external shape of the structures (when preserved). Some crests locally bifurcate. Some faint higher order cycles (4-5) might be deciphered; each cycle containing about 12-15 crests. The crests are strongly reminiscent of the *circuli* in the teleosts elasmoid scales. Similarly, some radial thin clefts suggest scale *radii*, although they may be artefacts. Very thin, numerous dark radial or oblique fibre-like structures are locally observed, although they may also be artefacts, at least in part. They could express the plywood-like organisation of the collagenous fiber bundles forming the underlying basal plate of the scale. No vasular or cell spaces could be deciphered.

Comments. Stensiö (1969: 646-659) described macroscopically and commented the scales in *Coccosteus* Agassiz, 1844-1845 and other Placoderms. He noted the limited histological knowledge of this material at that time and interpreted the condition in *Coccosteus* scales as a secondary simplification by reduction of the deeper components of the more typical three layered dermal skeleton (Stensiö 1969: 652-653). Whatever it may be, the structures strongly agree in general aspect with teleosts elasmoid scales of the cycloid subtype (e.g., Meunier 1981; Sire 1986).

Selachii

3. "Lamna fossil. Longitudinal section showing cellular appearance" (n.b. original label in English). Ink label: 1938-630 (Fig. 1C).

Description. A longitudinal section through an elongate, thin tooth-like organ, about 12 mm long and 3 mm wide at its base. The section shows two different tissue types, *a* and *b*.

Tissue *a*: all the periphery is formed by a homogeneous tissue of constant thickness, birefringent under crossed nicols. This tissue is itself divided in three regions. *a1*: the most external one is characterized by very numerous thin dark *canaliculi* perpendicular to the free surface. *a2*: the middle one is almost devoid of *canaliculi* and shows a faint organisation of the tissue as very thin "sheets" layered parallel to the free surface. *a3*: the inner one, with a complement of canaliculi similar to *a1* but far less numerous. This lesser density allows observing some branching patterns of the canaliculi, several branches uniting from the periphery towards the center.

Tissue *b*: the internal part of the organ is made of a cone which almost reaches the surface at the tip of the tooth. This cone is formed by a highly birefringent vascularized tissue. Numerous vascular canals of small diameter are lining the limit between tissues *a* and *b*. Large and small vascular canals with irregular branching patterns are spread deeper within tissue *b*. Actually, there is no structural discontinuity at the limit between tissues *a* and *b*, but only a change in the orientation of *canaliculi* and tissue fibers, plus vascularity restricted to tissue *b*. The *canaliculi* are numerous in tissue *b*, but highly irregular, forming locally a very dense meshwork. They are far less numerous or almost lacking in the material immediately surrounding the vascular canals. There is nothing like a pulp cavity in the structure.

Comments. This thin section is very interesting from an historical-technological point of view. It is still technically excellent. The glass plate is not standard but very small (54 × 17mm). There is no cover slip and the section itself is only protected by a blue paper glued on both faces of the glass plate, with a circular opening around the section itself. This paper also bears the original label in English. Very likely the section was processed in Great Britain sometimes during the early development of the thin section technique.

Histologically, we interpret "tissue *a*" as a kind of orthodentine, forming the so-called "manteldentin" at the periphery of a tooth. "Tissue *b*" would be a so-called "circumpulpar dentin", actually a vasodentin, with centripetal deposition of dentin around vascular canals, the denteons of Ørvig (e.g., 1967), analogous to the primary osteons of bone. There is no evidence of any enameloid.

"AMPHIBIANS"
Temnospondylii

4. "*Archegosaurus latirostris* de Lebach 1870-480". Pencil number: 1073, ink label: Anat. Comp. 1875.

According to the species name "*latirostris*" (unvalid) and the locality, "*Archegosaurus latirostris* de Lebach, could be a juvenile *Archegosaurus decheni* (Steyer pers. comm.).

*Description***.** Two partial cross sections of simple labyrinthodont teeth, still partially embeded in the matrix. The pulp cavity is free, with about 12 short radial expansions of dentine protruding in it. Each inward expansion roughly coincides with a slight groove at the external surface of tooth. Tooth material is monorefringent under crossed nicols. There is no distinct coating of enamel. A thin region of globular dentin forms the tooth material at a small distance from its external surface. Inside, the tooth is formed of orthodentin with very long, thin, strait *canaliculi* within and between the radial expansions. Overall, the material agrees well with Schultze's (1969) illustrations of *Lyrocephaliscus* Wiman, 1910 (Schultze 1969: pl. 21 fig. 3, pl. 22 fig. 2), a Trematosaur.

5. "*Archegosaurus latirostris* de Lebach 1870-480". Pencil number: 1073, ink label: Anat. Comp. 1875 (Fig. 1D).

Description. One isolated tooth free of matrix. This cross section may come from a region somehow closer to the tooth tip. It shows about 20 radial expansions into the free pulp cavity. Long expansions tend to alternate with short ones, and the long ones slightly undulate. Again, no enamel could be deciphered. However the section slightly shows the radial expansions of the external dentine forming the core of the radial fences.

6. (N-1) – "Archegosaure de Lebach, crâne". No numbers, no pencil indication.

Description. About 10 osseous fragments are scattered under the coverslip. In most fragments the bone tissue is sectioned longitudinally. Osteocyte lacunae, more or less plump or elongate in shape, are set in line with the parallel fibered bone tissue. Some vascular canals, forming primary and secondary osteons are also sectioned longitudinally. In two fragments, the structure is more complex, with several vascular canals parallel to each others or faintly converging in a fan-shaped arrangement. Sharpey's fibers are numerous after a faint *annulus*. This structure is suggestive of the bone not far away from a tooth insertion.

7. "*Labyrinthodon* – Wurtemberg. Os crânien". Pencil number: 1074, ink label: 1938-613. Anat. Comp. 1875 (Fig. 1E).

Description. A few square millimetres probably from a horizontal (oblique) section in the external cortex of a dermal bone. The light brown bony material is mostly birefringent under crossed nicols, especially in regions around vascular canals (primary osteons). No secondary osteons (Haversian systems) are observed. Osteocytic lacunae are difficult to observe. Noticeable locally are Sharpey's fibers and superposition of undulating dark lines strongly suggesting *annuli* or LAGs (= lines of arrested growth), as well known among Stegocephalians (e.g., Ricqlès 1995b).

8. "*Labyrinthodon* du Wurtemberg. Écaille? céphalique." Pencil number: 1078, ink label: Anat. Comp. 1938-no.613.

Description. Probably a horizontal section in the external cortex of a dermal bone, broken in several small fragments, and further damaged by balsam shrinkage. Bone is strongly birefringent under crossed nicols, apparently demonstrating two orthogonal superimposed plies of bony lamellae.

9. "*Labyrinthodon* de Stuttgart. Écaille? temporale". Pencil number: 1077, ink label: 1938-613. Charles Marchand, Préparateur à Paris. (Fig. 1F)

Description. A good section from the free surface of a bone (with matrix) to about 3 mm deep in the cortex. No superficial ornamentation is obvious. The bone is generally birefringent under crossed nicols with a clear lamellar organisation. It contains about 16 superimposed rows of vascular canals of small diameter, sectioned longitudinally and circularly, and organized as primary osteons laid down in a "lamellar-zonal" matrix of periosteal origin. However, neither Sharpey's fibers, nor cyclical *annuli* could be observed. Secondary osteons seem to be lacking.

10. "*Trimerorachis insignis*. Permien du Texas". Pencil number: 1900. Ink label: Anat. Comp. 1878. Mr Cope.

Description. A poorly preserved bone fragment, probably sectioned vertically. What might have been the external, ornamented surface appears to have been mostly replaced by fan shaped, radiating black mineral structures which could be superficially mistaken for Sharpey's fiber bundles. Actually, very little of the external bone is preserved. Most of the specimen is formed by thin, remodelled endosteal bone trabeculae forming a highly cancellous tissue. In many places, osteocytic lacunae appear to have experienced localized widening, probably the result of *post mortem* destruction. Indeed, evidence of boring canals of mycelial origin can be observed locally.

Comments. Occurrence of *Trimerorachis* in the collection and the presence of Professor Edward D. Cope's name on the section label demonstrate the relationships among French and American paleontologists of the era.

11. "*Prototriton* de Gaudry. Permien d'Autun". Pencil number: 1075, ink label: 1938-613.

Description. A section containing several "*Prototriton*" (*sic*) bones still in their relative positions in the matrix. What can be observed suggests a complete small skeleton sectioned frontally, e.g., parallel to the bed plate in which it lies dorso-ventrally. Unfortunately the technical quality of the section is poor. It nevertheless allows deciphering occurrence of several bones and teeth. At least eight teeth can be observed *in situ* on teeth-bearing bones. The teeth are non labyrinthodont in structure, with a very thin dentin surrounding a relatively large pulp cavity. They appear to be pedicellate as among most Lissamphibians and a region of intensive remodelling, where a tooth base ankyloses on the dentigerous bone is visible. On the other hand neither enamel or enameloid, nor bicuspidate structure could be observed. Various parts of the skeleton, including dermal bones, and short and long endoskeletal bones, are sectioned more or less at random. Bone tissue shows little details but appears to have been poorly vascularized. Some long bones sectioned longitudinally may show sequence of endochondral ossification in the calcified cartilage of metaphyses. However the poor quality of the section and randomness of orientations preclude detailed observations.

Comments. The cover slip of this section is not round (as on most sections in the collection) but rectangular, as in modern thin sections. The endoskeletal bone structures preserved in this specimen may be compared to those of post metamorphic Urodeles (Ricqlès 1965).

12. "*Prototriton* de Gaudry. Permien d'Autun". No numbers.

Description. A large thin section, obviously from the same material as above (11). Preservation is very poor (see Comments). The section is rather thick but allows deciphering a longitudinal section in a limb with the stylo-zeugopodials in articulation (no autopodial is preserved).

Comments. This section has a large oval-shaped coverslip. This has largely separated from the glass plate over time and gently curled. The balsam is badly cracked and the section will have to be intensively cured for further preservation and observation.

13. (N-2) – *Plathyosaurus* (?) Ink label: "fossil bone Plathyosaurus" (in English). No number.

Description. A small (4 × 4 mm) fragment of cancellous bone. This spongy bone tissue is formed by rather coarse irregular trabeculae, leaving between them irregularly elongate spaces. The bone tissue has a great cellular density and shows extensive erosion/reconstruction cycles, as well as osteon-like structures within the thick trabeculae. Some aspects within the trabeculae are suggestive of *globuli ossei*. If so this tissue would originate in part from previous endochondral ossification.

Comments. Another thin section of English origin, exactly similar to section 14 (N-3) (see below). It is not possible to decipher the exact label name; both "Plathyosaurus" and "Plathioposaurus" can be read. The former name does not appear to match any genus name coined to a fossil Amphibian or Reptile during the 19th century. The later name appears close to *Platyposaurus*, which would be a synonym given by Lydekker, 1890 to *Platyops* Twelvetrees, 1880, a Permian "Rachitome" (Lehman 1955).

"REPTILES"
Ichthyosauria

14. (N-3) – *Ichthyosaurus*. Ink label "fossil bone Ichthyosaurus" (in English). No number.

Description. A bone tissue fragment of 5 × 5 mm. This is a microcancellous bone tissue spatially organized along a very regular "honeycomb" pattern. The thickness of the section prevents from observing details of the tissue itself.

Comments. One of several sections probably pertaining to Paul Gervais' collection but of English origin. The section is set on a standard (7.6 × 2.5 cm) glass plate with a round cover slip. The glass is entirely covered (and protected) by a red paper below, a red and gold paper above; with the label "C. M. TOPPING" appearing twice into circles on top.

15. "*Ichthyosaurus communis* d'Angleterre, côte." Pencil number: 983, ink label: 1938 no. 619.

Description. A good cross section of a small bone. The section is irregularly oval, about 5 mm in its largest diameter, and with one flat, slightly concave face. The cortex merges very gently with the more cancellous central region, as usual among aquatic tetrapods (Ricqlès & Buffrénil 2001). The outer cortex is primary in structure, containing longitudinally oriented primary osteons embedded in a woven tissue, radially oriented in the thickest par of the cortex. In the thiner (more slowly growing) regions, the cortex shows less vascularity, no radial orientation and some evidence of cyclical deposition. The medullar region is rather dense, small marrow cavities being set apart by thick, irregular secondary trabeculae of endosteal bone tissue. No remnants of cartilage are observed.

Comment. The thick convoluted trabeculae in the medullary region agree with the (non pathological) "osteosclerotic" condition often observed among aquatic tetrapods (Ricqlès & Buffrénil 2001).

16. "Ichthyosaure du Spitzberg, vertèbre". Pencil number: 965, ink label: 1938-619.

Description. Only cancellous bone tissue can be observed in cross section. This is a "mature" bone tissue with evidence of erosion/reconstruction cycles forming areolar secondary endosteal trabeculae. Some structures agree with the large endosteal secondary osteons lining the marrow sinuses often observed at the periphery of the medullar region in many large tetrapods.

Comments. Pollution by grinding powder hinders detailled observations. The structures are rather similar to the ones observed in an adult Plesiosaur phalanx (see Ricqlès & Buffrénil 2001: pl. 4, fig. F.).

17. "Ichthyosaure du Spitzberg, vertèbre". Pencil number: 985, ink label: 1938-619.

Description. A large portion of cancellous bone retaining its microanatomical organisation, possibly suggesting longitudinal orientation of bone trabeculae along the section, in a vertebral centrum. Otherwise the section is too thick to show histological details.

18. "Ichthyosaure du Spitzberg, côte". Pencil number: 984, ink label: 1938-619.

Description. A partial cross section of a bone of at least 10 mm in diameter. A central free marrow cavity (diameter 4 mm) contains a few bone trabeculae. The remains of the cortex is 5 mm thick and entirely formed by a very cancellous tissue, somewhat organized radially and longitudinally. No histological details can be deciphered because of bone opacity.

19. (N-4) – "Ichthyosaur 16 25 fofsil" (sic) (ink label on blue paper). Museum, Anatomie comparée (printed label on white paper) with pencil number: 1065 (Fig. 2A).

Description. A partial cross section from a large tooth (partial diameter 14 mm), close to its base. The tooth has a complex, "folded" structure, showing 9-10 partly preserved folds of dentine circling a large pulp cavity entirely filled by finely cancellous bony tissue. Each individual fold is a U-shaped mass of orthodentine of about one millimetre thick, the top of the U opens towards a small pulp cavity. The orthodentine has typical dentinal tubules, oriented from the periphery to the pulp cavity along radial curves, crossed by several (6 to 8) "growth lines" parallel to the external surface of the folds. Close to the surface, a thin coating of very dark dentine appears to be globular and is capped by a very thin sheet of a strongly birefringent hard tissue with a slightly irregular surface. Between the folds a distinct bone-like tissue contains cell spaces and vascular canals, apparently in structural continuity with the highly birefringent thin sheet mentioned above. This osseous tissue (topologically located outside the dentine) is in continuity with the finely trabecular bone filling the pulp cavity. The dentine folds are isolated from each others at the level of this cross section.

Comments. This section is of a rather good quality. It is mounted on a tiny glass plate, with original label on blue paper, as section no. 3 "*Lamna*" fossil (see above) but better prepared. There is no coverslip and the section is thus technically very similar to section no. 3 and may have the same British origin. The tissue between the dentine folds may be interpreted either as a cellular cementum (as suggested by its specialized fibre systems) or as bone of attachment, nevertheless it merges with the regular bone inside the pulp cavity. There is no clear indication of enamel.

These structures agree with later descriptions of ichthyosaurian teeth by Schultze (1969: 111-115, text fig. 18 and pl. XVI figs 1, 2) and Schmidt & Kiel (1971).

Plesiosauria

20. "Plesiosaure. Apophyse épineuse de vertèbre dorsale." Pencil number: 986, ink label: 1938 no. 627 (Fig. 2B).

Description. Bone tissue is observed on a 20 × 5 mm surface. This section is of fairly good technical quality and allows detailed observations. The preserved free surface of the bone is flat and formed by a very thin cortex which likely experienced subperiosteal resorption. This cortex has the same histological structure as the inner trabeculae which merge with it locally. Inside the bone, the tissue is cancellous, formed of very irregular trabeculae. These trabeculae are of endochondral origin, as evidenced by the

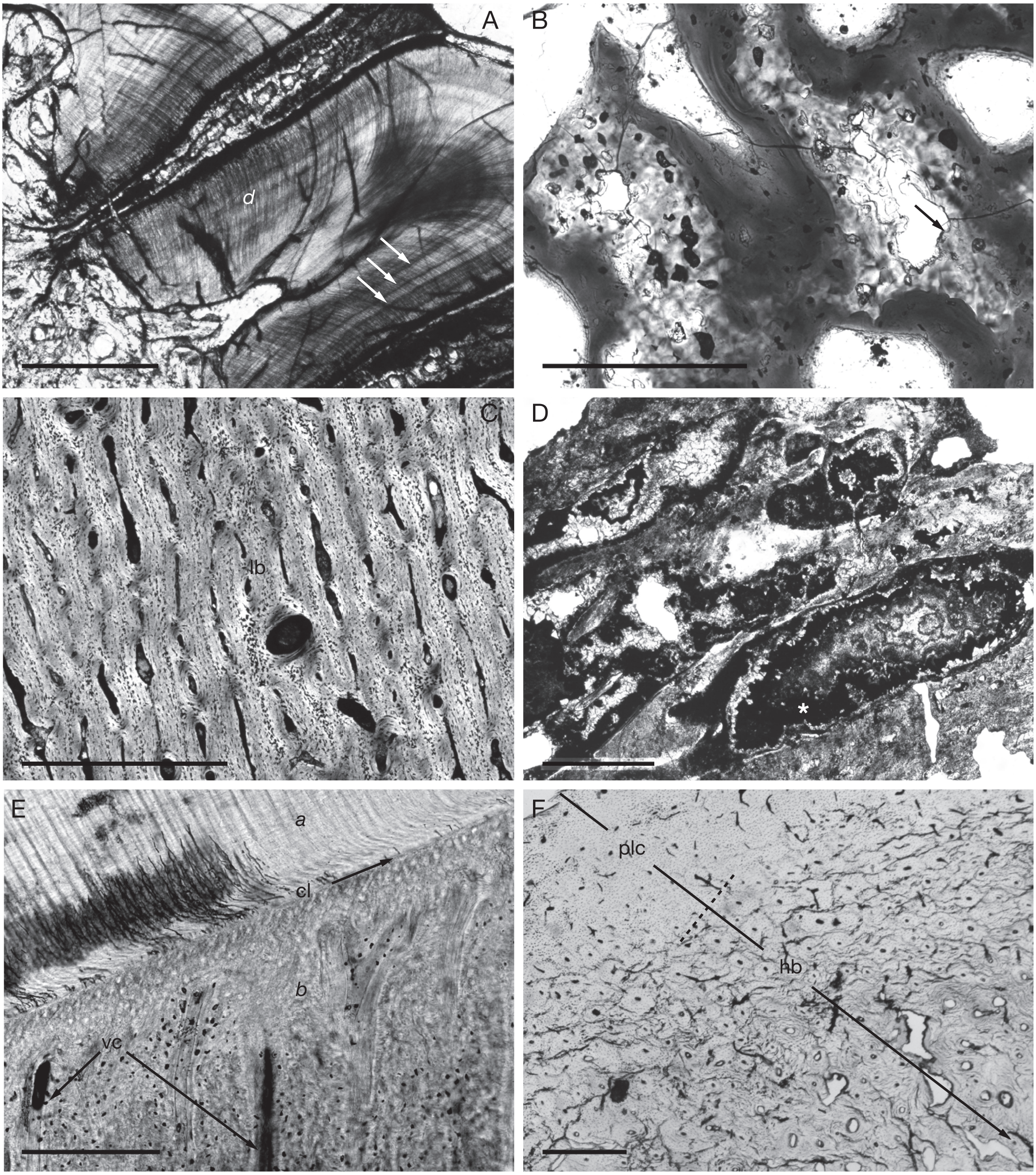

FIG. 2. — **A**, Ichthyosaur tooth (section no. 19), cross section in ordinary transmitted light, conspicuous growth marks (arrow heads) are present in the dentine; **B**, neural spine of a plesiosaur (section no. 20), cross section in ordinary transmitted light, the cores of the trabeculae still contain remnants of calcified cartilage matrix (arrow); **C**, *Iguanodon* Mantell, 1809 femur (section no. 25), cross section in ordinary transmitted light, the bone tissue is of the laminar type (**lb**); **D**, section of an undetermined bone from *Rhabdodon* Matheron, 1869. (section no. 26), the deep cortex (at the lower right corner of the photo) is extensively eroded and broad resorption bays (**asterisk**) are created; **E**, *Megatherium* Cuvier, 1796 tooth (section no. 36), ***a*** and ***b*** designate respectively tissues ***a*** and ***b***, as described in the text, the sparse remants of tissue *c* are not visible on this picture, cementing line (**cl**), vascular canals (**vc**); **F**, humerus of a bradypoid (section no. 38), cross section in ordinary transmitted light, primary grossly lamellar cortex (**plc**), Haversian bone (**hb**). Scale bars: A, 0.55 mm; B, 0.36 mm; C, 0.85 mm; D, 1 mm; E, 0.20 mm; F, 0.60 mm.

presence in their core of many island of calcified cartilage, with their clusters of large chondrocytes lacunae. The globular mineralisation of the cartilage matrix is also conspicuous, as well as *globuli ossei* localized at the interface between bone and cartilage (cf. Buffrénil *et al.* 1990).

Comments. The resorbing trabeculae forming the cortex retain an endochondral component. This structure is comparable to the surface of long bone metaphyseal regions which have to reduce their outer diameter (modeling) during the growth in length of the bones, so that the overall morphology of the bones can be maintained while metaphyseal regions are sequentially relocated (Enlow 1963).

21. (N-5) – Pliosaur. Ink label: "Plesiosaur Plesiosaur (the two words striked of) maxill. inf. Pliosaur". Anat. Comp. 1878. Pencil label: 987.

Description. A cross section of a rather compact bone fragment (jaw), about 17 mm long and 6 mm maximal width, in part contained in matrix. The preservation is fair, although the balsam has badly shrunk and cracked below the cover plate. The subperiosteal bone tissue shows incorporation of new vascular canals, Sharpey's fibers and "growth cycles". The osseous tissue shows evidence of *post mortem* degradation, suggesting that the bone was stranded on shore before ultimate fossilization. The inner bone is extensively converted into Haversian systems and contains large "marrow" sinuses, one tooth socket and some tooth material. However it has entirely experienced diagenesis and no dental tissue structure remains.

Comments. A striking artifact is provoked locally by the schrinken balsam, that displays appearance of a globular tooth with an "onion sheets" structure under low magnification.

22. (N-6) – *Pliosaurus*. Ink label: "*Pliosaurus grandis* du Havre, mach. Inf-re." Anat. comp. (no date, no number).

Description. A longitudinal (oblique) section in fairly dense bone, about 10 × 7 mm. The tissue has numerous elongate periosteocytic lacunae. It contains numerous vascular canals, roughly parallel to each others, with some evidence of secondary reconstruction around them. A more cancellous region with some irregularly shaped sinuses carved into dense secondary tissues corresponds to the endosteal margin.

Comments. Superficial (sub periosteal) bone layers do not seem to be preserved in the section.

Dinosauria

23. (N-7) – *Iguanodon*. Ink label: "Fossil bone *Iguanodon*". No pencil number. No date, with the label "– C. M. TOPPING –" appearing twice in circles on red and gold paper covering the top of the glass slide (Fig. 1A).

Description. A 8 × 8 mm cross section in coarse cancellous bone. The section is rather thick but the bone structure can be deciphered. The bone trabeculae are irregular and thick, with small marrow spaces between them. The bone tissue is secondary and remodeled. It appears mostly endosteal in origin.

Comments. One of the early thin sections of British origin in P. Gervais' collection, and one of three with the same, careful technical setting under red and gold paper. The material should come from an *Iguanodon* Mantell, 1825 fragment from England antedating the Bernissart discovery; it is so impossible that this specimen comes from the Belgium material. However, the origin of this specimen is not precisely known (England, Isle of White?).

24. "*Iguanodon* fémur". Ink label: 1938 no. 620, MNHN 1875 (figured in Taquet 2001).

Description. A cross section probably in the external cortex from the shaft of a long bone. Bone tissue is entirely primary in structure. The section is polluted by abrasive grains but the structures can nevertheless be observed. The bone tissue with a dense, homogeneous and regular vascularisation organized as primary osteons, is typically laminar to sub-plexiform. The bone surface, as preserved, shows no evidence of an external fundamental system or a decrease in appositional rate. However it might not represent the natural subperiosteal surface of the bone. No lines of arrested growth, or Haversian substitution are clearly visible.

Comments. The structure suggests an immature, actively growing individual.

25. (N-8) – *Iguanodon*. Ink label: "*Iguanodon* femur". Mus. Nat. Hist. Nat. 1876. No numbers. (Fig. 2C).

Description. An excellent thin section in compact bone, about 10 × 9 mm, plus some additional fragments. The main part of the section is a cross section through a massive cortical bone entirely formed by primary (periosteal) bone tissue of laminar to sub-plexiform types. Only a few vascular canals have experienced Haversian reconstruction. Five small additional fragments under the same cover slip figure the same tissue, but cut tangentially, parallel to the bone surface. They show three complex (and difficult to interpret) interwoven components: 1) the fibrous component of periosteal origin; 2) the lamellar component of the primary osteons (endosteal component); and 3) the vascular component locally appearing as a reticulum (e.g., Ricqlès 1972: figs 6, 7).

Comments. The structure, similar to section 24 (see above), should originate from the same material. It also suggests a fast, massive, almost continuous new bone apposition in a presumably juvenile to half grown individual. This thin section, again, raises the issue of the origin of the material. It looks to have been processed in Paris, along most others from Gervais' collection, possibly by E. Bourgogne or C. Marchand (although no label suggests this). If so, and if the material indeed belongs to *Iguanodon*, it should have come from a fragment sent from England. An alternative is that the material comes from Southern France (see below) and was labelled *Iguanodon* by comparison with other sections, published or not.

26. (N-9) – *Rhabdodon*. Ink label: "Rhabdodon, vertèbre de Villeveyrac" Mus. Nat Hist. Nat., Anat. Comp. 1876. (Fig. 2D).

Description. Two small irregular fragments under a square coverslip. The bone tissue is mostly cancellous, and only one small region seems to agree with a bone cortex of primary (periosteal) origin. This cortex is densely vascularized by up to five rows of primary osteons organized into a vaguely laminar pattern. The spongiosa starts abruptly in the deep cortex, which is dissected by large marrow cavities. The endosteal trabeculae are very remodelled. The whole bone experienced extensive *post mortem* erosion by boring organisms.

Comments. Taquet (2001), dealing with early discoveries of Dinosaurs from Southern France, notably by the geologist Philippe Matheron, commented the likely occurrence of *Rhabdodon* Matheron, 1869 at Villeveyrac (Herault) (Taquet 2001: 620), as well as Matheron's relationships with Paul Gervais (cf. Gervais 1877 in Taquet 2001) about those dinosaurian remains. This thin section confirms their relationships.

27. (N-10) – Dinosaur indet. Ink label: "Reptile de la Nerthe (Matheron) marne (?) inf. Eugène Bourgogne, préparateur à Paris". No date, no pencil number (Fig. 1A).

Description. A thin section of triangular shape, about 10 × 6 mm. Most of the section is formed by a dark matrix, containing bony fragments. The tissue, sectioned longitudinally or obliquely, is highly birefringent under crossed nicols. It is an intensively reconstructed bone tissue that may be Haversian or secondary endosteal.

Comments. From La Nerthe tunnel, Matheron described fragments of both "*Hypselosaurus*", a Sauropod, and *Rhabdodon,* an Ornithopod (cf. Taquet 2001: 614-615). The secondary nature of the tissue would agree with a Dinosaurian origin. The section likely comes from the material given by Matheron to P. Gervais in 1876 which thus would have contained not only eggshells fragments (Taquet 2001: 616) but also bone fragments.

28. (N-11) – Dinosaur indet. Ink label: "Dinosaurien? Vertèbre du Garumnien de Esperaza par

Mr. Leymerie. Museum d'Hist. Nat. Anat. Comp. 1876" (Fig. 1B).

Description. A small bone fragment, about 7 × 5 mm in longitudinal section. The tissue is highly birefringent throughout. A small region may correspond to the deep primary cortex, with a few Sharpey's fibers and rather abundant anastomosing vascular canals sectioned longitudinally. However, most of the section is secondary endosteal and would form the external part of a rather dense spongiosa.

Comment. Again, this section does not bear much "diagnostic" characters but the structure could generally agree with a dinosaurian origin. Taquet (2001: 620) quotes the letter dated July 1877 of Mr. Leymerie to Paul Gervais discussing the bone fragments from Fa and Esperaza (Aude) from which this section comes.

Mammalia
"Edentates", Xenarthra
Glyptodontoidea

29. *Glyptodon* "cubitus". Pencil number: 48, ink label: 1938-612. Anat. Comp. 1878.

Description. A bone cross section, semi-circular in shape of 23 mm diameter. Although tissue preservation is poor overall, it allows precise microanatomical and histological analysis, at least locally. Contrast between what are usually a central cancellous region opposed to a dense cortex is low here. The cortex is locally highly cancelous via large radial, circular and longitudinal canals. Conversely the inner bone tissue is rather dense, with thick bony trabeculae and relatively small marrow spaces. A part of the cortex is primary, with a plexiform vascular network. Large vascular canals with incipient osteonal deposition open under at the surface of the cortex. This suggests that sub-periosteal accretion was still actively proceeding when the animal died. At some distance from the surface, circular vascular canals experience resorption. Inner bone is formed by complex, remodelled endosteal trabeculae rather than typical Haversian systems.

Comments. The section suggests an immature, fast growing bone, perhaps exposed to peculiar biomechanical demands for a land dwelling mammal.

30. *Glyptodon* "cubitus". Pencil number: 48, ink label: 1938-612. Anat. Comp. 1878.

Description. A longitudinal section (12 × 10 mm) in compact bone. The section agrees with the description above. It documents the high vascularisation of the periosteal bone tissue via longitudinal, circular and some radial canals, and also the development of Sharpey's fibers.

31. *Glyptodon* "cubitus". Pencil number: 48, ink label: 1938-612. Anat. Comp. 1878.

Description. A small longitudinal section (4 × 10 mm in two parts) in compact bone. The natural subperiosteal surface of the bone is exposed on one side of the section, while the endosteal (perimedullar) region is exposed on the other side. What can be deciphered is consistent with the preceding section.

32. *Glyptodon* "cubitus". No pencil number. Ink label: Anat. Comp. 1878.

Description. A small longitudinal section (7 × 9 mm) in compact bone. In this better preserved section, the primary structure of the densely vascularized bone cortex is easily observed.

33. *Glyptodon* "cubitus". No pencil number. Ink label: Anat. Comp. 1878.

Description. A larger longitudinal section (14 × 9 mm) in compact bone. No primary bone at the subperiosteal surface is observed. The section is entirely composed by the inner secondary bone tissue. The stout longitudinally organized endosteal trabeculae leave between them only relatively small marrow spaces.

Tardigrada

34. *Megatherium* "cubitus". Pencil number: 42, Ink label: Anat. Comp. 1925-291, 1878 (crossed?) no. 42.

Description. A small (7 × 4 mm) longitudinal section in compact bone. The mounting balsam has extensively cracked, which does not impair observations too much. Bone tissue is highly birefringent and mostly organized longitudinally. Preservation of the tissue is not excellent because of some boring *post mortem* organisms. Evidence for multiple scalopped cementing lines concurs to analyze the tissue as dense Haversian.

35. *Megatherium*. Pencil number: 43, Ink label: 1925-291, 43, G. Marchand, Préparateur, rue Censier 16ter à Paris.

Description. A large irregular section in tooth material under an oval coverslip. Irrespective of the anatomical organization which is hard to decipher, a tissue (*a*) forms a narrow band (about 2 mm thick) sandwitched within a much thicker hard tissue (*b*). A very poorly preserved tissue (*c*) lies at the periphery of tissue (*b*). Generally, preservation is not perfect, with obvious localized *post mortem* destructions, but the histological structures can nevertheless be assessed, at least in tissues (*a*) and (*b*) (see below, section 36).

Tissue (*a*) is monorefringent. It is crossed by very numerous fine, non undulating canals, or very elongate cell spaces, with a distinctly observable diameter, running parallel to each others and with indications of short branching of oblique lateral expansions. On one side, tissue (*a*) merges in contiguity with tissue (*b*) by a very thin region where tissue (*a*) canals almost disappear. On the other side, tissue (*a*) is set apart from tissue (*b*) by a very regular, non undulating "cementing line". Tissue (*b*) is cellular and vascular. Cell spaces are numerous, plump and slightly polygonal; they are embedded in a birefringent matrix showing two orthogonal fibrillar directions. The matrix is also permeated by a large number of "canals". These are mostly parallel to each others and run towards tissue (*a*). Close to the cementing line with tissue (*a*), they change their direction and tend to run parallel to the cementing line. Around each "canal", the tissue matrix is strongly birefringent, demonstrating a primary osteon-like structure with two successive orthogonal directions of fibers. Tissue (*c*), sometimes observable at the periphery of tissue (*b*) is monorefringent and badly preserved. Many sand grains permeate the "tissue" which otherwise would show remnants of a dark cloudy matrix with some vascular canals locally.

36. "Megatherium No. 23" (some other words are undecipherable and had been crossed; Fig. 2E).

Description. A very small section, prepared with blue paper as section no. 3 "*Lamna* fossil" (see above). It shows about 4 × 3 mm of tooth material. Description would match tissues *a* and *b* above but orientation in the structure differs; moreover, preservation and optical qualities are better. The "canals" in tissue B are here crossed longitudinally and show some branchings. *Canaliculi* in tissues *a* and *b* meet at an angle at the level of the cementing line between them.

Comments. Since Owen's time (1840-45), the peculiar tooth histology of "edentates" has been a subject of study. According to traditional views (Schmidt & Kiel 1971: 148-152, figs 104, 105), tissue (*a*) would match the hard or "compact" dentin forming the tooth crests; tissue (*b*) would be the so-called vascular dentin while tissue (*c*) could represent remains of cementum.

37. *Megatheroida*? de Charlestone (sic). Pencil number: 44, ink label: 1925-292, 44. Anat. Comp. 1878.

Description. A longitudinal section (16 × 9 mm) in rather compact bone. The well preserved bone tissue is formed of secondary osteons with clear cementing lines at their periphery. The osteons are sectioned at various angles. Large oval-shaped bays, lined by endosteal coating, suggest a perimedular margin.

Comments. The city name given on the label is obviously a misspelling for Charleston (USA). The fossil would thus be from the coastal region of Georgia. Large Megatheriids are indeed known from SE North America, after the "great interchange" (e.g., Spillmann 1948: *Eremotherium*; Hoffstetter 1958: 612, 613, 635).

38. "Bradypoide de Mr. Filhol (Quercy) Humerus". Pencil number: 68, ink label: 1925-68. Anat. Comp. 1878 (Fig. 2F).

Description. A cross section in compact bone, of a roughly triangular shape, with 9 mm of bone surface extending 6 mm in bone depth. In this good thin section, the primary cortex is formed by a grossly lamellar tissue of periosteal origin. Bone fibers alternate under crossed nicols. Vascularisation is provided by small primary osteons organized longitudinally. The canals are arranged in about five, poorly defined concentric rows. Short radial vascular anastomoses connect some canals. A dense Haversian tissue with typical, well-lamellated secondary osteons, spreads by places in the primary cortex up to its surface. The same tissue also forms the remaining deep cortex. At the endosteal margin, the deep cortex is limited by large perimedullar cavities lined by thick endosteal trabeculae.

Comments. The primary cortex suggests radial growth at very moderate rate, moreover, extensive Haversian substitution does not suggest a juvenile condition. However, the lack of a typical "external fundamental system" and the relatively small amount of superimposed generations of secondary osteons both suggest a less than fully mature condition. Amprino & Godina (1947: 351-52, 452, figs 64, 66) describe the histology of *Bradypus* Linnaeus, 1758 femur and tibia as densely Haversian with locally slow growing primary bone at the periphery. This does not allow substantiating histologically the taxonomic status of Filhol's "Bradypoid".

39. *Lestodon*, "crâne". Pencil number: 47, ink label: 1925-289. Anat. Comp. 1878 no. 47.

Description. A longitudinal (oblique) section (19 × 2 to 5 mm) in compact bone. The well-preserved tissue is organized as a cortex formed by secondary osteons sectioned longitudinally and obliquely. A region extending from this cortex has its secondary osteons sectioned transversely. There is no evidence of a high number of superimposed generations of osteons.

40. *Lestodon*, "crâne". Pencil number: 47, ink label: 1925-289. Anat. Comp. 1878 no. 47.

Description. A small section (5 × 3 mm plus detached fragment) in rather compact bone. The section is similar to the preceding one, but the structures are cut more transversely. Secondary osteons appear well delineated, in cross section, from neighbouring tissues. The tissue may be "compacted coarse cancellous bone" (Enlow 1963) rather than truly Haversian.

41. *Lestodon*, "crâne". Pencil number: 47, ink label: 1925-289. Anat. Comp. 1878 no. 47.

Description. A large, irregular section (15 × 20 mm) of a dense, broken bony material (and perhaps teeth). As in preceding sections, the well preserved tissue is highly birefringent, with most fibers of a given osteon apparently organized longitudinally, as are also the osteocyte lacunae. The cell canaliculi are mostly oriented perpendicular to the fibres. All the bone appears as built of secondary osteons, forming very distinct "pipes" in an overall compact bone tissue, both in longitudinal and cross sections. This aspect reflects the presence, in the thin peripheral layer of each osteon, of fibres orthogonal to the longitudinally-organized fibres forming most of the osteons. No tissue in the section can be interpreted as dentine or cement.

42. *Lestodon*, "crâne". Pencil number: 47, ink label: 1925-289. Anat. Comp. 1878 no. 47.

Description. A large (15 × 12 mm) rhomboid, longitudinal (oblique) section in compact bone. The thinner section has the same structure as the preceding one.

43. *Lestodon* (?) *armatus*. Pencil number: 49, ink label: 1938-612. Anat. Comp. 1877.

Description. Two small fragments (2 × 2 mm) in tooth material in cross section. The thick wall of a hollow cylinder is apparently preserved. Action of boring organisms is evident. The tissue is slightly birefringent. It contains numerous cell lacunae, no vascular canal and is entirely permeated by long, thin fibres oriented radially.

Comments. Occurrence of numerous autochthonous cell lacunae identifies the tissue as cementum rather than dentin.

44. *Lestodon* "cubitus". No pencil nb. Ink label: Anat. Comp. 1878.

Description. An elongate (22 × 5 mm) longitudinal section in compact bone. The putative natural surface of the cortex is badly preserved because of *post mortem* boring organisms, which precludes histological analysis. Deeper, the better preserved tissue is apparently of the dense Haversian type, with secondary osteons cut longitudinally or transversely. This tissue forms a dense but thin cortex. Still deeper, a well developed endosteal margin is formed by large perimedullar cavities lined by secondary finely-fibered endosteal bone tissue.

45. *Scelidotherium*. Pencil number: 46, ink label: 1938-612.

Description. A longitudinal section (9 × 5 mm) in compact bone. The tissue is slightly birefringent. A very thin primary cortex contains a few primary vascular canals and some Sharpey's fibers. This cortex is immediately replaced below the surface by Haversian tissue forming the rest of the cortex thickness. Scalopped cementing lines at the periphery of the secondary osteons are well marked. The osteocytic lacunae included in osteonal lamellae are not all organized longitudinally. Instead, their orientations appear to alternate from lamella to lamella within and between osteons. No endosteal margin is preserved.

46. *Scelidotherium* "cubitus". No pencil number, ink label: Anat. Comp. 1878.

Description. A slightly larger (10 × 7 mm) longitudinal section in compact bone. No remain from the superficial cortex is preserved. Otherwise bone structure is similar to that of the preceding section, which can be assumed as coming from the same bone.

47. *Mylodon*. Pencil number: none, ink label: Mus. Anat. Comp. 1938-612. G. Marchand, Préparateur.

Description. A rather small (9 × 5 mm) cross section in compact tissue. Structures are almost entirely obliterated by the poor tissue preservation. Only a thin, grossly lamellated external cortex with few longitudinal vascular canals, and possibly radial Sharpey's fibers, may be deciphered.

48. *Mylodon*, "os du crâne". Pencil number: 50, ink label: 1938-612. Anat. Comp. 1879.

Description. A small (8 × 5 mm) section of fairly dense bone organized as thick trabeculae. Bone tissue is strongly birefringent and finely fibered. Some very large, well-defined secondary osteons are observed in cross and longitudinal sections, over a background of stout secondary endosteal trabeculae orthogonal to the osteons just mentioned. There is no clear superficial cortex of periosteal origin. High magnification shows the pervasive, if still discrete, occurrence and action of *post mortem* boring micro-organisms.

49. *Mylodon*, "os du crâne". Pencil number: 50, ink label: 1938-612. Anat. Comp. 1879.

Description. A large (10 × 6 mm) section in thick, highly birefringent bone trabeculae. Structures are similar to those observed in the preceding section. The large secondary osteons form a complex 3D meshwork.

50. *Mylodon*, "os du crâne". Pencil number: 50, ink label: 1938-612. Anat. Comp. 1879 (broken).

Description. Three small bone fragments have similar structures than in the two preceding sections. Two fragments are mostly organized as longitudinal sections while in the third one the structures are mostly observed in cross section.

51. *Mylodon*, "côte". Pencil number: 54, ink label: 1925-213 (or 293?). Anat. Comp. 1878.

Description. A longitudinal section (15 × 6 mm) in compact bone. The highly birefringent bone tissue is entirely formed of a dense packing of secondary osteons, all sectioned longitudinally. A tiny fragment nearby is a cross section of the same.

52. *Mylodon*, "côte". Pencil number: 54, ink label: 1925- 293. Anat. Comp. 1878.

Description. Three fragments of rib in cross section. Apart from a putative, small and very thin remain of the external bone surface, all the tissue is dense Haversian. The tissue is largely monorefringent with exception for the most external region of the secondary osteons that shows high birefringence. Several generations of osteons are observed, as well as fully open erosion rooms, suggesting a still active erosion/reconstruction process.

53. *Mylodon*, "omoplate". Pencil number: 53, ink label: 1925- 293. Anat. Comp. 1878. (Fig. 3A).

Description. Two fragments in cross section. This dense Haversian bone gradually merges laterally into a more concellous (inner) tissue formed of strong endosteal trabeculae. The Haversian tissue is more anisotropic than that of the rib, suggesting a different spatial organisation of its (former) collagenous fibers. The free bone surface, as preserved locally, is formed of a very thin primary tissue, rich in Sharpey's fibers, broadly replaced below the surface by Haversian substitution.

54. *Mylodon*, "omoplate". Pencil number: 53, ink label: 1925-293. Anat. Comp. 1878.

Description. A larger (12 × 13 mm plus isolated fragments) longitudinal section in compact bone. The tissue matches the dense Haversian structure observed in cross section. A few oblique to transversal osteon orientations and the pattern of anisotropy of the tissue suggest a more complex spatial organisation of bone fibers than that in the rib.

55. *Mylodon*, "humerus". Pencil number: 52, ink label: 1925-293. Anat. Comp. 1878.

Description. A small (5 × 8 mm) cross section of cortex and perimedullar cancellous region. The thin cortex is entirely dense Haversian in structure, with a resorptive sub-periosteal surface; hence no primary (periosteal) bone tissue is preserved. Large, regularly flattened erosion bays, lined by thick deposits of endosteal tissues, form the underlying spongiosa, comprising five bone trabeculae parallel to the cortex and to each others. Within the trabeculae, extensive remnants of the inner Haversian cortex are preserved.

56. *Mylodon*, "humerus". Pencil number: 52, ink label: 1925- 293. Anat. Comp. 1878.

Description. A slightly larger (9 × 10 mm) longitudinal (tangential) section in well vascularized compact bone. The tissue is highly birefringent and is formed of secondary osteons and endosteal deposits rather regularly organized. Many secondary osteons appear to be composed of parallel-fibered rather than finely lamellar tissue.

57 to 59. *Mylodon*, "cubitus". Pencil number: 55, ink label: 1925- 293. Anat. Comp. 1878.

Descriptions. Three longitudinal thin sections in dense compact (cortical) bone. Extensive *post mortem* destruction by boring micro-organisms precludes accurate description. Only the lumen of thin, parallel oriented, vascular (Haversian) canals is preserved, in addition to scattered islands where the background of bone tissue is decipherable, especially in the thickest section.

60 to 62. *Mylodon*, "cubitus". Pencil number: 55, ink label: 1925- 293. Anat. Comp. 1878.

Descriptions. Three cross sections in compact cortical bone tissue. Similar circumstances caused slightly less devastating results for observation in the cross sections than in the longitudinal ones. From the periphery, the cortex varies in thickness from 5 to 10 mm. A very thin lamellar external fundamental system appears; otherwise the cortex is densely Haversian throughout. The periphery of each secondary osteon tends to be better preserved than the core of the osteon.

63 to 73. *Mylodon*, "plaque cutanée". Pencil number: 51, ink label: 1938-612. Muséum. Anat. Comp.

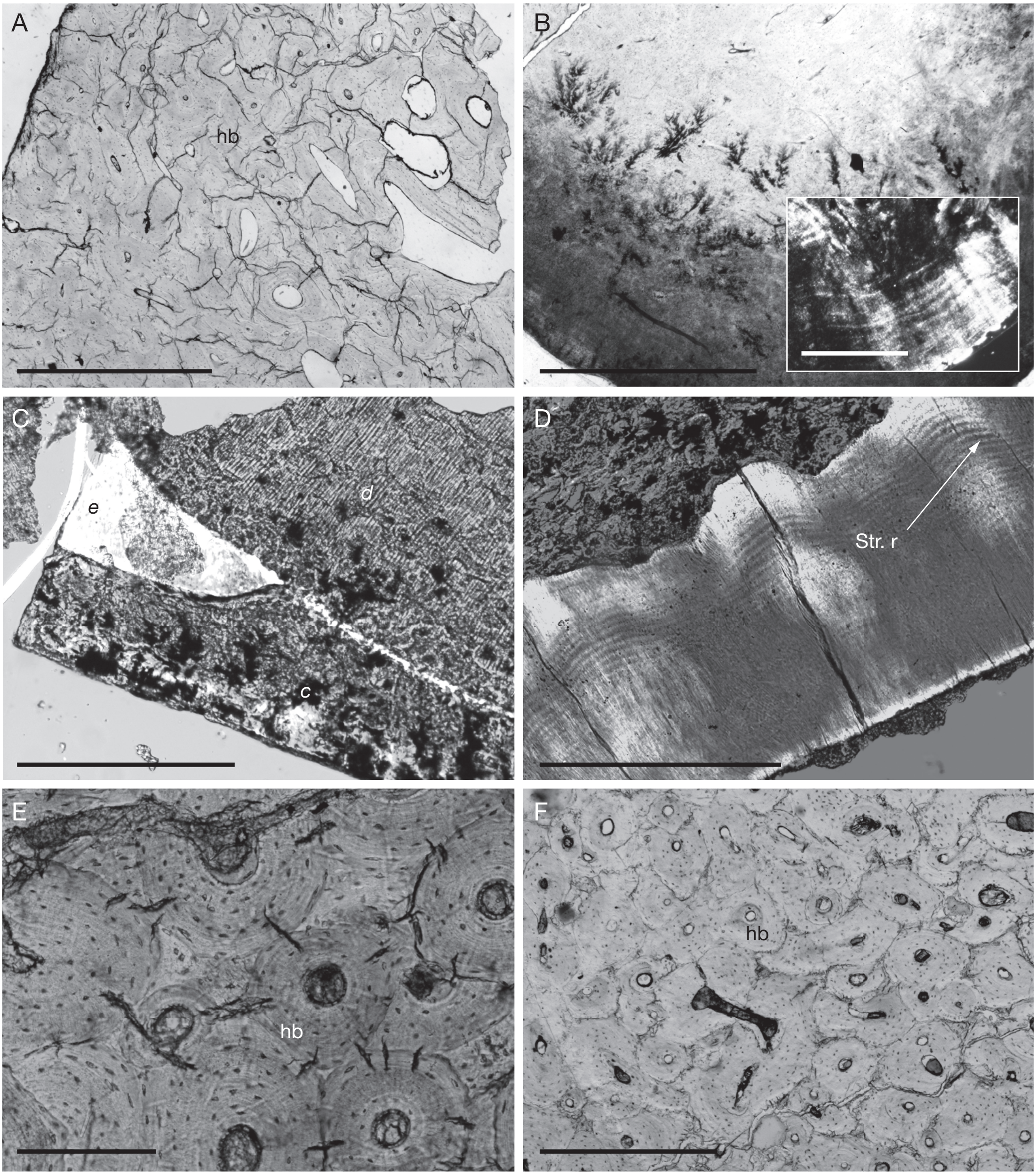

FIG. 3. — **A**, Scapula of *Mylodon* Owen, 1859 (section no. 53),cross section in ordinary transmitted light, the bone tissue is of the dense Haversian type; **B**, *Mylodon* osteoderm (section no. 67), main frame: radial section in ordinary transmitted light; detail: polarized transmitted light revealing cyclic growth marks in the outer cortex; **C**, *Typotherium* Gervais, 1867, a junior synonym of *Mesotherium* Serres, 1867 molar (section no. 75) at low enlargement, at the crown-root junction, three different tissues can be observed in ordinary transmitted light: orthodentine (***d***), cement (***c***), and wedged between the two formers, a triangular splinter of enamel (***e***); **D**, closer view at the striae of Retzius (**Str. r**) in the enamel of *Typotherium* molar, same section as above, transmitted polarized light; **E**, cetacean rib (section no. 82), cross section in ordinary transmitted light, bone tissue is of a dense Haversian type (**hb**); **F**, *Macrotherium* Lartet, 1837, a synonym of *Anisodon* Lartet, 1851 ulna (section no. 89), cross section in ordinary transmitted light. Dense Haversian tissue (**hb**). Scale bars: A, 1.15 mm; B main, 2.10 mm; B inset, 2 mm; C, D, 1 mm; E, 0.30 mm; F, 0.40 mm.

G. Marchand, Préparateur. (no. 67 is illustrated on Fig. 3B).

Descriptions. Eleven thin sections (one broken) in osteoderms. Each section is sub-circular, varying in diameter from 5 to 10 mm. The material is compact, with no central cavities forming a spongy region. The periphery of the osteoderm is formed by an extremely dense, compact tissue, almost non vascular, with radial fibres, perpendicular to the surface. The tissue is organized into numerous (> 12) successive thin strata, parallel to the surface. This organization appears to result from the alternation of thinner, translucent, and thicker more opaque strata, that differ in their general orientation, rather than in the nature of their fibrillar material (as also suggested by reactions under crossed nicols). In some cases this stratification results into a more clear-cut alternation of opaque zones and translucent very thin lines; the zones becoming thinner and thinner towards bone surface. Cell spaces are numerous but not conspicuous. This organization may be followed, more or less unchanged, down into the core of some osteoderms. In others, the general system of radial fibers becomes more conspicuous in the deeper regions, forming very elongate, sometimes fan shaped systems of compact fibers bundles. Those systems are set apart and lined by others, orthogonal to them, and forming together a complex 3D dense meshwork. A faint system of vasular canals occurs in the osteoderms, especially in the deep regions that were formed during early osteoderm development. The canals are irregularly oriented, with some short anastomoses between them. They appear to be either of the primary simple vascular canals type, or to develop as primary osteons. Haversian reconstruction, if any, seems to be exceedingly rare. Some *post mortem* cracks have been filled by a dark mineral (Manganese oxide?) which locally forms "ferns leafs-like" images. Locally, this material has naturally stained the structures in a faithful way, either from the surface or from the inner cracks, enhancing the optical contrast between the neighbouring fibrillar systems.

Comments. The osteoderms appear to be formed by a rather specialized type of dense primary bony tissue, also observed in some dinosaurs osteoderms (Ricqlès *et al.* 2001), where an extensive system of closely packed fibers takes prevalence over a weak system of vascularisation. The core of the osteoderm may have been initially formed here by the metaplastic ossification of the preexisting fibers of the *stratum compactum* of the dermis. Subsequent growth may have taken place by further deposition of new material at the periphery of the core, although there is a clear fibrillar continuity between deep and more superficial regions. Growth cycles at the periphery of the osteoderms strongly resemble the *annuli* and zones described in the bones of many extant ectotherms (Castanet *et al.* 1993), where they have been demonstrated to be annual in many cases. The whole comparative analysis of osteoderms formation and growth among various tetrapod groups still remains a little surveyed problem.

Notungulates

74. *Toxodon* "cubitus". Ink label: Anat. Comp. 1878.

Description. A small (9 × 5 mm) longitudinal section in compact bone. Most of the fine structure has been destroyed by *post mortem* boring organisms. A very thin but well-vascularized primary cortex, with vascular canals running in several directions, is replaced at a small distance from the bone surface by longitudinally organized Haversian tissue.

75. *Typotherium* "3ème mol. sup. gauche, coupe transv." Pencil number: 276, ink label: Anat. Comp. 1938-583 (Fig. 3C, D).

Description. A large tooth thin section with a rectangular coverslip. The tooth is broken in several fragments by the technical process but tissue structures can be observed. Most of the material, cone shaped, appears to be orthodentine, although preservation of the tissue is very poor, due to *post mortem* invasions. This cone appears to have been covered by a thin (about 400 µm) continuous sheet of a highly birefringent tissue which remained *in situ*, at least locally (Fig. 3C), and did not suffered invasion by boring organisms. The tissue shows a very fine radial striation throughout and faint suggestion of an irregular globular structuring of its matrix. No obvious "prisms" could be recognized. On its external surface (opposed to what we interpret as dentin) this tissue may have an irregular surface, with some undulations, bulgings and shallow grooves locally. In some tooth fragments, this tissue displays, in transmitted polarized light, at least 17 to 20 regularly spaced incremental layers (interval: 25 to 30 µm) that are sharply defined in the strata close to the undulated surface, but tend to vanish towards the opposite surface (Fig. 3D). This tissue is interpreted as an enamel of some sort, and the striation that it displays consists in striae of Retzius. Externally, a third tissue, very poorly preserved, as is dentin, shows cell spaces, short fibre-like striations, and some local evidence of cementing lines. It is interpreted as cementum. The dental region shown on Fig. 3C is of special interest because it shows the end of enamel as an edge at the crown-collar junction, after which the cementum is directly capping the dentin, with only a line of discontinuity between them.

76. *Typotherium* "molaire inf. (section verticale)". Pencil number: 275, ink label: 1938-583, Charles Marchand, Préparateur à Paris.

Description. A small tooth under a circular coverslip and dark mounting medium. The tissue preservation is correct but tooth exploded during the technical process, with several fragments becoming superimposed. Obliquity of the section in the enamel and cementum provides further details: the enamel shows cycles of diffuse, cloudy transverse "bands" in polarized light, but no obvious prisms. In the cementum, plump cementocytes lacunae and bundles of long fibers are associated with numerous simple vasular canals of small diameter, running parallel to each others. The cementum is thus vascular. Its location in connection with enamel suggests it is crown rather than root cementum.

77. *Typotherium* "os incisif, coupe transversale, structure altérée". Pencil mumber: 267, ink label: 1938-583.

Description. A small triangular (side 7 mm) thin section in spongy bone. As already recognized on the label, the intensity of *post mortem* destruction by boring organisms makes histological study difficult, although the overall microanatomical organization of bone trabeculae (and bone porosity) can be still easily assessed under crossed nicols.

78. *Typotherium* "os incisif, coupe transversale, structure altérée". Pencil number: 274, ink label: 1938-583.

Description. A small quadrangular (side 7 mm) thin section in compact bone. Same comments as above.

79. *Typotherium* "cubitus". Pencil number: 273, ink label: 1938-583. Anat. Comp. 1878.

Description. A quadrangular (side 11 mm) longitudinal thin section in compact bone. This section is badly, but not completely, invaded by *post mortem* boring organisms. The remain of the bone tissue suggests a longitudinal section in a dense Haversian tissue, with prevalence of longitudinal orientation of bone fibers. Apparent active biological resorption of the bone may rather represent the deceptive effect of boring organisms.

80. *Typotherium* "cubitus". Pencil number: 273, ink label: 1938-583. Anat. Comp. 1878.

Description. A large quadrangular (broken in two, sides 11 × 7 mm) longitudinal thin section in compact bone. Same comments as above.

81. *Typotherium* "cubitus". Pencil number: 273, ink label: 1938-583. Anat. Comp. 1878.

Description. A large irregular oval (16 × 9 mm) cross section in compact bone. Parts of the free surface of the external cortex are preserved. Unfortunately, the poor tissue preservation again precludes detailed observations. The thin sub-periosteal primary cortex contains a few longitudinally oriented primary osteons. Otherwise all the bone appears to have been remodeled into dense Haversian tissue.

Cetacea

82. "Côte fossile d'un Cétacé, section en travers". Pencil number: 263. Charles Marchand Préparateur (Fig. 3E).

Description. A cross section in compact bone tissue. The section is irregular in shape, about 8 × 5 mm. It seems that an original external free surface of the bone is preserved. The external cortex is characterized by many osteons in a periosteal tissue containing many Sharpey's fibers. A few osteons appear to be primary, longitudinally oriented and lying comformably within the periosteal tissue. However, many osteons are secondary, as evidenced by their inconformity with neighbouring structures. Deeper in the bone, most osteons are secondary, although some primary tissue, with Sharpey's fibers, locally form an "intersticial system" between them. Most secondary osteons are well defined, with a small diameter Haversian canal in the middle. Very few wide open erosion rooms are observed and there is no generalized superposition of several generations of osteons.

Comments. The tissue can be described as "dense Haversian bone" although there are probably more primary osteons than suggested by a quick casual observation and secondary osteon overlaping is not overwhelming. Most secondary osteons would be thus of "first generation", suggesting a not so mature tissue. As frequent in fossil dense Haversian tissues (especially from Hadrosaurs "ossified tendons") numerous short radial cracks unite the peripheries of neighbouring secondary osteons, crossing the cementing line limiting each secondary osteon.

83. "Côte fossile d'un Cétacé, section en travers". Pencil number: 116, ink label: Anat. Comp. 116.

Description. A smaller cross section in compact bone from the same material as above (82) but slightly thinner, allowing sharper observation, but with no preserved peripheral cortex. A few wide open erosion rooms and some "third generation" secondary osteons are observed.

84. *Champsodelphis macrogenius*? "terrains de...". Ink label: Anat. Comp. 1876.

Description. An irregular and ovoid cross section in a tooth 6 × 3 mm. Most of the section is formed of a highly birefringent tissue, surrounding an oval central structure about 2 × 1 mm. The external tissue is entirely non-vascular but densely cellular, and entirely permeated by an extremely large number of thin, slightly undulating and very long radial fibres. Many circumferential lines, closer to each others towards the periphery, are resolved as associated with cracks in the tissue. Although those lines are artefactual, at least in part, they strongly suggest lines of cyclical deposition.

The inner tissues are sharply delineated from the external one by a clear discontinuity. Deeper to this discontinuity, a first thin layer is amorphous, isotropic and featureless. Then a second thicker discontinuity circles the most internal tissue. The latter is highly birefringent and surrounds a tiny, central free pulp cavity. The internal tissue appears mostly globular, especially close to its periphery. Birefringence underlines both radial and circumferential organizations. Successive circumferential regions of relatively more globular or more inotropic mineralizations (*sensu* Ørvig 1967) seem to alternate. Elongate, very thin radial fibres can be observed, perhaps as numerous, but far less obvious, than in the surrounding cellular tissue.

Comments. *Champsodelphis* Gervais 1848 *in* Gervais 1848-1852 was erected on material from the middle to the upper Miocene of Europe (Simpson 1945). By comparison with available data (e.g., Schmidt & Kiel 1971) we interpret the cellular, non vascular tissue in the periphery as a very thick coat of cementum. Radial fibres there would be the anchoring fibres, akin to Sharpey's fibres. The inner tissue can be interpreted as orthodentine, although of a highly globular variety. The thin amorphous coating at the periphery remains puzzling. It appears to be natural and well *in situ* between cementum and dentin. Its optical properties do not suggest enamel, an interpretation which would also be contradicted by its surrounding by the cementum.

Perissodactyls, Chalicotheria

85. "*Macrotherium* du Gers". Charles Marchand, Préparateur à Paris. Pencil number: 277, ink label: 1938-588.

Description. A thin section in a large tooth, broken in several fragments, the largest being about 10 × 10 mm. Preservation is poor because of breakage during preparation and later shrinkage of the balsam. It nevertheless allows detailed observations locally. A thin coating of cementum is still located over the dentine in one place, and detached in another. The cementum is cellular, non vascular, slightly birefringent, and contains thin radial fibers. The region in contact with dentine differentiates into thin alternating layers where the relative amount of cementocytes, fibers and ground substance differ. In most other regions, cementum has been extensively altered by *post mortem* boring organisms. The dentine forms a very thick (several millimetres) birefringent orthodentine, with numerous, very long and gently undulating canaliculi, with little change from the periphery to the pulp cavity. At least 40 alternatively darker and lighter «growth bands », parallel to each others and to the dentin surface, are visible (but better expressed in the periphery) in ordinary and polarized light. They are supplemented by at least two "lines of arrested growth" locally forming clearer discontinuities. There is no enamel on the section.

Comments. *Macrotherium* Lartet, 1837 is the same as *Chalicotherium* Kaup, 1833. Material from the Gers (Sansan) allowed deciphering the puzzle of the Chalicotheria. *Macrotherium* was known by post-cranial material only, while only skull and teeth material were apparently available for *Chalicotherium* (both from Sansan). Finally, the discovery of sub-complete skeleton in connection at Sansan by Filhol in 1887 demonstrated the common origin of the cranial and post-cranial material (e.g., Viret 1958: 413-420). In connection with the above story, it is of interest that this thin section of tooth is nevertheless labelled "*Macrotherium* du Gers". As no tooth section bears a date, it is not possible to conclude that attribution of teeth to *Macrotherium* (rather than to *Chalicotherium*) was already done prior to Filhol's discovery (1887). Nevertheless, dates on the thin sections from *Macrotherium* post-cranial bones in this collection (1878) make it a possibility.

86. "*Macrotherium*, cubitus". Pencil number: 266, ink label: 1938-588. Anat. Comp. 1878.

Description. A small (8 × 6 mm) longitudinal thin section in compact bone. Most of the structure appears to be formed by longitudinal section in highly birefringent secondary osteons, although cementing lines at their periphery are not obvious. Longitudinal orientation of bones fibers in the osteons is overwhelming. Between them, a more monorefringent interstitial tissue may be the remnant of periosteal bone, as suggested by faint indications of localized Sharpey's fibers.

87. "*Macrotherium*, cubitus". Pencil number: 266, ink label: 1938-588. Anat. Comp. 1878.

Description. A small (9 × 8 mm) longitudinal thin section in compact bone. The structures are generally similar as in previous section, with perhaps less evidence of interstitial remnants of periostal bone and more evidence of localized resorptions taking place in the secondary osteons.

88. "*Macrotherium*", cubitus. No pencil number. Ink label: Anat. Comp. 1878.

Description. A longer (14 × 7 mm) longitudinal thin section in compact bone. The structures are similar to the ones of the two preceding sections, with a better expression of the elongate and branching paths of the Haversian canals (one in the middle of each secondary osteon).

89. "*Macrotherium*", cubitus. No pencil number. Ink label: Anat. Comp. 1878 (Fig. 3F).

Description. A small (10 × 5 mm) cross section in compact bone. The natural periphery of the cortex is preserved. Primary bone tissue of periosteal origin is locally preserved close to the bone surface. Elsewhere, it has been eroded away, degraded by *post mortem* organisms, and replaced *in vivo* by Haversian tissue. As preserved, primary bone appears to be parallel-fibered, with few vascularisation. No typical "external fundamental system" is obvious. Most of the bone is composed of dense Haversian tissue, with superposition of several generations of secondary osteons, locally. The overall very weak birefringence of the bulk of the osteons suggests that most fibers are perpendicular to the section.

Comments. Structures in the cross and longitudinal sections agree with the hypothesis that they all come from the same region in the same bone shaft, as also suggested by evidence of sawing planes along some sections. Extreme prevalence of the organization of the bone fibres along a longitudinal pathway may be tentatively linked to the peculiarities of front arm elongation and likely specialized biomechanics in Chalicotheres.

Chalicotherioidea

Pernatherium. This genus, described by Gervais (1876), is classified by Simpson (1945) as *Chalicotheriidae incertae sedis* (Eocene of Europe).

90 and 91. *Pernatherium.* Pencil number: 279, ink label: 1938-593. Anat. Comp. 1878.

92. *Pernatherium*. Anat. Comp. 1878.

93. *Pernatherium* "calcaneum" (? p.G 1.). Anat. Comp. 1878.

94. *Pernatherium* "calcaneum" (P.G). Anat. Comp. 1878.

Descriptions. The five sections seem to come from the same material, if not from the same bone. Sections 93 and 94 are the only ones bearing anatomical information (calcaneum). Section 90 shows almost identical structures with 93 and 94, and will be described with them; 91 and 92 are different.

Calcaneum sections (93, 94 and, very likely, 90) show cross sections of a rather spongy bone, about 13 × 8 mm in surface, at most. Natural surface of the bone is partly preserved as a flat to gently convex cortex, ornamented by an extremely rough, spiky structure. The cortex contains a few irregular primary osteons embedded in a periosteal tissue dominated by extremely abundant Sharpey's fibers. The fibers are mostly organized perpendicularly or obliquely to the free surface of the bone. They are also organized as superimposed zones, suggesting bursts or cycles of bone deposition, and are well developed in the bone spikes protruding from the general surface. Erosion-reconstruction of the cortex is demonstrated by numerous secondary osteons. The superficial cortex merges with a more concellous secondary tissue forming the bulk of the bone. However this tissue can hardly be described as a spongiosa because its trabeculae are thick and occupy a larger volume than the cavities in between. The tissue is secondary, irregular, formed of endosteal trabeculae forming more or less typical secondary osteons. Interstitial islands of periosteal bone with extensive amounts of Sharpey's fibers are nevertheless present deep in the bone, far away from the preserved cortex. There is no evidence of articular surface or endochondral components.

Comments. The structure fits with an endoskeletal short bone, with little contrast between a compact cortex and a spongy medulla. The cortex structure strongly suggests a region of dense, extensive connective tissue attachment, probably the tendon of a powerful muscle. The obvious biomechanical involvement of the bone as a whole is also suggested by the general robustness of its trabecular system.

Section 91 is a fairly large (14 × 7 mm) longitudinal section in compact bone. The tissue is optically very "active", showing high birefringence even under uncrossed nicols. Most of the bone appears to be primary and parallel-fibered, with a homogeneous mass reaction under crossed nicols. The tissue is permeated by a few longitudinal vascular canals. Some canals are crossed transversally and appear as small primary or secondary osteons. No Sharpey's fibers or lines of arrested growth are obvious. Towards one end of the section, the tissue becomes very progressively invaded by more and more numerous and large secondary osteons, observed in longitudinal section but slightly obliquely.

This structure suggests a long bone cortex. The longitudinal section would be slightly oblique relative to the bone structure, from a more external region (dominated by primary periosteal bone tissue) to a deeper region (dominated by secondary osteons).

Section 92 is a longitudinal section in compact bone, smaller than 91, triangular in shape with each side about 10 mm. As in 91 and even more, the tissue is highly birefringent. Vascular canals are cut longitudinally and transversely. The bone tissue is entirely endosteal, with complex evidences of multiple erosion/reconstruction sequences and secondary osteon-like structures cut longitudinally and obliquely.

The simplest interpretation is that this section comes from the same material as 91, cut parallel to it but slightly deeper into the bone in the perimedullar region (endosteal margin), hence only containing endosteal secondary material.

(?) Equoidea

95. (N-12) – "*Ephippus* (sic) *gigas* Hyperostosose dr l'antr bord (?) interne". Ink label: Muséum Hist. Nat. Anat. Comp. 1875 (no pencil number)

Description. This puzzling section, almost translucent, appears to have received some staining, perhaps by fuschin. The tentative description herewith is purely provisional.

A lateral part of the section appears to comprise cancellous bone. This merges in the medial part of the section into a dense tissue permeated by small (vascular?) cavities set in extremely orderly longitudinal rows parallel to each others. The tissue also contains numerous tiny cell spaces set regularly in pace with the above mentioned longitudinal rows. Finally, the tissue is entirely permeated by numerous small branching canals, slightly larger in diameter than the supposed cell spaces, but smaller than the putative vascular spaces. Again, this system is orderly set in pace with the general structure of the tissue but runs generally perpendicular to the longitudinal rows.

Comments. *Epihippus* Marsh, 1877 is a "primitive" horse from Middle to Late Eocene of Western North America, known by fragmentary material (e.g., Viret 1958; Mc Fadden 1992). It is not clear whether this thin section actually comes from this taxon or not.

The structure is puzzling; it could be tentatively interpreted as a tangential section into the ossified part of a large tendon at the level of its insertion into bone. The numerous branching canals perpendicular to the general longitudinal organization of the tissue are best interpreted as evidence of a massive *post mortem* invasion by boring micro-organisms, the invasion being spatially constrained by the strongly ordered longitudinal organization of the tendon-like tissue.

Sirenia

96. "Côte fossile d'un Halitherium". Pencil number 246, ink label: Anat. Comp. 1938 no. 626.

Description. A 10 × 15 mm cross section in compact bone. Cell spaces and their canaliculi are well underlined by *post mortem* deposition of dark mineral salts, but the whole bone is microfragmented and the numerous cracks hinder observations. Only a small region may represent the external cortex. The few primary bone left is very poorly vascularized, already replaced by secondary osteons. Many highly irregular, grey-brown coloured secondary osteons strongly contrast with a more translucent yellowish background of dense bone tissue. This background is formed by densely packed irregular bony trabeculae and secondary osteons. The structure may thus derive from a compacted coarse cancellous tissue of endosteal origin (Enlow 1963) rather than from a "regular" cortex turned into dense Haversian bone. No remains of calcified cartilage or endochondral ossification could be observed.

Comments.This very compact, irregular secondary tissue fits the general pattern of "pachyosteosclerosis" common in parts of the Sirenian skeleton (e.g., Ricqlès & Buffrénil 2001). The strong differential natural colouring of some secondary osteons and other structures underlines the *in vivo* differences in bone matrix mineralisation, the latest (youngest) secondary osteons laid down being less mineralized than the older (more mature) ones that form most of the more translucent "background".

Proboscidea

97. "Mastodonte de Sansan, cubitus". Pencil number: 271, ink label: 1938-582. Anat. Comp. 1878.

Description. A thin bony "scale" probably detached or sawed from a shaft and sectioned transversely. The section (9 × 2 mm) is technically good. One side of the section, flat and perhaps sawed off, is entirely Haversian with small secondary osteons and a few, much larger, irregular ones. Deeper in the section, the bone is entirely formed by larger and larger endosteal osteons, ending into large, broken endosteal trabeculae.

Comments. The structure strongly suggests a perimedullar region in the endosteal margin.

98. "Mastodonte de Sansan, cubitus". Pencil number: 271, ink label: 1938-582. Anat. Comp. 1878.

Description. A larger section about 10 × 12 mm. The bone, sectioned longitudinally, is compact and displays a complex structure, with large, longitudinally sectioned secondary osteons spreading in a complex of dense endosteal trabeculae.

Comments. This longitudinal section matches the bone organization in an endosteal margin.

99. "Mastodonte de Sansan, cubitus". Pencil number: 271, ink label: 1938-582. Anat. Comp. 1878.

Description. A large section about 13 × 12 mm. The bone is sectioned longitudinally. The structures, similar to those of no. 98, are typical of a well developed endosteal margin.

100. "*Mastodon arvernensis*, cubitus". Pencil number: 270, ink label: 1938-582 . Anat. Comp. 1878.

Description. A small and technically good cross section about 5 × 7 mm, in compact bone. The free surface of the bone cortex is not available. The tissue is entirely dense Haversian. Several generations of secondary osteons are locally visible, together with active erosion bays and secondary osteons at various stages of deposition. Osteonal lamellation and cell lacunae with *canaliculi* are generally well marked. The periphery of most osteons is brightly birefringent.

101. "*Mastodon arvernensis*, cubitus". Pencil number: 270, ink label: 1938-582. Anat. Comp. 1878.

Description. A longitudinal section of 19 × 12 mm in bone cortex. The section contains two fragments with different structures. One fragment, covered by sediment, shows the free external surface of the cortex on its two sides (because of tangential effect of the section in a convex structure). This superficial cortex is largely monorefringent, and contains a few longitudinally and circularly oriented primary vascular canals, and numerous Sharpey's fibers. Deeper in the cortex, the structure becomes almost entirely Haversian. The external cementing lines of the secondary osteons are clear, as well as their central Haversian canal and its anastomoses branching laterally. This is well developed in the second fragment.

102. "*Elephas meridionalis* du Gard, Radius". Pencil number: 269, ink label: 1938-592. Anat. Comp. 1878.

Description. A longitudinal section (14 × 10 mm) in a relatively spongy bone. The section is entirely composed of secondary endosteal trabeculae, probably from the periphery of the marrow cavity.

103. "*Elephas meridionalis* du Gard, Radius". Pencil number: 269, ink label: 1938-592. Anat. Comp. 1878.

Description. A cross section in cortical bone and endosteal margin. The section broke during the technical process, which hinders observations. The free surface of the bone and its external-most cortex are lacking. Tiny remains of the periosteal bone tissue can nevertheless be observed locally: they contain longitudinally and circularly oriented small primary osteons embedded in an apparent lamellar matrix containing Sharpey's fibres. No fibro-lamellar organization of the laminar or plexiform subtypes could be deciphered. Most cortical bone is densely Haversian. This secondary cortex gently merges, very progressively, into a well-developed endosteal margin, with larger and larger endosteal osteons and large secondary endosteal trabeculae.

Comments. The sections seem to come from the very large skeleton of *E. meridionalis* (synomym of *Mammuthus meridionalis* Nesti, 1825) found in Durfort (Gard) and mounted in the Galerie de Paléontologie of the MNHN (see Gaudry 1893).

104. "*Dinotherium teutobochus*, humerus". Pencil number: 272, ink label: 1938-587. Anat. Comp. 1878.

Description. A small (4 × 6 mm) longitudinal section that apparently comes from an endosteal margin subject to diffuse erosion. However, a small region is formed by periosteal tissue with Sharpey's fibers, and possibly a "bright line" of the laminar bone pattern. The numerous osteocytic lacunae and canaliculi are of exceptional sharpness.

105. "*Dinotherium teutobochus*, humerus". Pencil number: 272, ink label: 1938-587. Anat. Comp. 1878.

Description. A larger (about 16 × 9 mm) and very thin cross section in bone cortex. No remains of the bone free surface are left. The whole section is formed of typical dense Haversian tissue. Several generations of secondary osteons are present. Osteon size becomes larger towards a region likely closer from the endosteal margin.

106. "*Dinotherium teutobochus*, humerus". Pencil number: 272, ink label: 1938-587. Anat. Comp. 1878.

Description. A small (10 × 3 mm plus fragment) longitudinal section probably from the endosteal margin.

107. "*Dinotherium teutobochus*, humerus". Pencil number: 272, ink label: 1938-587. Anat. Comp. 1878.

Description. A small (7 × 5 mm) cross section in cancellous bone. The tissue is formed of complex endosteal trabeculae, with extensive evidence of erosion/reconstruction cycles. In the thickness of some trabeculae, typical smaller secondary osteons were laid down. Between the network of trabeculae, a rather regular pattern of circular marrow spaces is produced.

Comments. No remains of either periosteal bone or tissues of endochondral origin are left within the trabeculae, which suggests a perimedullar spongiosa from the bone shaft.

108. "Dinotherium de Pikermi". No label and date.

Description. A large (about 20 × 10 mm) longitudinal section, in poor condition. Both bad *post mortem* preservation, technical and curation problems (the balsam is badly cracked) prevent meaningful comments. The cover slip was rectangular and apparently disapeared. Observation at high magnification confirms the generalized invasion of the bone tissue by *post mortem* boring organisms.

109. (N-13) – "Ivoire fossile lot no. 1650. 1866, Charles Marchand Préparateur à Paris". Pencil label: 34 no. 99.

Description. A section of 10 × 5 mm in a homogeneous dentinal tissue. Macroscopically, the whole section is divided by numerous wide undulating lines, roughly parallel to each others. They can be observed only in polarized light (crossed nicols) and are produced by the regular ordering of the dentinal tubules over great distances. The numerous tiny dentinal tubules appear to be sectioned transversally and somehow obliquely. The tissue is pervaded by numerous black spots with stellate, irregular limits, which appear to be metallic oxides.

ASSESSMENT AND CONCLUDING REMARKS

Paul Gervais' comparative collection of thin sections from fossil bone and teeth retains a current interest in many ways. First, it documents Gervais' own curiosity and attention towards a subject - comparative hard tissues histology - still relatively new and little known at his time, where he obviously hoped to find new tools and possibilities to identify and diagnose fossil material. His similar interest for the comparative microstructures of reptilian and avian eggshells during the same period (Taquet 2001) supports this view. The fact that Gervais realized that the very limited knowledge available at his time on eggshells structure precluded reaching firm taxonomic conclusions (Taquet 2001) may have extended to his assessment of the situation regarding bone and teeth histology. This could explain why Gervais ultimately made little use of his collection of thin sections at the time (Gervais 1875a, b; see also Crémière 2004 for more general comments on microscopical researches at MNHN during the last decades of the 19th century).

As for the eggshell collection, in most cases, Paul Gervais took great care of the orientation of the sections relative to the structures: very often, longitudinal and cross sections were performed from the same specimen. For some 70% of the sections from mammalian limb bones, he focused on the ulna (cubitus), and thus seems to have sought some sort of standardization. It is unknown whether he had special reasons (other than operational) to concentrate on that bone.

In line with Paul Gervais's main scientific interests in paleontology, the mammals occupy a prevalent place in the collection (almost 80%). Amphibians (9%), Reptiles (11%), and especially fishes *sensu lato* (less than 3%) occupy a very minor position, exemplifying a long tradition in French vertebrate paleontology, where "lower vertebrates" were somehow restricted to the inferior condition that the expression implies (Ricqlès 2006). This would be accordant with the general "progressionnist" views of life that the early French evolutionary paleontologists, notably Albert Gaudry, promoted at the time (e.g., Gaudry 1878). At best, non mammalian vertebrates appear here as a small comparative background. A few dinosaurian bone sections, however, document Paul Gervais' relationships with Matheron (and others) and his likely hopes to decipher histologically the significance of the large bone and eggshell fragments from the Cretaceous of Southern France. Within Mammals, the balance among the main Orders is also interesting, even puzzling: while the Carnivores and Primates are lacking, an enormous percentage (45%) is devoted to the South American Mammals, Notongulates and Edentates, *sensu lato*. Among Ungulates the prevalence of Perissodactyls over Artiodactyls may also raise questions. Of course, all the above assumes that the present survey of extant sections is a faithful reflection of the original collections, which is still unknown (see Introduction). Indeed, Gervais's short histological publications of 1875 focus on a specialized issue: hyperostosis, which is dealt with in a well balanced way among the various vertebrates groups (including fishes). The sections described by Gervais in that paper do not belong to the list of sections currently found and described herewith.

For all these reasons, it seems that the collection was built up following some circumstancial constraints rather than trying to establish a well balanced and general systematic coverage of mammalian (and vertebrate) bone and teeth histodiversity. The collection may mostly reflect Gervais' own long term focal interests (e.g., 1855, 1873, 1874), but also special opportunities and questions, such as problems arising from the discoveries in Sansan (Gers) site, and from the availability of the fossils (notably those from South America) to become permanent displays in the Galerie de Paléontologie at MNHN (opening in 1898), etc. Similar opportunities may have arisen from the discoveries by Matheron and others of dinosaurian remains in the Cretaceous of Provence-Languedoc (e.g., Taquet 2001). However, Gervais' willingness to acquire histological material for comparison from England is a testimony of the depth of his involvement in such researches.

From a histological point of view, many sections were of excellent technical quality, at least initially. After more than 120 years, most of them are still readily usable. Problems were obviously encountered with heterogeneous materials, such as teeth, which often suffered dislocation due to the lack of an efficient embedding medium before sawing and grinding. Nevertheless, even in such cases, histology can be deciphered. A high percentage of the thin sections (about 25% of mammalian bones and teeth) exhibit bad to very bad *post mortem* preservation, a significant ratio that may have somewhat discouraged Paul Gervais to extend his paleohistological inquiry further. The great prevalence of dense Haversian bone tissue in many sections from Mammals, combined with little evidence of the actual histodiversity of primary (periosteal) bone deposits in this group, may have also induced Gervais to relinquish from initial hopes of taxonomic determination from bone histology.

Since Gervais' histological endeavors, a full century has elapsed, during which a significant body of knowledge on the comparative histology of hard tissues in mammals was collected (e.g., Foote 1916, Amprino & Godina 1947, Enlow & Brown 1956-58, Schmidt & Kiel 1971). It is remarkable that his collection of thin sections completes our knowledge of hard tissue histology in some fossil mammalian groups, on questions that still remain poorly documented in modern literature, as far as we know. This clearly exemplifies the patrimonial and scientific value of historical comparative paleohistological collections.

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REFERENCES

AMPRINO R. & GODINA G. 1947. — La struttura della ossa nei vertebrate. Ricerche comparative negli amfibi e negli amnioti. *Commentationes Pontificia Academia Scientiarum* 11: 329-467.

BONIS L. DE, LEBEAU M. O. & RICQLÈS A. DE 1972. — Étude de la répartition des types de tissus osseux chez les vertébrés tétrapodes au moyen de l'analyse factorielle des correspondances. *Comptes Rendus Académie des Sciences Paris* D, 274: 3084-3087.

BUFFRÉNIL V. DE, RICQLÈS A. DE, RAY C., DOMNING D. 1990. — Bone histology of the ribs of the Archaeocetes (Mammalia: Cetacea). *Journal of Vertebrate Paleontology* 10: 455-466.

CASTANET J., FRANCILLON-VIEILLOT H., MEUNIER F. J. & RICQLÈS A. DE 1993. — Bone and individual aging, *in* HALL B. K. (ed.), *Bone*. Vol 7. CRC Press, Boca Raton, Fl.: 245-283.

CRÉMIÈRE C. 2004. — *La Science au Musée, L'anatomie comparée au Jardin du Roi puis au Muséum national d'Histoire naturelle de Paris, 1745-1898*. Thèse de Muséologie, Muséum national d'Histoire naturelle, France, 407 p.

ENLOW D. H. 1963. — *Principles of Bone Remodeling.* Ch. C. Thomas, Springfield, 131 p.

ENLOW D. H. & BROWN S. O. 1956. — A comparative histological study of fossil and recent bone tissues Part I, *Texas Journal of Sciences* 8: 403-443.

ENLOW D. H. & BROWN S. O. 1957. — A comparative histological study of fossil and recent bone tissues Part II, *Texas Journal of Sciences* 9: 185-214.

ENLOW D. H. & BROWN S. O. 1958. — A comparative histological study of fossil and recent bone tissues Part III, *Texas Journal of Sciences* 10: 187-230.

FOOTE J. S. 1916. — A contribution to the comparative histology of the femur. *Smithsonian Contribributions to Knowledge* 2382: 1-242.

GAUDRY A. 1878. — *Les enchaînements du monde animal dans les temps géologiques* III. *Mammifères tertiaires*. F. Savy, Paris, 323 p.

GAUDRY A. 1893. — L'Éléphant de Durfort (Gard). *Volume commémoratif du centenaire de la fondation du Muséum national d'Histoire naturelle*. Imprimerie nationale, Paris: 5-25.

GERVAIS P. 1855. — Recherches sur les Mammifères fossiles de l'Amérique méridionale, *in Extrait de la Zoologie de l'expédition dans les parties centrales de l'Amérique du Sud de Francis de Castelnau*. P. Bertrand, Paris, 62 p.

GERVAIS P. 1873. — Mémoire sur plusieurs espèces de mammifères fossiles propres à l'Amérique méridionale. *Mémoires de la Société géologique de France* (2) vol 9 (5): 1-43.

GERVAIS P. 1874. — *Lestodon trigonidens* et *Valgipes deformis*. *Journal de Zoologie* 3: 161-164.

GERVAIS P. 1875a. — De l'hyperostose chez l'homme et chez les animaux (1: mammifères, oiseaux, reptiles). *Journal de Zoologie* 4: 272-284.

GERVAIS P. 1875b. — De l'hyperostose chez l'homme et chez les animaux (2: poissons). *Journal de Zoologie* 4: 445-462.

HOFFSTETTER R. 1958. — Xenarthra, *in* PIVETEAU J. (ed.), *Traité de Paléontologie*. Volume VI (2). Masson et Cie, Paris: 535-636.

LAURENT G. 1996. — Paul Gervais 1816-1879, *in* TORT P. (ed.), *Dictionnaire du darwinisme et de l'Évolution*.

Volume II. Presses universitaires de France, Paris: 1904-1909.

LEHMAN J. P. 1955. — Rachitomes, *in* PIVETEAU J. (ed.), *Traité de Paléontologie*. Volume V. Masson et Cie, Paris: 67-125.

MAC FADDEN B. J. 1992. — *Fossil Horses, Systematics, Paleobiology and Evolution of the Family Equidae*. Cambridge University Press, 369 p.

MEUNIER F. J. 1981. — Données générales sur la structure de l'écaille et l'organisation spatiale des fibres de collagène de la plaque basale chez les Osteichthyens actuels. *Ichthyophysiologica Acta* 5: 41-49.

ØRVIG T. 1967. — Phylogeny of tooth tissues: evolution of some calcified tissues in early vertebrates, *in* MILES A. E. W. (ed.), *Structural and Chemical organization of Teeth. Volume 1*. Academic Press, New York; London: 45-110.

OWEN R. 1845. — *Odontography or a Treatise on the Comparative Anatomy of the Teeth; their Physiological Relations, Mode of Development, and Microscopic Structure in the Vertebrate Animals*. 2 volumes. H. Baillère, London, 655 p., 118 pls.

RICQLÈS A. DE 1965. — La formation des os longs des membres de *Pleurodeles waltlii*, (Michah.), 2ème partie. *Bulletin de la Société Zoologique de France* 90 (2-3): 267-286.

RICQLÈS A. DE 1972. — Recherches paléohistologiques sur les os longs des tétrapodes. III Titanosuchiens, Dinocephales et Dicynodontes. *Annales de Paléontologie* (Vertébrés) 58 (1): 17-60.

RICQLÈS A. DE 1987. — On recherche… lames minces. *Bulletin de l'Association des Paléontologues Français* 15: 13-17.

RICQLÈS A. DE 1994. — A. Meyendorff, A. F. de Lapparent, Ch. L. Camp et les premières recherches paléohistologiques sur les dinosaures du Sahara. *Annales de Paléontologie* 80 (2): 143-153.

RICQLÈS A. DE 1995a. — Les vertébrés des Grès de Harding : ce que Vaillant a pu observer. *Geobios* Mémoire spécial 19: 51-56.

RICQLÈS A. DE 1995b. — Les tissus squelettiques, *in* GRASSÉ P. (ed.), *Traité de Zoologie XIV (1 A) Amphibiens*. Masson et Cie, Paris: 49-96.

RICQLÈS A. DE 2006. — Paléohistologie et paléobiochimie des vertébrés dans les Annales de Paléontologie. *Annales de Paléontologie* 92: 187-196.

RICQLÈS A. DE 2007. — Fifty years after Enlow and Brown's *Comparative histological study of fossil and recent bone tissues* (1956-58): a review of Professor Donald H. Enlow's contribution to paleohistology and comparative histology of bone. *Comptes rendus Palevol* 6: 591-601.

RICQLÈS A. DE & BUFFRÉNIL V. DE 2001. —Bone histology, heterochronies and the return of Tetrapods to life in water: where are we? *in* MAZIN J. M. & BUFFRÉNIL V. DE (eds), *Secondary Adaptation of Tetrapods to Life in Water*. Verlag Dr F. Pfeill, München: 289-310.

RICQLÈS A. DE, PEREDA-SUBERBIOLA X., GASPARINI Z., OLIVERO E. 2001. — Histology of dermal ossifications in an ankylosaurian dinosaur from the late Cretaceous of Antarctica, *in* VIIth International Symposium on Mesozoic Terrestrial Ecosystems. *Asociacion Paleontologica Argentina*, Special Pap. No. 7, Buenos Aires: 171-174.

SCHMIDT W. J. & KIEL A. 1971. — *Polarizing microscopy of dental tissues.* Pergamon Press, Oxford, 584 p.

SCHULTZE H. P. 1969. — Die Faltenzähne der Rhipidistiiden Crossoptrygier, der Tetrapoden und die Actinopterygier-Gattung *Lepisosteus*. *Palaeontographia Italica* 65: 63-136.

SIMPSON G. G. 1945. — The principles of classification and a classification of Mammals. *Bulletin of the American Museum of Natural History*, 85: 1-350.

SIRE J.-Y. 1986. — Ontogenic development of surface ornementation in the scales of *Hemichromis bimaculatus* (Cichlidae). *Journal of Fish Biology* 28: 713-724.

SPILLMANN F. 1948. — Beiträge zur Kenntnis eines neues gravigraden Riesensteppentieres. (*Eremotherium carolinense* gen. et spec. nov.). *Paleobiologia* 8: 231-279.

STEEL L. 2003. — John Queckett sections and the earliest pterosaur histological studies, *in* BUFFETAUT E. & MAZIN J.-M. (eds) Evolution and palaeobiology of pterosaurs. *Geological Society Special Publications* 217: 325-334.

STENSIÖ E. 1969. — Placodermata, Arthrodires, *in* PIVETEAU J. (ed.) *Traité de Paléontologie. Volume IV (2)*. Masson et Cie, Paris: 71-692.

TAQUET P. 2001. — Philippe Matheron et Paul Gervais : deux pionniers de la découverte et de l'étude des os et des oeufs de dinosaures de Provence (France). *Geodiversitas* 23 (4): 611-623.

VIRET J. 1958. — Perissodactyla, *in* PIVETEAU J. (ed.), *Traité de Paléontologie. VoIume VI. fasc. 2*. Masson et Cie, Paris: 368-475.

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