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Middle left: Vascular zonal bone with lamellated annuli and non-lamellated zones. Local development in a right radius; transverse section; C-LQ 109.

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Bottom: Calcified cartilage showing the rounded form of the spaces (lacunae) once occupied by chondrocytes. Proximal end of a fibula; longitudinal section; C-LQ 014.

In all sections the direction of the external surface is upward.

Bone Histology of the Cleveland-Lloyd Dinosaurs and of Dinosaurs in General, Part I: Introduction: Introduction to Bone Tissues

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ABSTRACT

This paper is intended as the first part of a planned three-part study of the bone of Cleveland-Lloyd and other dinosaurs, and has been written as a general introduction to dinosaurian bone histology. After an account of the nature of bone, of various processes and factors that affect it, and the ways in which bone tissues can be classified, those found in dinosaurs are examined. Above fibrillar level, 10 main types are distinguished: (1) normal primary compact bone (periosteal bone s.l.), with uniform, lamellated, fibro-lamellar, zonal, and accretionary varieties; (2) compact Haversian bone, with partial and dense varieties; (3) endochondral bone; (4) reconstructed (Haversian) cancellous bone; (5) compacted cancellous bone; (6) endosteal lining bone, with compact and cancellous varieties; (7) endosteal surface bone; (8) dental (alveolar) bone; (9) metaplastic bone, with intratendinous and intracartilaginous varieties; and (10) other special tissues. Further text discusses the nature of "ossified tendons" and describes special tissue patterns found in cavernous ("pneumatic") bones and osteoderms. Some examples of pathological tissues are also described, but an overall survey of dinosaurian bone pathology is not attempted. In a discussion of physiology, extensive Haversian bone is not thought to be evidence of endothermy, and the only sure implication of the endotherm-like growth of many dinosaurs is held to be the possession of cardiovascular and hemal systems able to support such growth. Two appendices then deal with historical perspectives and some nomenclatural problems.

INTRODUCTION

This paper has been written as the first part of a planned three-part study of the bone of Cleveland-Lloyd and other dinosaurs. Originally, two separate projects in these fields were envisaged; but when it emerged that Cleveland-Lloyd material yields good illustrations of most of the tissues found in other forms, it seemed logical to combine them. This part has been written as a general introduction to dinosaurian bone histology, both as background to the planned further parts and as an aid for others wishing to make similar studies. As currently planned, Part II will deal with the bone of *Allosaurus*, and Part III with other Cleveland-Lloyd genera.

Cleveland-Lloyd dinosaurs sampled include *Allosaurus, Apatosaurus, Camarasaurus, Camptosaurus, Ceratosaurus, Haplocanthosaurus, Marshosaurus, Stegosaurus, Stokesosaurus*, and small unidentified theropods. Other dinosaurs sampled include *Albertosaurus; Anatosaurus; Aristosuchus; Baryonyx; Daspletosaurus; Euskelosaurus; Hypsilophodon; Iguanodon; Massospondylus; Megalosaurus; Ornithomimus; Orthomerus; Polacanthus; Rhabdodon; Sauropelta; Sauror-nitholestes; Stegoceras; Syntarsus; Tyrannosaurus;* and *Valdosaurus;* plus generically indeterminate bones from Bajocian, Bathonian, and Wealden (? Barremian) sauropods; an Oxfordian theropod (? *Eustreptospondylus*); a Wealden carnosaur; small Wealden and Late Cretaceous theropods; hadrosaurs from Alaska, Alberta, and Montana; an ankylosaur; and a ceratopian. Only *Allosaurus* (67 bones) and *Iguanodon* (43 bones) were sampled extensively, the others being represented by one to several bones only. In the latter group, most samples were from limb bones, with additional ribs, girdle bones, or vertebrae in some cases; but ankylosaurs, pachycephalosaurs, and ceratopians were represented only by armor, one skull cap, and one scapula, respectively. From this it will be seen that this paper is based mainly on data from ornithopods, sauropods, and theropods; but, since these groups showed no evident differences except in occasional special tissues, it seems likely that others will follow the same patterns.

Outlining results, the range of tissues found in the samples is wide and is roughly equivalent to those now found in crocodilians, ratites, and medium-sized and large mammals together. The broad spectrum approach to sampling

yielded a wider range of tissue types than the studies of single genera (*Allosaurus, Iguanodon*), but mostly in the case of special tissues (e.g., from armor). Most of the tissues in the total range determined are present in the Cleveland-Lloyd genera, and most of these in turn were found in various bones of *Allosaurus*. The large sample from this genus has yielded more information about the bone tissues of one animal than is available from many modern ones. As in other dinosaurs (cf. de Ricqlès, 1980, Table 1), the primary compact bone of the Cleveland-Lloyd genera was mainly non-zonal fibro-lamellar bone, but local developments of zonal "growth rings" were found in *Allosaurus, Camarasaurus,* and *Stegosaurus*. Limb bones of *Allosaurus* show little or no sign of growth slowing before ceasing, but others from *Camarasaurus* and *Stegosaurus* show it first becoming intermittent, and one from *Ceratosaurus* shows a late switch to slow accretion. The microstructure of the same *Ceratosaurus* bone implies that high vascularity does not always mean fast growth. *Allosaurus* and *Ceratosaurus* vertebrae have yielded data on how their cavernous ("pneumatic") structures arose in ontogeny, plus evidence that hollow limb bones of these genera were not pneumatic. Jaw sections from *Allosaurus, Camarasaurus,* and *Camptosaurus* show that socket formation involved a special alveolar bone tissue, as in "thecodontians" and crocodiles, while the *Allosaurus* sections show theropod interdental plates as formed from upgrowths of this tissue. *Allosaurus* and *Haplocanthosaurus* vertebrae show that bone underlying scars left by the interspinous ligament was intratendinous metaplastic bone, ossified from the ligament, while lateral osteoderms ascribed to *Ceratosaurus* and *Stegosaurus* show structures suggesting ossification from different types of hide. An example of osteoporotic bone was found in a scapula of *Apatosaurus*.

In new results from non-Cleveland-Lloyd genera, an "ossified tendon" of *Iguanodon* was found to be built wholly from osteoblastic bone, and thus not to be an ossified tendon in the metaplastic sense. A skull cap of *Stegoceras* was built from highly vascular fibro-lamellar bone, more suggestive of a heat-exchanging structure than of head-butting habits. Osteoderms from *Polacanthus* and an unnamed ankylosaur seem to have been ossified from crocodile-like hides, but one from *Sauropelta* was built from normal bone tissues. New pathological conditions include aberrantly developed "Haversian systems" (secondary osteons) and a tumor in a cavernous vertebra.

ACKNOWLEDGMENTS

MATERIAL STUDIED: REGISTRATIONS, ETC.

C-LQ designations used in this paper were given to specimens lent to the writer for study from a collection then held at the Utah Division of State History, Salt Lake City. At the time of writing, this material is with Jim Madsen pending institutional location. Any necessary revision of registration numbers will be published when available. Registration numbers of figured non-Cleveland-Lloyd specimens are in the figure captions, as are also those of samples figured in other papers (e.g., Reid, 1984a). Abbreviations used are B.M.(N.H.): British Museum (Natural History), London; OUM: Oxford University Museum, Oxford, England; R.T.M.P.: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; SM: Sandown Museum, Isle of Wight, England. Samples cited but not figured are mainly in the collection of the British Museum (Natural History) or the writer's own collection, with a few in those of the Sandown Museum and the Royal Tyrrell Museum. The writer's collection is kept at his private address but will ultimately go to the Ulster Museum, Belfast, Northern Ireland.

INTRODUCING DINOSAURIAN BONE, ITS GENERAL NATURE, HOW BONE TISSUES ARE CLASSIFIED, AND WHAT TYPES OCCUR IN DINOSAURS

This chapter provides an introduction to dinosaurian bone histology for readers wishing to work in this field or simply to understand the future descriptive text. It can also be used as a general introduction to bone, since these animals had all the main types known from tetrapods, except for special ones from flying and marine forms. All photographic figures are of dinosaurian bone, and most are of Cleveland-Lloyd material. Two appendices deal with the historical background and with various other usages and problems. It might be thought more logical to have treated the historical background first, but, so placed, it would only be meaningful to persons already familiar with the technical terms involved.

A secondary purpose of this section is to show how the usage of some technical terms has varied between different authors. The term laminar, for instance, has four different meanings in papers by Foote (1916), Gross (1934), Enlow and Brown (1956), and de Ricqlès (1974); of four types of bone called Haversian by Foote (1916), only one is Haversian in current usage (see, e.g., Enlow and Brown, 1956; Currey, 1960; de Ricqlès, 1974). In advance of full discussion, the following points may be noted:

1. The term primary is used as meaning produced during growth. Bone laid down slowly on external bone surfaces after normal growth has ceased is termed accretionary, not secondary.

2. The term secondary is applied to internal spaces formed by bone resorption and to bone tissues and structures formed within them after preexisting bone has been resorbed. Primary tissues whose original condition is modified by later internal bone deposition, or by internal bone resorption without deposition of new bone, are said to show secondary conditions, but are not called secondary tissues.

3. The term lamellar bone means the *lamelläre Schalenknochen* of Weidenreich (1930) and not the Type I (lamellar) bone of Foote (1916) that is called lamellated bone.

4. The term laminar bone means the *laminäre Periostknochen* of Gross (1934), called plexiform bone by Enlow and Brown (1956), and not the laminar type of Enlow and Brown (1956) and Enlow (1969), which here is called zonal bone.

5. The term Haversian bone means secondary bone built from the structures now called secondary osteons (Gross, 1934), whose cross sections are the "typical Haversian systems" of medical literature. So defined, the term comprises compact forms of Gross's secondary osteon-bone

(1934, as *sekundäre Osteonknochen*) and Type III, C, only of Foote's (1916) "Haversian" types.

For convenience, the rest of this section is divided into numbered subchapters.

1. GENERAL NATURE OF BONE

Bone is a mineralized connective tissue, produced typically by deposition of hydroxyapatite microcrystals on a framework of collagen fibers. In tetrapods it normally also contains living cells known as osteocytes, which occur scattered through it and occupy spaces called osteocyte lacunae. The lacunae are connected by networks of very fine tubules termed canaliculi, into which branching processes extend from the osteocytes (Fig. 6).

Except in special cases, bone is deposited from external and internal coating tissues, termed the periosteum and endosteum, respectively. Before mineralization, these produce both its collagen content and a mucopolysaccharide groundmass, which together form material known as osteoid. Bone deposition is controlled by cells known as osteoblasts, some of which become osteocytes through the growing bone enclosing them. The periosteum and endosteum originate from the embryonic perichondrium when bones have cartilaginous prototypes, or directly from mesodermal tissue when they do not.

In special cases, cartilage or fibrous tissues are ossified through chondrocytes or fibrocytes apparently assuming the mineralizing function of osteoblasts. Bone formed in this manner makes only minor contributions to the bones of the normal skeleton, but ossification of fibrous tissues produces splint bones in some birds and is seen in some dinosaurian armor. Almost any tissue can also become ossified pathologically.

2. STUDY AIMS AND METHODS

Bone histology in its broad sense comprises the study of histology and structure in particular bones, including local variations in both, and of variations found between different bones, different individuals, different animals, and different groups of animals. The features studied are essentially those that can be seen with normal optical microscopy. Electron microscopy can also be used but is chiefly useful at cytological level or in studying mineral microstructure or taphonomic or diagenetic alterations.

Modern bone can be studied by means of ground sections, or decalcified and then cut and stained like normal soft tissue. Sections of both types can be studied with crossed polarizers when tissues with different arrangements of collagen fibers show different extinction patterns. Fossil bone is studied mainly by means of ground sections. Organic contents are commonly limited to biochemical traces or lacking, but it often still shows both

gross structure and mineral microstructure, even in mineralized specimens, and then shows the same extinction patterns as modern bone. Sometimes details can be easier to see than in modern bone, due to diagenetic staining or to infilling of osteocyte lacunae and canaliculi by dark minerals (e.g., Fig. 6). Preliminary studies can be made by means of acetate peels before preparing ground sections, especially if enough organic material remains for bones to show a dark coloration. Stains such as eosin or alizarin red will sometimes bring out details, but results are unpredictable.

Bone is never uniform in character through the whole of the skeleton but shows variations in structure and histology between different bones, different parts of the same bone, and sometimes also bones of different ages. Establishing its range of variation in any given animal is one of the aims of bone histology. Ideally, such studies should be based on representative examples of all types of bone seen in the skeleton, with each example studied comprehensively and samples taken from several individuals of different known ages. In practice, the bone of most tetrapods, including dinosaurs, is known only from casual sampling, which cannot yield an overall picture of their bone and is potentially misleading if it varies appreciably. In this study, data from 67 bones of *Allosaurus* provides a more complete picture than is currently available for any other dinosaur; but this is only a fraction of the data that could be obtained, for example, by serial sectioning complete examples of every bone studied.

Study of bone histology can also be used to investigate the ways in which bones grow (e.g., Enlow, 1962a); in fossils, it can sometimes yield data on ligaments and muscles that cannot be had by other means. It has also been claimed to throw light on thermal physiology (e.g., de Ricqlès, 1974, 1980) but yields equivocal results in dinosaurs. For example, bone from *Allosaurus* and *Camarasaurus* could be that of endotherms in some Cleveland-Lloyd samples, but shows typical reptilian "growth rings" in others.

3. BONE CLASSIFICATION AND NOMENCLATURE: FIRST PART

Classification and nomenclature of bone has been based on a variety of characters, including place and mode of origin, gross structure, microscopical structure, and details of vascular supply. Different methods have been used by different authors, and changes have inevitably followed advances. Concepts used here derive mainly from work by Seitz (1907), Biedermann (1913), Weidenreich (1923, 1930), Gross (1934), Enlow and Brown (1956), Smith (1960), Haines and Mohouiddin (1968), and de Ricqlès (1974, 1975), although some have older sources (e.g., Tomes and de Morgan, 1853).

For beginners, three warnings may be useful here. First, much bone nomenclature gives names to segments of continuous spectra of tissue types in which the named types intergrade through intermediates. This applies, for instance, to histological nomenclature based on how the collagen fibers are arranged. Second, certain named types (e.g., fibro-lamellar bone, de Ricqlès, 1974) are distinguished by combinations ·of characters, which can also vary independently. If they do, one can again meet with tissues that do not fit compartmentalized nomenclature. Third, as noted already, some authors have used terms in conflicting ways. This applies especially to the terms primary, secondary, lamellar, laminar, and Haversian, hence making it important to determine the sense in which they are used by particular authors. For example, so-called "Haversian" bone of Foote's (1916) Type III, Ic, is not Haversian bone in the sense of Enlow and Brown (1956), but a tissue of de Ricqlès' (1974) fibro-lamellar type, and Foote's records of "Haversian" bone from birds must be seen in this light. Other conflicting usages that may be encountered are examined in Appendix B below. Last, it may be noted that the term bone tissues is used in both histological and structural senses. For example, the tissue called Haversian bone is built from structural units called secondary osteons, which are formed histologically from the tissue called lamellar bone.

3A. Mode of Origin

First, a distinction may be made between osteoblastic bone, produced by normal osteoblasts, and metaplastic bone (Haines and Mohouiddin, 1968) formed through other cells (chondrocytes, fibrocytes) apparently assuming the function of osteoblasts. Osteoblastic bone may be classed as periosteal or endosteal, according to whether it is formed on external or internal surfaces, coated by the periosteum or endosteum, respectively. Metaplastic ossification can be intracartilaginous or intratendinous, according to the nature of the tissue affected.

A further distinction may then be made between primary bone, formed during growth, and secondary bone that may replace it later, after primary bone has been subjected to internal bone resorption. Bone formed during growth is mostly osteoblastic bone, of periosteal or endosteal origin, but small amounts of metaplastic bone may be formed in external situations. Bone formed as bones grow in thickness may be wholly periosteal in origin or mixed bone that is partly periosteal but partly endosteal, due to the periosteal bone enclosing spaces in which endosteal bone is formed later. Endosteal bone that replaces cartilage during growth (e.g., as bones grow in length) is called endochondral bone.

In this usage of the term secondary, internal replacement is specified because periosteal bone is replacive if it spreads over areas of external bone resorption produced by the external remodelling that maintains or adjusts the shapes of bones (see also sections 4 and 10). So defined, primary and secondary tissues mostly do not intergrade, but there are two situations in which the distinction between these can break down. First, this can occur in parts where the external periosteum is laterally continuous with the internal endosteum, when vascular or pneumatic channels pass through compact bone. The commonest case is seen where major blood vessels enter bones through passageways termed nutrient canals. These become enlarged by resorption during growth and can then become lined with replacive bone, which is laterally continuous with the latest periosteal bone. This replacive bone can in turn be continuous laterally with bone-forming structures termed secondary osteons, or Haversian systems (see sections 5d and 7), or with secondary bone lining a medullary (marrow) cavity (section 11). A similar situation can occur in the pneumatic bones of birds, with periosteal bone and internal lining bone continuous laterally through pneumatopores, and in the supposedly pneumatic vertebrae of pterosaurs and saurischian dinosaurs (section 13). Second, interruptions in the growth of structures termed primary osteons (section 5d) can lead to their showing features seen normally in secondary osteons.

3B. Fibrillar Structure

The arrangement of collagen fibers in bone, studied classically by Weidenreich (1923, 1930), is termed fibrillar structure or fibrillar organization. The fibers are typically grouped in bundles, and a general distinction can be made between finely and coarsely bundled tissues (Pritchard, 1956; = *Schalenknochen* and *Faserknochen*, Weidenreich, 1923). These types are then subdivided into

(1) lamellar finely bundled bone, with fiber bundles arranged in layers one bundle thick and running in crossing directions in successive layers;

(2) parallel-fibered finely bundled bone, with all bundles running in one direction;

(3) parallel-fibered coarsely bundled bone; and

(4) woven coarsely bundled bone, with fiber bundles interwoven.

A final category of finely and coarsely bundled bone is then added for mixed tissues. Alternative brief names for types 1–4 are lamellar, fine parallel-fibered, coarse parallel-fibered, and woven bone, and types 1–3 can be said to comprise non-lamellar bone.

This classification gives a useful broad picture but makes the range of conditions found in practice seem simpler than it is. Fiber bundles, for instance, can be simple

or spirally twisted, and even in lamellar bone some bundles may switch from one layer to another. Woven bone with no regular arrangement of fiber bundles can grade into tissues in which they show radial or plumose arrangements, or into stratified tissues that appear parallel-fibered in transverse or longitudinal sections. In text below, the term intermediate is applied to tissues showing transitions between different nominal types. The Weidenreich-Pritchard nomenclature also does not distinguish between osteoblastic and metaplastic tissues, and some coarsely bundled types especially are metaplastic (e.g., Fig. 57: parallel-fibered coarsely bundled bone, formed by ossification of an interspinous ligament in *Haplocanthosaurus;* C-LQ 110). In simpler variant systems, Pritchard (1972) grouped tissues between unstratified woven bone and lamellar bone as bundle bone, whereas de Ricqlès (1975) instead distinguished only fibrous (= woven), parallel-fibered, and lamellar types.

In paleontology it is commonly not possible to observe fibrillar structure directly because of degradation of collagen after death, but inferential use can be made of extinction patterns seen with crossed polarizers and of the form and arrangement of osteocyte lacunae.

1. With crossed polarizers, lamellar bone shows a characteristic pattern of fine light and dark banding, except for showing total extinction over a few degrees at ca. 90° intervals. When the banding is concentric, as in cylindrical structures, this produces a four-armed dark "axial cross" (Fig. 7). Osteocytes and their lacunae may show flattening parallel with this banding or may be elongate-fusiform although appearing flattened in side views. In either case, they may or may not occur in regular layers. In cylindrical structures, canaliculi may run radially.

2. Parallel-fibered tissues typically show uniform extinction between positions of maximum and minimum transmission, but may show parallel light and dark streaking at minimum transmission when coarsely bundled. Osteocyte lacunae are commonly flattened or elongate, as in lamellar bone, but may not be if the bone is metaplastic. Coarsely bundled tissues may also show obvious parallel fiber bundles, without use of crossed polarizers (Fig. 8).

3. Woven bone may show total extinction in all positions of the stage, or two sets of very fine light and dark lines arranged in crossing directions, or various patterns of light and dark streaks or patches that change position as the stage is rotated. The osteocyte lacunae show no flattening or elongation and no layered arrangement, except in special cases in which such bone is formed in very thin sheets (e.g., in laminar fibro-lamellar bone: see 6(3) below). The lacunae may also be larger and more closely packed than in other tissues (Fig. 9).

Some tissues, however, can have different appearances in different sections, as in, for example, *Allosaurus* femur

C-LQ 112 (Figs. 10–13). When viewed in transverse section with crossed polarizers, dense bone with a laminar vascular network (see 5 below) shows fine irregular light and dark circumferential streaking at maximum transmission, and more or less total extinction on rotation through 45°. In longitudinal section, transmission is uniform when maximum, although again becoming zero on rotation, whereas tangential views show varying patterns of patchy and streaky extinction. Osteocyte lacunae range from elongate fusiform to irregularly rounded, with elongate forms most prevalent in longitudinal sections and lying parallel with the external surface in longitudinal and transverse sections. In tangential views (Fig. 12), however, most are of the two extreme types, with frequent local variations in which type predominates. Some of the elongate lacunae are aligned longitudinally, but others lie in varying directions or are aligned around small vascular canals that run radially inward (Volkmann's canals: see (5b) below). The overall picture is thus more complex than might be thought from a transverse section only; this potentially applies to any bone studied only in transverse section. In this case, it suggests a stratified intermediate tissue in which fiber bundles lay parallel with the surface with a general longitudinal alignment but are also reticulating circumferentially.

A second problem is loss or alteration of extinction patterns by biological or diagenetic degradation. Many of the Cleveland-Lloyd samples show only local traces of the patterns expected in fresh bone, and some show complete extinction in all positions of the stage. In bone with "Haversian systems" (Figs. 7, 34, 35; see 7 below), a common form of degradation is for only the innermost and outermost parts to show traces of lamellar bone, from which they are formed, with bone between showing total extinction. Alternatively, structures normally formed from lamellar bone may show the uniform extinction of parallel-fibered bone, with no sure evidence of whether or not this is due to alteration (Figs. 14, 15).

In modern osteoblastic bone, fibrillar variations reflect growth rates, with slowest and fastest growth shown by lamellar bone and unstratified woven bone respectively (Pritchard, 1956, 1972). This is likely to have been so in dinosaurs, although no proof is possible. Lamellar bone used to be described as essentially a replacive tissue (e.g., Pritchard, 1956), but its formation during growth in some cases is now recognized (Gross, 1934; Currey, 1960; Smith, 1960; Pritchard, 1972). Woven bone is seen typically as a primary tissue or in special situations, occurring, e.g., as foetal bone, as a framework in mixed bone formed later (fibro-lamellar bone: see 6(3) below), as dental bone, in antlers, or in fracture callus or reactive growths. After early life, normal periosteal bone is sometimes lamellar bone but more commonly an intermediate tissue, and only

unstratified woven bone when it forms a framework in mixed bone. Normal endosteal bone is typically formed from lamellar bone, sometimes varied as fine parallel-fibered bone. Metaplastic bone shows coarsely bundled parallel-fibered or woven textures when formed from tendons or ligaments, but may be non-fibrous if formed from cartilage.

4. GROSS STRUCTURE: INTERACTING PROCESSES

The gross tissue structure of adult bones depends on three types of processes, which vary in relative importance in different cases:

(1) growth processes, producing periosteal bone or both periosteal and endochondral bone, and also varying types of periosteal bone;

(2) internal remodelling or reconstruction, in which bone is either simply resorbed or first resorbed and then replaced by new endosteal bone; and

(3) external remodelling, which maintains or adjusts the shape of bones during growth by means of external bone resorption and can trigger internal changes where it occurs.

These three kinds of processes produce different tissues, which can be used to show their relative importance in determining final structure. They reflect a complex balance between the activities of the bone-forming osteoblasts and bone-resorbing cells termed osteoclasts and various factors that affect them. As seen above (3a), a distinction can be made between primary bone tissues, formed during growth, and secondary tissues, formed later. Tissues produced during growth and by internal reconstruction are generally most important, but a type formed in response to external remodelling (compacted cancellous bone; see 10 below) can be extensive in mammalian bones.

External remodelling of bones occurs mainly during growth, but may also continue in minor ways after growth ceases. Internal reconstruction can be growth-linked in that marrow or air spaces can only expand by bone resorption, but it also occurs independently and need not, for instance, stop if growth ceases when a maximum size is reached. It also appears to be affected by many other factors. For example, it is typically most extensive in large terrestrial animals and least developed in small ones and marine forms, and it is usually less developed in the largest modern reptiles than in mammals of similar size. Here, the indicated factors are size, habit, and thermal physiology. Reconstructed bone can also be extensive from an early stage or develop progressively through life or be mainly seen in old bones.

5. BONE CLASSIFICATION AND NOMENCLATURE: SECOND PART

A series of gross textural and structural features of bone next need to be examined as background to descriptions of individual tissues that follow.

5A. Gross Texture

The most familiar contrast in gross tissue textures is seen in bones that have dense external parts, called compact bone, and a spongy internal tissue called cancellous bone. Alternative names for these tissues are cortical and medullary bone, or compacta and spongiosa. In flat bones, cancellous internal bone is sometimes called diploë. The struts of bone forming networks in cross sections of cancellous bone are trabeculae, and the spaces between them are inter-trabecular spaces or cancelli. The terms fine-cancellous and coarse-cancellous are used for textural variants. Some tissues are characteristically either finely or coarsely cancellous, but no sharp distinction can be made on a textural basis only.

In origin, compact bone may be (a) primary bone, produced at the periosteal surface as bones grow in thickness; (b) a tissue produced by compaction (see 10 below) of medullary cancellous bone, in response to external bone resorption; (c) bone of endosteal origin, deposited on the walls of a medullary (marrow) or pneumatic cavity; (d) metaplastic bone, where ligaments or tendons are attached; or (e) a reconstructed tissue termed Haversian bone (see 7 below), which replaces other compact tissues. Cancellous bone may be (a) endochondral primary bone, formed, for example, as limb bones grow in length; (b) a reconstructed tissue (secondary cancellous bone: see 9 below), which replaces endochondral bone or compact tissues; (c) a tissue produced from compact bone by internal resorption only, without secondary bone deposition (e.g., Fig. 8); or (d) one of a number of special tissues (e.g., dental bone: see 14 below). At their most complex, individual bones may show many of these types in different parts, plus intergradations between cancellous and compacted bone or secondary cancellous and Haversian bone.

5B. Vascularity

A second common feature of bones is the presence in compact bone of small tubular passageways, which in life contain capillary blood vessels and are termed vascular canals. Bone is vascular when they are present and avascular in their absence (e.g., Figs. 10, 14, 17).

Vascular canals are commonly called Haversian canals, from having first been described by Clopton Havers (1691), or called Volkmann's canals when they enter bone surfaces. As shown by Seitz (1907), they have two different origins. Primary vascular canals contain capillaries that become enclosed in primary compact bone as bones grow in thickness, without involvement of any reconstruction process. Secondary vascular canals are produced when Haversian bone (see 7 below) replaces older compact tissues and contains a new capillary network that arises during this process. The canals seen in sections of compact bone may be all primary, all secondary, or a mixture of both types; but Volkmann's canals are normally primary, except where external resorption has exposed Haversian bone.

Some nomenclature is based on the way in which vascular canals are arranged. If they form an irregular network, with no special alignments, the pattern is said to be reticular. In three other patterns, most of the canals run parallel with the external surface. In bone described as showing parallel canals, they run side by side with widely spaced junctions and are typically aligned longitudinally in bones or processes with long axes. A regular succession of two-dimensional networks, lying parallel with the surface, forms a laminar pattern (Figs. 10, 16) or a plexiform pattern if additional radial canals connect the networks (Fig. 18). Bone with all the canals aligned radially can also occur, but is not known from dinosaurs. Laminar and plexiform patterns are formed by enclosure of successive periosteal vascular networks and hence are typically restricted to primary bone, but bone with parallel or reticulate canals may be primary or secondary.

5C. Discontinuities

Many bones also show structural discontinuities, marked in sections by linear features termed cementing or apposition lines. These are again of two kinds. If the deposition of bone is simply interrupted and then resumed, without bone resorption intervening, the interruption is marked by an interruption line, or resting line. These are seen chiefly in bone of periosteal origin, formed as bones grow in thickness, although sometimes in other tissues (e.g., medullary lining bone: see 11 below). Resorption of bone, either external or internal, produces a resorption surface, and, if new deposition then takes place on this surface, the junction between old and new bone is a reversal line. The term reversal is used here because resorption and regrowth take place in opposite directions. Bone deposited after resorption is identified by having boundaries formed by reversal lines, which are cut across or into other tissues and truncate structures seen in them. The alternative term cementing lines refers to the fact that such junctions may show thin layers of non-fibrous cement (Fig. 19), which is ossified from the osteoid matrix.

5D. Osteons (Figures 7, 9, 14, 15, 19, 28–32, 34–36)

Bone deposited in internal bone-lined spaces is said to form osteons (Biedermann, 1913) and is called osteonic bone. Again, these structures have two origins (Gross, 1934). Some, described as primary osteons, are formed in large vascular spaces enclosed during periosteal growth, but others, termed secondary osteons, are formed in spaces produced by internal bone resorption. Primary osteons are formed in continuity with bone surrounding them and hence have no sharp peripheral boundaries (Fig. 9), but secondary osteons, because of their origin, are always bounded by reversal lines (Figs. 19, 34–36). Both are typically formed from lamellar bone, although fine parallel-fibered bone may occur peripherally or more extensively. Some primary osteons are simple cylinders, with a single central vascular canal, but others have irregular cross sections or form radial or circumferential plates and then contain several canals (Smith, 1960). Primary osteons occur principally in compact bone formed during growth (e.g., fibro-lamellar bone: section 6b) and otherwise are of periosteal origin. Secondary osteons build reconstructed tissues, which can be either compact or cancellous. Secondary compact bone (Haversian bone) is built from cylindrical secondary osteons, with central secondary canals whose cross sections are the "Haversian systems" (Todd and Bowman, 1846) of classic bone nomenclature. In secondary cancellous bone (see 9 below), thin-walled tubular osteons may form the linings of inter-trabecular spaces, and intergrades can occur between these osteons and typical "Haversian systems."

In compact bone formed partly from primary osteons, the distinction between primary and secondary tissues can show a partial breakdown through formation of the osteons being preceded or interrupted by a pause in bone formation, or by such pauses being accompanied by slight bone resorption. Structures that are primary osteons by homology can then show sharp peripheral or internal boundaries, which are reversal lines if resorption has occurred, despite not being products of a normal reconstruction process. Such features are seen mainly as local abnormalities only, but can sometimes occur more extensively.

Various combinations of these features (5a–5d), together with differences in fibrillar structure and origin, distinguish a series of gross tissue types described below. All the main types listed, and most of their variants, occur in the Cleveland-Lloyd dinosaurs. Except where specified, all the tissues described are of osteoblastic origin.

6. NORMAL PRIMARY COMPACT BONE (PERIOSTEAL BONE *SENSU* GROSS, 1934, AS *PERIOSTKNOCHEN*) (FIGS. 9–33)

Normal primary compact bone is formed in parts where the external surfaces of bones are coated by the soft periosteum and can consist entirely of periosteal bone or in part of bone forming primary osteons. In the latter case, the osteonic bone may form the major part of the tissue. The term normal here means non-metaplastic.

Some primary compact bone is structurally featureless, if vascular patterns are discounted, and may be termed uniform bone. Other examples can show any of three main types of gross structure or some combination of two or all of them.

6A. Lamellated bone "(Zonare Periostknochen, Gross, 1934, in Part; Lamellar-Zonal Bone, de Ricqlès, 1974, in Part)" (Figs. 17, 20)

This term lamellated bone is used here for periosteal bone in which fine lamellations, which parallel the external surface, can be seen without use of crossed polarizers and do not correspond with the finer lamellations sometimes seen in true lamellar bone. The lamellations typically disappear when they are viewed with crossed polarizers, and the bone shows as a parallel-fibered or stratified tissue. Bone of this type can form the whole of the compact bone (Figs. 17, 20) or occur as intercalations termed annuli between layers of non-lamellated bone (Fig. 21).

In some of the writer's material (Figs. 17, 23), this type of lamellation appears to be due simply to small-scale cyclical variations in mineral microstructure, which postmortem staining can accentuate; but a variant named pseudo-lamellar bone by Enlow (1969, pp. 57–58) has a distinct minor resting line between each lamella. In the Cleveland-Lloyd material, this type seems to be present in *Allosaurus* pubis C-LQ 113 (Fig. 20), unless the appearance of resting lines is due to crushing having separated lamellae slightly. A *Ceratosaurus* limb bone (?femur: C-LQ 115: Fig. 22) shows a thin external layer of such bone formed at the end of normal growth, providing one of the few known examples of this kind of change in dinosaurs.

6B. Fibro-Lamellar Bone and Related Tissues (Figs. 9–16, 18, 28–32)

This group comprises the fibro-lamellar bone of de Ricqlès (1974) plus intergrades between it and uniform bone. The term fibro-lamellar is also used here irrespective of whether formation of the tissue is continuous or periodic.

Fibro-lamellar bone is a highly vascular tissue, which grows quickly, and is formed initially as finely cancellous bone built from woven bone. Being cancellous allows a given volume of periosteal bone s.s. to grow outward more rapidly than it could if laid down solidly. The tissue is then compacted by slower internal deposition of finely bundled bone, which is usually lamellar bone, and grows in toward enclosed blood capillaries to form primary osteons (e.g.,

Fig. 9). Cross sections of simple examples resemble true "Haversian systems" but are distinguished by the absence of a sharp peripheral boundary formed by a reversal line (compare, e.g., Figs. 9 and 34). The form of the osteons depends on those of the spaces they form in, which may reticulate irregularly or form parallel longitudinal tunnels or circumferential or radial clefts. The resulting types of osteons are termed irregular, cylindrical, circumferential, and radial (Smith, 1960), and tissues showing these types are here termed reticular, parallel osteoned, laminar, and radiate, respectively. Many bones show one of these patterns exclusively, but others can show mixtures of different types of osteons or intermediates between named types. Cylindrical osteons typically show a single central vascular canal, but the other types usually show more than one. Cylindrical, circumferential, and radial osteons appear mainly as separate units in cross sections, but all branch and reticulate when traced in three dimensions.

Under this nomenclature, bone termed laminar is the laminar periosteal bone of Gross (1934), which Enlow and Brown (1956) called plexiform bone, but not the "laminar" bone of Enlow and Brown (1956) or of Enlow (1969), which is vascular zonal bone (see 6c). De Ricqlès (1974, 1975) divides laminar bone *sensu* Gross into plexiform and laminar varieties, according to the presence or absence of conspicuous radial canals, but these conditions are completely intergrading, and whether radial canals are conspicuous in transverse sections can depend on whether they lie in the plane of section or pass through it obliquely. In limb bones and vertebral centra (e.g., Fig. 18), this can in turn depend on where a bone is sectioned, since their orientation may change from one end of the bone to the other.

In other developments, variations occur in the proportions of periosteal bone s.s. and osteonic bone. In bone seen in Figure 30, for instance, lamellar bone forming osteons, marked by small dark "axial crosses," form only a minor part of the tissue. However, in Figure 9, for example, the periosteal framework, seen as dark trabeculae, is instead the minor component. Still more extreme forms can seem to be built almost wholly from osteonic bone, with little sign of a coherent primary framework. In variations of a different sort, fibro-lamellar bone s.s. can grade into tissues with no true (i.e., unstratified) woven framework, its place being taken by a stratified tissue; such bone can grade in turn into uniform tissues, with no woven framework or osteons. Such tissues can be deceptively similar to true fibro-lamellar bone due to showing the same vascular patterns; figures in literature that seem to show it should be treated with caution unless a true woven framework can be recognized (as in, for example, Gross, 1934, Fig. 17, from *Brachiosaurus*). Fast growth is also only implied if a true woven framework is present.

In modern forms, typical fibro-lamellar bone is seen mainly in large mammals and ratites, in which it is formed continuously unless growth is interrupted by events in the lives of individuals. All the named types occur, but parallel-osteoned and laminar patterns are commonest. Some development of simple primary osteons may also occur in flying birds. Histologically fibro-lamellar bone is also produced discontinuously by young crocodiles and some turtles, which experience periodic rapid growth, and is then usually parallel-osteoned with a low osteonic content. A "plexiform" (laminar) pattern may also occur in young crocodiles (Enlow, 1969). Many dinosaurs, up to brachiosaur sizes, resemble large mammals in showing fibro-lamellar bone formed continuously, apart from irregular interruptions. Again, the common types are parallel-osteoned and laminar bone, with reticular bone mainly seen locally and radiate bone so far unrecorded. The simpler tissue variants also occur. The Cleveland-Lloyd dinosaurs follow this pattern, and the *Allosaurus* sample shows its whole range occurring in one dinosaur. In another notable case, apparent laminar bone from a *Ceratosaurus* limb bone (C-LQ 115) was formed entirely from a stratified ("parallel-fibered") tissue, and so presumably did not grow quickly despite a high vascularity.

In the laminar bone of mammals, thin layers of clear acellular bone described as forming "bright lines" are usually seen within the woven bone between successive layers of circumferential osteons (cf. Currey, 1960, pp. 344–356 and Figs. 2, 3). These features appear to mark alternations of fast growth and slow accretion so that formation of the tissue shows a form of cyclicity. No "bright lines" were seen in dinosaurs the writer has sampled, in which growth of the woven framework seems instead to have been continuous.

6C. Zonal Bone s.s. (Zonare Periostknochen, Gross, 1934, in Part; Laminar Bone, Enlow and Brown, 1956, and Enlow, 1969 [Not Gross, 1934]; Lamellar-Zonal Bone, de Ricqlès, 1974, in Part) (Figs. 21, 23–27)

The term zonal is used here for periosteal bone tissues s.l. which show cyclically developed major "growth rings," or zones, bounded by resting lines, annuli, or both, in exclusion of lamellated tissues which do not. Lamellation and zonation are admittedly often associated and sometimes hard to distinguish (e.g., Fig. 27), but they are different phenomena, sometimes easily distinguished (e.g., Figs. 21, 23), and it is preferable to have different terms for overall patterns and tissues. In Figure 23, for instance, the broad pattern is zonal, whereas bone forming the zones is lamellated.

The simplest zonal tissues show resting lines in avascular bone or in bone in which a vascular network does not reflect

the zonal pattern (Fig. 23). More advanced examples have alternating annuli and zones, with vascular canals confined to zones except when crossing between them, and the bone in zones non-lamellated (Fig. 21). In the most advanced cases, bone in zones shows primary osteons and may be fully fibro-lamellar. Annuli are usually built from lamellated bone in one to several layers (e.g., Fig. 21), but may also be formed from clear bone with no sharp boundaries. They usually occur under resting lines when these are also present and then mark growth slowing before ceasing, but they may also occur on both sides of a resting line or only outside it.

In modern forms zonation is seen most typically in reptiles, in some of which (e.g., crocodiles) it is known to be annual. Zones with primary osteons are known from some turtles and from crocodiles (Enlow, 1969), which may form clearly fibro-lamellar bone when young. In mammals, annual zonation is known chiefly from marine forms that encounter cold conditions (e.g., Phocoena: de Buffrenil, 1982) and small terrestrial forms from cool regions (Klevezal and Kleinenberg, 1969), in both of which it shows typically in closely spaced resting lines in avascular bone. Vascular zonal bone is known from specially thickened (pachyostotic) ribs of the manatee Trichechus (Fawcett, 1942) and, in fossils, from archaeocete whales (de Buffrenil and others 1990). No clearly zonal tissues are known from birds. Vascular zonal bone is widely distributed in dinosaurs (Reid, 1990), but is much less common than non-zonal fibro-lamellar bone and is known mainly from bones other than limb bones (e.g., Fig. 26: Camarasaurus, chevron bone C-LQ 060). Genera in which it is known from limb bones are the ornithopods Orthomerus and Rhabdodon and the theropods Baryonyx, Saurornitholestes, and Syntarsus (Chinsamy, 1990; Reid, 1990, 1993).

A problem here is that dinosaurian bones can show broad "growth rings" that do not appear to be part of a cyclical pattern. This was argued by de Ricqlès (1980) in the case of bones figured by Madsen (1976, Fig. 24) from Cleveland-Lloyd allosaurs and is confirmed by the present study. They are conspicuous, for instance, in Allosaurus tibia C-LQ 104 and pubis C-LQ 113; but they have no constant pattern between different bones and are lacking in, for example, Allosaurus femur C-LQ 096. This points plainly to their having a purely individual basis, while in Allosaurus radius C-LQ 109, a very local development of apparently genuine zonal bone (Fig. 21) shows four zones passing laterally into one broader "growth ring" (Reid, 1990). The identification of zonal bone in dinosaurs must hence always be somewhat tentative, in isolated bones especially, although reasonably likely to be justified if an appreciable number (e.g., 10 or more) of apparent zones form a regular sequence (e.g., Reid, 1990, Fig. 1).

6D. Accretionary Bone (Figs. 22, 33)

In animals that stop growing after reaching a maximum size, minor thickening of bones may still occur by slow accretion of small amounts of bone on periosteal surfaces. Such accretionary bone is usually avascular, or nearly so, and may consist of a thin external cover of lamellated bone or of thin layers of uniform or lamellated bone separated by resting lines or resorption lines. Interruption lines of these sorts occur because accretion can be intermittent or alternate with slight resorption.

Accretionary bone is uncommon in dinosaurs, whose bones often show no sign of growth slowing before ceasing, but is recorded from a tibia of Brachiosaurus (Gross, 1934, Fig. 15, upper part), an Iguanodon chevron bone (Reid, 1984a, Fig. 7, top; Fig. 33 here), and leg bones of three small theropods: Syntarsus (Chinsamy, 1990, Fig. 40, arrowed), Troodon (Varricchio, 1993, Fig. 4, top), and Saurornitholestes (Reid, 1993, Fig. 2, top). In the Cleveland-Lloyd material none was seen in Allosaurus, despite a large sample, but a new example was found in a Ceratosaurus limb bone (Fig. 22, top; C-LQ 115). In all cases, a switch from active growth to slow accretion is implied, but what else is implied can be doubtful. First, when found in isolated bones (e.g., C-LQ 115), such tissue might be either a characteristic of the species or a feature of a single individual. The writer's Iguanodon material, for instance, showed only one example in 43 bones sectioned. Second, as seen by Chinsamy (1990), it could point to growth ceasing at maturity, as in mammals; but if dinosaurs normally grew throughout their lives, as was thought by de Ricqlès (1980, p. 132), it might instead mark old age in animals long past maturity. The best indication to date of actual definitive growth is from a tibia of Saurornitholestes (Reid, 1993), which appears to show rapid growth for six or seven years, followed by slow accretion only for twelve more; but this reading depends on assuming a sequence of resting lines to be annual, which might not be correct.

6E. Influence of Growth Rates

As with fibrillar structure, variations between different types of primary compact bone reflect differences in growth rates. Lamellated bone is typically a slowly formed tissue, whereas fibro-lamellar tissues are characteristically fast growing. Zonal bone marks cyclically intermittent growth if the zones are defined by resting lines, or alternately faster and slower growth if zones alternate with annuli. Fast-growing tissues are always highly vascular, but the opposite does not always apply.

After early ontogeny, bone formed periosteally may be constant in character throughout growth (as, for example, in human bones) or change in character progressively as growth continues. In crocodiles, for instance, early zones

seen in juveniles may show primary osteons in a matrix of woven bone, but the bone laid down later changes progressively to lamellated bone, in which vascular canals become progressively less frequent. Resting lines between zones may also become progressively closer until lamellation and zonation become indistinguishable. This sequence reflects a progressively slowing rate of bone accretion. In dinosaurs, the formation of fibro-lamellar bone was sometimes followed by a switch to forming zonal bone (Reid, 1990), implying a change from relatively fast continuous growth to slower intermittent growth.

In zonal bone, local variations in growth rate may result in zones being asymmetrical, and, for example, several times thicker on one side of a bone than on the other. In such cases, however, a similar pattern could also be due to "lateral drifting" (Enlow, 1962a), in which bone was resorbed on one side before each zone was formed. It is important then to check whether interruption lines between zones show any signs of truncating structures seen in the underlying tissue, such as osteons or a stratified alignment of osteocyte lacunae. If they do not, asymmetrical growth can be assumed. It can sometimes also be confirmed by having caused structural changes, if, for example, zones show lamellated bone where thinnest but non-lamellated tissue where thickest.

Little data is available on measured growth rates, but, for instance, a human femur, in which the periosteal bone formed after infancy is dense, finely lamellated bone, takes about 20 years to reach ca. 2.5 cm shaft diameter. For comparison, the femur of a bullock, in which the primary compact bone is laminar fibro-lamellar bone, can reach ca. 4 cm in only three years; however, that of a *Crocodylus porosus*, showing the changing growth pattern described above, had taken at least 70 years to reach 4.3 cm (M. W. J. Ferguson, pers. comm., 1984). In a sauropod pubis that grew asymmetrically (Reid, 1981, Fig. 1), the thickness of zones ranges from ca. 0.25–2.2 mm, but these thickness were presumably formed in less than a year, even if the zones are taken as annual, and the same applies to any other measurement from zonal thicknesses. There is also no apparent way of measuring how fast dinosaurs formed fibro-lamellar bone because of its lack of zonation. It could have formed as quickly as in large fast-growing mammals and birds, as assumed by de Ricqlès (e.g., 1974, 1980), but there is no proof of this, and a hybrid tissue found in part of a sauropod humerus (de Ricqlès, 1983), with a zonal pattern superimposed on laminar fibro-lamellar bone, showed only 2–12 layers of osteons per zone in the part that showed zonation. Further, tissues resembling fibro-lamellar bone but lacking a framework of woven bone (see 6c above) presumably grew more slowly than fibro-lamellar bone proper. Hence, the growth of dinosaurs with fibro-lamellar and related types of primary compact

bone should not be assumed to have always been as rapid as in the fastest-growing modern forms.

7. COMPACT HAVERSIAN BONE (HAVERSIAN BONE *SENSU* ENLOW AND BROWN, 1956; HAVERSIAN TYPE III, C ONLY, FOOTE, 1916 [*NOT* HIS TYPES III, IA-C]; *SEKUNDÄRE OSTEONKNOCHEN*, GROSS, 1934) (FIGS. 7, 19, 34–36)

Haversian bone is compact bone built from secondary osteons ("Haversian systems"), which replaces other compact tissues by a process termed Haversian reconstruction. Most commonly, the tissue replaced is primary compact bone, but any compact or compacted tissue may be affected.

In normal primary compact bone, reconstruction begins in the deepest (= oldest) parts and may be confined to them or spread outward to varying extents. At first, certain primary canals are enlarged by bone resorption, carried out by endosteal osteoclasts, and produce cavities seen in cross sections as rounded resorption spaces (the "Haversian spaces" of Tomes and de Morgan, 1853). These can be several to many times larger than the original vascular canals (Fig. 36). Bone resorption then ceases and is followed by deposition of lamellar bone, which grows inward to form cylindrical secondary osteons with single central vascular canals. The affected part of the vascular network also usually takes on a new pattern as resorption proceeds. At first, bone surrounding the osteons, termed interstitial bone, is still primary bone (Fig. 36); but, with further repetitions of the process, this is progressively replaced, and resorption spaces start to encroach on older secondary osteons. The ultimate result is a tissue formed entirely from the last-formed secondary osteons and the interstitial remnants of partly resorbed older ones (partial Haversian systems, Tomes and de Morgan, 1853; *Haversche interstitielle Lamellen*, Kölliker, 1889; *Osteonfragmente*, Weidenreich, 1923), comprising fully developed or dense Haversian bone (Figs. 19, 34, 35). In this tissue, reconstruction may continue until death or cease earlier. The same pattern of replacement is followed when tissues other than primary bone are affected.

Osteons forming Haversian bone are commonly oriented more or less parallel to surfaces, and longitudinally in bones or parts of bones with long axes. Locally, however, they may run toward the surface at angles of up to 90°, and may then be found to follow the direction of included tendinous fibers. Other variants have the osteons interwoven, in irregular ways or in bundles. Although appearing as separate units ("Haversian systems") in cross section, they branch and anastomose at intervals, as do the secondary vascular canals that they contain.

Less intense production of secondary osteons leads to tissues showing various proportions of unreplaced and

replacive bone, with a range from examples showing only scattered secondary osteons to bone in which unreplaced tissue is only seen interstitially. The term partial Haversian bone is convenient for the latter type, although it cannot be precisely defined except in terms of some arbitrary percentage. Every gradation between bone with scattered secondary osteons and dense Haversian bone may occur in bones from one animal or in different parts of the same bone. In dinosaurs, for instance, it is common for compact bone to show an outward gradation from dense Haversian bone in the deeper parts to unreplaced primary bone near the surface, through partial Haversian bone and bone with scattered secondary osteons.

In modern forms, levels and patterns of Haversian reconstruction vary widely, in ways implying the influence of a complex of interacting factors. It is generally most conspicuous in mammals, and weakly developed or lacking in amphibians and reptiles, hence suggesting the influence of the higher metabolic rates of mammals (cf. Bakker, 1972; de Ricqlès, 1974); but it is also slightly developed or lacking in mammals smaller than cats, despite the smallest forms having the highest metabolic rates (McNab, 1978). This points to size and, hence, weight as an interacting factor. Growth rates may also have an influence, since Haversian bone is less developed in, for example, fast-growing cattle than in slowly growing human bones. Age also seems to be a factor, since reconstruction is often more extensive in old animals than in young ones. Great age could explain how a tortoise (Reid, 1987, Fig. 3b) developed Haversian bone to human levels. Reconstruction may also be localized under areas where muscles are attached or in parts where the bone cells have died (Currey, 1962; Enlow, 1962a); while according to Currey (1960), reconstruction itself triggers more reconstruction by interfering with blood supplies and hence causing death of bone cells.

Dinosaurs often show Haversian bone developed as extensively as is usual in large mammals, but sections from the shafts of large limb bones may also show little reconstruction. This is so, for instance, in bone figured by Madsen (1976, Fig. 24) from a tibia and fibula of *Allosaurus*, in which most of the compact bone is unreplaced primary bone. Also, the writer (unpublished) has a mid-shaft section from an *Iguanodon* tibia, 6.5 X 7.8 cm thick where sectioned, showing only a few scattered secondary osteons in parts near the medullary cavity. Contrastingly, *Allosaurus* surangular C-LQ 041 is a mainly solid bone, formed chiefly from dense Haversian bone. In dinosaurian limb bones known to the writer, reconstruction seems generally more extensive when bones are cored by reconstructed cancellous bone (see 9 below) than when there is a medullary cavity. It may also increase laterally,

from shafts (diaphyses) toward terminal parts (metaphyses). Some bones also show radial segments of partial or dense Haversian bone under areas where muscles were attached. The two main blocks seen in an *Iguanodon* femur (Reid, 1984a, Figs. 19, 22), for instance, underlie the fourth trochanter and a lateral muscle scar and mark the insertions of the caudi-femoralis muscles and the origin of an external femoro-tibialis. Reconstruction becoming more extensive with age is known from *Brachiosaurus* (Gross, 1934), but is not evident in the Cleveland-Lloyd allosaurs sampled. In some bones, unfilled resorption spaces seem to show that reconstruction continued throughout life, but, in others, which show Haversian bone, their absence implies that it ceased before death.

8. ENDOCHONDRAL BONE (FIGS. 1, 37–42)

Endochondral bone is cancellous bone produced during growth by a process through which bone replaces cartilage in contact with endosteal tissue (Figs. 39, 41). After early ossification, the main sites in which it is formed are under articular cartilages, on both sides of epiphysial plates when these are present, and at sutures where sutured bones have cartilage between them. Although replacive, it is counted as primary bone because of being formed during growth and because its formation involves no resorption of preexisting bone.

In normal cartilage, the cartilage cells (chondrocytes) are mostly widely spaced, but toward zones of replacement they multiply and hypertrophy, becoming packed close together in columns (Fig. 38) or without any order (Figs. 1, 39, 41). This cartilage then becomes calcified, and most chondrocytes die. The calcified cartilage is attacked from below by osteoclast-like endosteal cells termed chondroclasts, which produce an internal resorption surface on parts of which bone is next deposited. The form of this surface varies from gently undulating through deeply pitted to conditions in which simple or branching tubules run into the calcified cartilage. These variations reflect the thickness of the calcified cartilage, which may be several to many cells deep. The bone formed is laid down on parts of the resorption surface where resorption has ceased temporarily, and is then left as the earliest endochondral trabeculae as the rest of the cartilage is removed (Figs. 39, 41).

When first formed, endochondral bone is usually finely cancellous, but it becomes coarser progressively through a process by which bone is resorbed in some parts whereas deposition continues in others. This process establishes the final pattern of endochondral trabeculae, which may then be modified further by secondary reconstruction (see 9 below). At first, the trabeculae may be cored by unresorbed cartilage, which may persist in forms in which internal

remodelling is limited (e.g., manatees, plesiosaurs), but it usually is progressively lost as endochondral remodelling proceeds. Some trabeculae may also show local "islands" of included calcified cartilage (Figs. 40, 42), and the presence of such cores or "islands" identifies bone as endochondral.

In dinosaurs, calcified cartilage and underlying endochondral bone occur commonly at articular surfaces in well-preserved material and at sutures such as the neurocentral sutures of vertebrae. The cartilage can be recognized as a finely foamlike tissue (Figs. 1, 38, 39, 41), with the "bubbles" representing the lacunae once occupied by chondrocytes. The external surfaces it forms often show a finely porous appearance (Fig. 81). In ornithopods (e.g., *Iguanodon, Hypsilophodon*), they may show a pattern in which small thin-walled and matrix-filled rings of endochondral bone are seen surrounded by calcified cartilage (Reid, 1984a, Fig. 25). This represents a pattern of ossification in which the first endochondral bone is formed on the walls of marrow-filled tubules, as in young crocodiles (cf. Haines, 1938, Figs. 6–8). Although cartilaginous, such terminal surfaces are not true articular surfaces, but represent the internal interface between lost uncalcified cartilage and the underlying calcified zone.

A notable difference between dinosaurian limb bones and those of mammals is the absence of bony epiphyses (Moodie, 1908; Reid, 1984a), and so of cartilaginous epiphysial plates between epiphyses and metaphyses. The growth in length of limb bones hence took place under the articular cartilages, as in crocodiles and turtles, instead of on the metaphyseal sides of epiphysial plates; and longitudinal sections may show radiating patterns of endochondral trabeculae ending under the terminal surfaces (e.g., Fig. 37) instead of stopping short of them. A consequence of this mode of growth is that dinosaurs would have been able to grow throughout their lives, like modern reptiles; and many appear to have done so, as thought by de Ricqlès (1980), since bones from even large individuals may show the formation of periosteal and endochondral bone apparently still in progress at death. Sexual maturity may hence have been reached long before maximum size, which would depend on maximum life span, and should not be trusted as a means of identifying adults. Similarly, fusion of epiphyses cannot be used to identify dinosaurs as adults.

9. RECONSTRUCTED CANCELLOUS BONE (HAVERSIAN CANCELLOUS BONE; CANCELLOUS SECONDARY OSTEON BONE), (FIGS. 43–45)

This tissue is formed by a variant of the process that produces compact Haversian bone, from which it only differs in being cancellous, and can replace bone of any other type. "Reconstructed" is specified because of the existence of a second type of secondary cancellous bone, which arises through trabeculae of endosteal bone growing out from the surfaces of medullary cavities (see 11 below).

That tissue of this type is secondary is most obvious when it replaces primary compact bone. Reconstruction begins with the appearance of large resorption spaces, separated by narrow partitions of persisting primary tissue. These spaces then become lined with centripetally deposited lamellar bone, forming large tubular secondary osteons that only differ from typical "Haversian systems" in having a wide central cavity (Fig. 43). Intergrades between these osteons and typical "Haversian systems" may also be formed. At first, primary bone occurs interstitially between the osteons (Fig. 43), but new resorption spaces remove it progressively and also begin to encroach on the earliest large osteons. Continuing reconstruction leads to the production of a tissue in which trabeculae have surfaces formed by the walls of the latest formed osteons, but also contain remnants of older ones, corresponding with the interstitial remnants seen in dense Haversian bone. Such trabeculae are said to show a brecciate structure (Fig. 44). The remnants can be recognized by being bounded by reversal lines, and by lamellar bone in them forming patterns like those seen in cross-bedding when trabeculae are viewed with crossed polarizers.

Replacement of endochondral bone is less obvious because of its being cancellous and subject to remodelling by resorption. It begins by deposition of secondary lamellar bone on trabecular resorption surfaces, and may continue until all endochondral bone has been replaced. In consequence, endochondral and purely secondary bone may intergrade through mixed tissues formed partly from primary and partly from secondary bone.

Reconstructed cancellous bone is extensively developed in dinosaurs and usually forms most of their cancellous bone except in metaphyses. In the latter, cancellous bone may still be mainly endochondral, but, in diaphyses with no medullary cavity, it is secondary in examples the writer has sectioned. In vertebrae, cancellous bone is usually secondary, except close to articular surfaces. In longitudinal sections of centra, these surfaces may be paralleled internally by several secondary trabecular plates, which may be stout enough to show some internal Haversian reconstruction. In bones in general, reconstructed cancellous bone may intergrade with dense Haversian bone or replace it without intergrading (Fig. 45). In the first case, ongoing reconstruction was presumably active in both tissues and their intergrades, whereas the second pattern points to replacement of Haversian bone in which reconstruction had ceased.

10. COMPACTED CANCELLOUS BONE
(FIGS. 46–48, 52)

In some situations, compact bone is formed from originally cancellous bone by the thickening of trabeculae until inter-trabecular spaces are reduced to narrow vascular channels (Fig. 46). This can happen in any type of cancellous bone. It most commonly occurs in response to external remodelling during growth, under areas where bone resorption would otherwise expose cancellous bone. The compacted bone can come to be exposed at the surface if all primary compact bone is resorbed. A similar compaction can occur in response to internal cavitation in pneumatic bones and in cavernous saurischian bones (Fig. 52, see section 13) that may have been pneumatic. An unrelated style of thickening or compaction, known as osteosclerosis, involves the suppression of internal reconstruction. This may occur pathologically or as a normal occurrence in marine forms (e.g., manatees, some plesiosaurs), whose bones are described as being pachyostotic (e.g., by Nopcsa, 1923). External remodelling processes that trigger compaction of cancellous bone include the metaphyseal bone resorption that maintains the shape of limb bones and the various patterns of "drifting" by which curvature may be adjusted (Enlow, 1962b). In mammals these processes can lead to large parts of the surfaces of limb bones being formed by compacted bone (cf. Enlow, 1962b, Pls. 2, 3), but this does not appear to have been so in dinosaurs because limb bones the writer has sectioned show only limited compaction in metaphyses and no compacted bone in diaphyses. Even bones that show obviously undercut surfaces on metaphyses may show little compaction under them, and it can also be lacking in girdle bones, in which it might be expected to be extensive. Conversely, shape adjustment by asymmetrical growth was apparently more prevalent than in mammals. None the less, some bones show characteristic remodelling patterns of the sorts described by Enlow (1962b). In the Cleveland-Lloyd material, for instance, parts of the distal metaphysis of *Allosaurus* femur C-LQ 092 show compacted cancellous bone overgrown by periosteal bone, which spread onto it from the diaphysis (Fig. 48). A transverse (antero-posterior) section of the proximal part of *Allosaurus* ischium C-LQ 066 shows no compacted bone, but a similar section from the distal part of pubis C-LQ 090 shows a typical "drifting" pattern, with accretion of periosteal bone in its anterior part but compacted bone under resorption surfaces further back (Fig. 46).

Compressional stressing may also sometimes have been a trigger factor, since a tyrannosaurid metatarsal among bones examined showed compacted bone under the articular surfaces, which it could have served to strengthen mechanically. Osteosclerotic compaction is not currently known from dinosaurs.

11. ENDOSTEAL LINING BONE (FIGS. 49, 52–54)

This term is a convenient group name for bone tissues that result from deposition of endosteal bone on the walls of medullary, pneumatic, or other large internal cavities that are produced by internal bone resorption. They are typically formed where the tissue resorbed is compact or compacted bone.

Medullary cavities first appear in the diaphyses of developing long bones and then expand both longitudinally and radially as growth proceeds. Longitudinal extension occurs mainly at the expense of cancellous bone, which may be endochondral or secondary, but, except in the earliest stages, the bone resorbed in radial expansion is mostly compact bone. This may be primary bone, if Haversian reconstruction is lacking, or Haversian bone if this is present. When resorption ceases, new endosteal bone may be laid down on the internal surface it produces. In its simplest form, this bone is deposited uniformly as medullary lining bone, which is said to form "internal circumferential lamellae" in traditional medical nomenclature (Fig. 49). It can also be seen as forming a special form of secondary osteon and is called a "marrow-osteon" (*Markosteon*) in German usage (e.g., Gross, 1934). The bone forming it is typically avascular and built from lamellar bone. Alternatively, spines or longitudinal ridges of bone may grow into the medullary cavity, where they may branch and unite to form coarsely cancellous bone that may also become compacted. This tissue is secondary in the sense of replacing resorbed bone, but it does not replace it directly and thus differs from reconstructed cancellous bone (9 above) in its mode of formation. Because of this difference, the trabeculae do not show brecciate structure. It is best described as secondary cancellous bone of medullary origin because the briefer term medullary cancellous bone is also applicable to endochondral and reconstructed tissues.

Bone tissues formed in the medullary cavity show varying relationships to others and one another because of the complex and interacting patterns that remodelling processes may follow (cf. Enlow, 1962b). Only simple lining bone may occur, but simple, cancellous, or compacted forms may be found in different parts of the same bone or even of one section. In diaphyses, their external boundary is typically a reversal line, representing the medullary resorption surface, but in metaphyses they may merge indistinguishably with cancellous bone of different origins, with simple lining bone becoming continuous with the bone of reconstructed trabeculae. The bounding reversal line may be obliterated through Haversian bone spreading

inward. Medullary linings may also be formed and re-sorbed repeatedly, either during growth or later, and some linings contain remnants of partially resorbed ones. In lateral drifting, bone may be formed on one side of a medullary cavity while resorption takes place on the other (e.g., Enlow, 1962b, Figs. 7, 12), and may come to be exposed at the periosteal surface if enough bone is resorbed there. The whole wall of the medullary cavity is then locally formed by bone laid down inside it. Again, compact or compacted bone with this origin may be partly or wholly replaced by Haversian bone.

Dinosaurs known to the writer do not show the more extreme conditions described by Enlow (1962b) from mammals, although hollow limb bones may show thin medullary linings and local patches of related cancellous bone. It does not, however, follow that more complex patterns will not be found in forms not yet investigated. Known medullary linings may show only one phase of deposition or show several cycles of resorption and redeposition. Because such cycles could occur, the presence of a simple lining only need not imply that growth had ceased, but the presence of a composite lining is reasonable evidence that medullary expansion was no longer taking place actively.

Thin sheets of typically avascular endosteal bone also line the pneumatic bones of birds, the pneumatic parts of elephant skulls, and the supposedly pneumatic bones of pterosaurs, theropods, and sauropods (see 13 below). This can again be termed lining bone, but should not be described as medullary unless cavities it lines are supposed to have been tissue-filled.

12. ENDOSTEAL SURFACE BONE

As an alternative to internal compaction of cancellous bone (10 above), Enlow (1962b, Fig. 17) found that metaphyseal resorption surfaces may be sealed by an inward moving sheet of endosteally deposited compact bone, into which underlying trabeculae are progressively incorporated. This type of tissue seems to be present on sharply undercut surfaces seen on the proximal metaphyses of *Allosaurus* femora C-LQ 092 and 111, in which the ends of truncated endochondral trabeculae are spanned by a thin sheet of avascular bone, and can be reasonably expected to occur in other similar situations.

13. CAVERNOUS BONES (FIGS. 50–54, 73–75)

This is a convenient general name for all bones containing large internal spaces that either are or may have been pneumatic. The main modern examples are hollow bones of birds, into which the air sac system extends, and the "honeycomb" bones of the roofs and sides of elephant skulls, which contain extended nasal sinuses. In the latter,

a honeycomb pattern of thin radial plates of compact bone (e.g., 0.5–2 mm thick) extends between the inner and outer surfaces, enclosing spaces (e.g., 1–3 cm wide) that communicate through gaps in the plates. Where the plates are thinnest, they are formed from two thin opposed sheets of endosteal lining bone; but elsewhere they show a coring stratum of compact secondary osteons ("Haversian systems"), which run parallel with the surfaces. Their structure is of interest as the nearest modern analogue of the structure seen in cavernous dinosaurian vertebrae and ribs, which can show honeycomb structures indistinguishable from those of elephants.

Cavernous vertebrae and ribs are known from theropods and sauropods and have been supposed to be pneumatic by various authors since Nopcsa (1917) and especially by Janensch (1947), who dealt mainly with sauropods but also noted their occurrence in theropods including *Allosaurus* (as "*Antrodemus*"). In addition to vertebrae that show massive open pleurocoels on either side of a median septum (e.g., Janensch, 1947, Figs. 2, *Brachiosaurus*, and 9, *Barosaurus*), the centra of others contain enclosed cavernous spaces (e.g., Figs. 50, 73: *Allosaurus*, unnumbered core and cervical C-LQ 095) into which lateral foramina open. These foramina can be seen as pneumatopores if the vertebrae are thought to be pneumatic. Plates between the internal spaces may run longitudinally or show no regular direction. In ribs, cavernosity is seen mainly in proximal parts, although a tubular cavity may also extend downward beyond the tuberculum (e.g., Figs. 74, 75: *Allosaurus*, C-LQ 125).

In vertebrae (Figs. 50–54, 73), cavernosity is seen typically in cervicals and dorsals, although the writer has a specimen that shows it in a sauropod caudal. The cavernous spaces arose by a special large-scale reconstruction process, which seems normally to have kept pace with growth. The process began with the production of large internal resorption spaces, up to several centimeters wide, which expanded until only thin partitions of bone remained between them (Fig. 50). Where their expansion was longitudinal, the bone resorbed was inevitably cancellous bone, which was usually endochondral bone formed under the articular surfaces. As resorption proceeded, the remaining cancellous bone was usually compacted (Fig. 52), and in some forms compaction preceded resorption. The Cleveland-Lloyd allosaurs, for instance, can show endochondral bone compacted within millimeter distances of the zone of ossification (Fig. 51). When resorption ceased, resorption surfaces next became coated with lining bone, seen initially outside sharp reversal lines (Fig. 52, top and bottom). Later, however, coring compacted bone was often replaced by Haversian bone, and this could then spread outward into the lining bone (Fig. 53). These patterns, with intercavernous plates cored by

compacted or Haversian bone, are seen throughout such vertebrae except near lateral surfaces, where coring bone may instead be of periosteal origin or Haversian tissue that replaced it before cavitation.

In further variations, intercavernous plates were sometimes locally resorbed and then replaced, producing large-scale brecciate patterns. They were also sometimes formed wholly from lining bone, except at points of junction, due presumably to cavities expanding until only soft endosteal tissue remained between them. Lining bone can be featureless lamellar bone, sometimes showing unusually thick lamellae (Fig. 52, top), or a tissue interrupted by numerous resting lines (Fig. 53). It is usually avascular but can also thicken locally into vascular bone, with reticular or laminar vascular patterns but no osteon system. Some examples can show a special form of pseudo-lamellation due to sheets of bone spreading laterally. This can be detected by the presence of layers in which elongate osteocyte lacunae show a plumose arrangement (Fig. 54). In a fragmentary vertebra from the Wealden (early Cretaceous) of England, thought to represent a sauropod, cavitation was beginning in reconstructed cancellous bone and so must have been delayed until this had replaced endochondral bone instead of closely following its formation.

Without certain proof, it seems very likely that such structures were pneumatic and imply the presence of a birdlike air sac system, as various authors have thought (e.g., Swinton, 1934; Romer, 1946; Janensch, 1947). The morphological resemblance to pneumatic bird bones is unmistakable, despite the difference in scale, and the compaction that accompanied cavitation in cavernous structures is not seen in marrow-filled bones. The writer also has material from another Wealden sauropod that is quite indistinguishable morphologically or histologically from bone from the pneumatic parts of modern elephant skulls, except by being fossilized. If accepted as pneumatic, such structures have three implications for saurischians. First, pneumatic parts of the skeleton would be substantially lighter than tissue-filled bones the same size. Second, an air sac system would imply enhanced respiratory efficiency and could be taken for evidence of aerobic activity metabolism. Third, enhanced respiratory efficiency would also mean an enhanced capacity for respiratory cooling, which would probably be important in dispersing excess heat in large forms. There is also a further implication that ornithischians may not have been entirely like saurischians physiologically, since they mostly lack cavernous structures.

The hollow limb bones of Cleveland-Lloyd allosaurs, in contrast, show no evident pneumatopores, and their internal cavities end metaphyseally in the manner of marrow-filled medullary cavities. These bones were thus probably not pneumatic. Similarly, cavities present in some caudal centra of *Allosaurus* (e.g., C-LQ 087) and *Ceratosaurus*

(C-LQ 088) appear to be simply marrow spaces, since they were formed by simple bone resorption and do not communicate with the exterior.

Cleveland-Lloyd sauropod vertebrae were not available for section, but showed typical cavernous structure in, for example, *Barosaurus,* with coring and lining bone seen readily with a hand lens.

14. DENTAL BONE (ALVEOLAR BONE) (FIGS. 55, 56, 76–79)

Four types of dental bone occur in fossil reptiles and are here termed bone of attachment, alveolar bone, cementum, and pulp bone. Explained briefly, bone of attachment is bone tissue seen under fixed teeth or also growing up around their bases in subthecodonts. Alveolar bone forms thecodont sockets when these are built from a tissue distinct from those forming the tooth-bearing bones. It is typically formed as cancellous bone initially but may later be compacted. It also commonly shows repeated resorption and replacement related to both growth and tooth eruption. Cementum normally coats the basal parts of free teeth and is usually seen as thin layers of avascular bone whose osteocytes are also known as cementocytes. In ichthyosaurs, however, it can form thick masses of vascular bone, and then even contain primary osteons. Pulp bone is cancellous bone seen inside ichthyosaur pulp cavities.

Of these, only alveolar bone was seen in the Cleveland-Lloyd samples (*Allosaurus* C-LQ 133, *Camarasaurus* C-LQ 089, *Camptosaurus* C-LQ 107, *Marshosaurus* C-LQ 126). Tooth emplacement in dinosaurs had broadly the same pattern as in crocodiles and in the earlier "thecodontians" from which it was presumably inherited. Teeth were formed in deep longitudinal grooves in the tooth-bearing bones, within which sockets were built mainly or entirely by alveolar bone. Continuous grooves may not be evident in surface views but are seen readily by comparing sections through and between sockets (e.g., Figs. 76, 78). Because the grooves could only expand by bone resorption, the basal contact between alveolar bone and other tissues is characteristically a reversal line, truncating underlying structures (Fig. 55). Sometimes the alveolar tissue shows a continuous basal layer of avascular or vascular bone, but usually branching trabeculae grow out directly from the contact. The resulting cancellous bone is initially built mainly or entirely from non-lamellar bone (Fig. 56), which is sometimes recognizably woven bone, although lamellar bone could be added later. Uncompacted alveolar bone is seen mainly in the deeper parts of sockets, around developing teeth and the roots of erupted ones (Figs. 76, 77, 79), although also wherever the tissue was growing actively. Compacted bone is more usual in the upper parts of sockets, in partitions between successive

sockets, and in interdental plates seen on the medial (lingual) sides of sockets in theropods (e.g., Fig. 78). Compacted bone may, however, show reversion to a cancellous state through internal bone resorption, recognizable if cancelli truncate structural lines in trabeculae. The lingual surfaces of interdental plates may be formed by exposed alveolar bone, or thinly overgrown with periosteal bone.

In any part, inward-facing surfaces of alveolar bone may show either active growth or resorption, which appear to have alternated in relation to both socket expansion and tooth eruption. At maximum diameters, the medial and lateral walls of sockets may show only a very thin lining of alveolar bone, which may show signs of resorption, or a resorption surface cut into tissue not of alveolar origin (Figs. 76, 77, 79). The deeper parts of sockets and partitions between them may show two or more generations of alveolar bone, with junctions formed by reversal lines marking periods of resorption and regrowth (Fig. 77). New teeth were formed on the medial sides of the erupted ones and are sometimes seen located in ovate resorption spaces (Fig. 79), which suggest resorption around the outer epithelium of an enamel organ. In some forms at least, new teeth were formed in alternating positions, and this was the basis of their arrangement in iguanodont and hadrosaur batteries. In hadrosaurs, the upper parts of the teeth were in lateral contact, without bone between them, but alveolar bone can still line the grooves that they occupied and extend around the bases of the teeth.

Regrettably, the writer has not been able to section teeth showing cementum, but it seems to be normal in character when present. Its absence in the Cleveland-Lloyd samples is due to these being limited to the crown of one large tooth, and otherwise to jaws showing immature teeth only.

15. METAPLASTIC BONE AND "OSSIFIED TENDONS" (FIGS. 57–60, 62, 63, 80, 81)

The term metaplastic bone was introduced by Haines and Mohouiddin (1968) for tissues classified as bone but formed in locations where osteoblasts are absent. The parent tissue affected could be cartilage or fibrous (tendinous) material forming tendons and ligaments. The name is derived from the medical term metaplasia, denoting the transformation of one fully formed tissue (e.g., cartilage) into another. Some medical authors (e.g., Willis, 1962) apply this term to abnormal cases only, but small amounts of metaplastic tissue are a normal constituent of some bones, including mammalian limb bones, and such tissue would have to be seen as produced by metaplasia even if it was not called metaplastic. Haines and Mohouiddin (1968), moreover, could cite records of normal occurrences dating back as far as 1848, some from the classic

work of Weidenreich (1923), and Hall (1984) described such ossification as being "the norm" in reptiles.

Metaplastic ossification and its products can be described as intracartilaginous or intratendinous, according to the nature of the parent tissue. A complication (Badi, 1972) is that ossification of fibrous tissue may be preceded by chondrification, converting it into fibro-cartilage, but this does not affect the general pattern. Cells from the parent tissue (chondrocytes, fibrocytes) may persist in the ossified material, becoming in effect osteocytes, and may emit short lateral processes, but the lacunae they occupy are not connected by the canalicular networks seen in osteoblastic bone. This is because these cells lack the fine protoplasmic connections that osteoblasts develop before enclosure as typical osteocytes. In fossils, however, this character cannot be trusted to identify metaplastic tissues because even slight deterioration of bone can obliterate canaliculi. The presence of canaliculi, in contrast, is good evidence that a tissue is not metaplastic, as in the case of a so-called "ossified tendon" described below.

Dinosaurs show various tissues that either were or could be metaplastic, in both the main skeleton and osteoderms. Only intratendinous metaplastic bone has so far been identified certainly, in part at least due to the difference between the epiphyses of dinosaurs and mammals. The intracartilaginous metaplastic bone described by Haines and Mohouiddin (1968) is derived from non-hypertrophic articular cartilages in mammalian epiphyses; this pattern cannot be expected in dinosaurs, in which growth in length of the limb bones, preceded by cartilage hypertrophy, took place under the articular cartilages instead of under separate epiphyseal plates underlying the epiphyses as in mammals (see 8 above). There are no other obvious places where such tissue should be found. Just possibly, some cellular inclusions seen in compact bone immediately next to calcified "epiphyseal" surfaces (e.g., Fig. 81; *Camptosaurus*, C-LQ 105) may have been chondrocytes originally, since such tissue, standing up slightly above the "epiphyseal" surface, will have been in lateral contact with uncalcified cartilage in life; but this could not be verified in the writer's material.

Intratendinous metaplastic bone, in contrast, is readily demonstrable in saurischians whose neural spines show interspinous ligament scars (e.g., Madsen, 1976, Pls. 19–22). Periosteal bone stops at the margins of such scars, and bone forming the surface across them is typically an avascular tissue densely packed with coarse longitudinal fiber bundles (Figs. 57, 58; *Haplocanthosaurus*, C-LQ 110). This tissue was obviously formed by ossification of material from the interspinous ligament and may show transverse banding reflecting its progressive extension. The parallel-fibered pattern is here also genuine and not a product of layering as it can be in periosteal tissues.

Across the scars, a highly irregular surface shows the form of the zone of ossification (Fig. 80, at left; *Allosaurus*, C-LQ 093). At varying distances behind this surface, the metaplastic tissue is replaced by secondary osteoblastic bone, often first seen in the form of compact "Haversian systems" (secondary osteons), in turn grading into related cancellous bone. Because of the lack of primary vascularity, the first secondary osteons seem to have been formed in spaces tunnelled through the metaplastic bone by osteoclasts. Where metaplastic tissue stands out beyond the margins of the scars (e.g., Madsen, 1976, Pl. 21, Fig. B), replacement by secondary cancellous bone can extend well forward into it, leaving only a thin external covering of metaplastic tissue (Fig. 80, at left).

Muscles and other ligaments and tendons seem usually to have been attached to normal periosteal bone, in which the only sign of their attachment is imbedded "Sharpey's fibers" (Fig. 61; *Allosaurus*, C-LQ 078), but intratendinous metaplastic bone was also sometimes formed where major muscles were attached. The clearest known examples are from an *Iguanodon* femur, in which bone forming the surface where caudifemoralis and femorotibialis muscles were attached was a densely fibrous and mainly avascular tissue, instead of the laminar fibro-lamellar bone that formed the surface elsewhere (Reid, 1984a; Fig. 37). In both areas, the fibers were aligned with the expected pull direction of the muscles. The writer also found similar tissue in some *Iguanodon* metaphyses (e.g., Reid, 1984a, Fig. 36, distal end of a humerus). In the femur, the surface areas formed by intratendinous bone were also notable for being underlain by sharply bounded radial segments of dense Haversian bone, alternating with intervening segments formed from laminar fibro-lamellar bone (Reid, 1984a, Figs. 19, 22). At first sight, the function of this pattern of Haversian replacement could be thought to be the maintenance of vascular continuity between the laminar segments; but the primary and secondary canals were not found to communicate, and the contrasting segments must have had separate blood supplies. A possible alternative explanation is that bone with few vascular canals and no canaliculi would be specially susceptible to cellular necrosis, which is one of the known triggers of Haversian reconstruction (Enlow, 1962a); and having major locomotory muscles attached to segments of dead bone would obviously not be satisfactory.

Two other tissues figured here appear to be of metaplastic origin. In some dinosaurian vertebrae, the neurocentral suture when open is thinly lined with typical calcified cartilage, under which endochondral bone was formed. In contrast, an *Iguanodon* caudal (Fig. 60) showed the suture bounded by a highly fibrous tissue, with fibers aligned across the suture, which was replaced by Haversian and not endochondral bone. In places, rows of small cellular inclusions could be seen between fibers. This pattern is strongly suggestive of an ossified form of fibro-cartilage. In another case, bone flooring subterminal parts of the neural canal in caudal vertebrae of *Allosaurus* (Fig. 59; C-LQ 087) and *Ceratosaurus* (C-LQ 088) was found to be a highly fibrous tissue with fibers sloped obliquely outward, again showing replacement from below by Haversian bone. This also seems to be a metaplastic tissue, which could have been either fibro-cartilage or purely fibrous originally.

Structures usually called "ossified tendons" are common in ornithischians, in which they seem to have braced the vertebral column laterally in the absence of an interspinous ligament like that of saurischians. The name used suggests structures produced by metaplasia, but whether this was really involved is uncertain. A possible intratendinous tissue was figured by Moodie (1928, Figs. 3, 5b) from *Ankylosaurus*, but other examples known to the writer are formed mainly from dense Haversian bone, with only traces of fibrous tissue, or, in one case, in part from a further primary tissue that cannot be of metaplastic origin. In this example, from *Iguanodon* (Figs. 62, 63), a cross section shows a structure like that of a rib, with a core of reconstructed cancellous bone grading outward into dense Haversian tissue and the outermost osteons from this intruding primary bone. The primary tissue shows scattered longitudinal fiber bundles when sectioned in that direction (Fig. 62), and transverse sectioning shows it as also highly vascular, with many parallel longitudinal canals and some enclosed by small primary osteons (Fig. 63). Fine parallel longitudinal grooving of the external surface, suggesting fibrosity, is in fact due to partly enclosed vascular channels, which superficial blood capillaries would have occupied in life. Apart from its fibrosity, this tissue has an obvious resemblance to normal periosteal bone, and its osteoblastic origin is confirmed by the osteocyte lacunae emitting typical branching canaliculi. Such bone is clearly not a form of intratendinous metaplastic bone and can only have resulted from osteoblasts appearing in tissue coating the surface of a tendon, producing a secondary periosteum; this must in turn have given rise to an endosteum for internal reconstruction to occur. Examples formed chiefly from dense Haversian bone, as found by Broili (1922) and Moodie (1928) in "*Trachodon*" (presumably *Anatosaurus*), could simply be similar structures with more complete Haversian replacement; and, while the original tendon may first have undergone metaplasia, there is no proof that it did. The initial process could instead have been comparable with the formation of tail rods in *Deinonychus*, seen by Ostrom (1969) as resulting from the vertebral periosteum having spread onto tendons attached to zygapophyses and chevron bones, although, since the ornithischian structures were

not outgrowths from other bones, a secondary periosteum on them would have arisen *de novo*. But, however their growth was initiated, the "ossified tendon" described from *Iguanodon* is clearly not an ossified tendon in the literal sense of that term.

16. OSTEODERMS AND ARMOR (FIGS. 8, 64–67)

Dermal ossifications seen in reptiles may be formed from osteoblastic or metaplastic bone, or mixtures of both. Hall (1984), citing Moss (1969), described intratendinous tissues as the rule, with periosteal secretion only rarely involved, but turtle and crocodile material the writer has sectioned showed only periosteal and reconstructed bone, as did fossil examples from both groups recorded by Gross (1934) and by Enlow and Brown (1957). Similarly, Ferguson (1984) found dorsal scutes of American alligators to show zoned periosteal bone in early years, with internal reconstruction beginning at about six to eight years of age and more extensive in females than in males—perhaps through demineralization during eggshell formation.

Only limited dinosaurian material has been available to the writer, but even this showed a range of different patterns. Material from the crest of a large *Stegosaurus* dorsal plate (C-LQ 085; Fig. 67) confirmed the finding of de Buffrenil and others (1986) that the upper parts are formed from periosteal bone and Haversian tissues, whereas a section through the base of a small plate (C-LQ 097; Fig. 8) showed the highly fibrous cancellous tissue that they found in the lower parts. Here, however, fiber bundles were aligned horizontally, rather than vertically or obliquely as in their example. As they showed, the contrast in tissue styles was due to the plates growing by accretion from below, as well as by lateral accretion in the upper parts. The fibrous tissue seen in the lower parts gives a very strong impression of being of metaplastic origin, and it also gives an impression of being formed initially as compact bone, despite the lack of a compact basal plate, because cancellous spaces in it cut through fiber bundles (Fig. 8; compare de Buffrenil and others, 1986, Fig. 5b). In contrast, a small flat lateral ossicle ascribed to *Stegosaurus* (Figs. 64, 65; C-LQ 128) showed bone formed from irregularly interwoven ossified fiber bundles, with some replacement by compact secondary osteons but no periosteal content. Flat-lying armor from the early ankylosaur *Polacanthus* (Wealden; Sandown Museum; no number) and an unnamed late Cretaceous species from Alberta again showed bone ossified from large irregularly interwoven fiber bundles, but a sample from *Sauropelta* (writer's collection) was instead formed mainly from reconstructed (Haversian) cancellous bone, with fiber bundles seen only in a thin basal layer of periosteal bone. A further contrasting pattern was seen in a lateral ossicle ascribed to *Cerato-*

saurus (Fig. 66; C-LQ 100), showing tissue of several different types. In the interior, a general groundmass is formed by finely fibrous vascular bone, with the fibers arranged radially except near the external surface, where they form crossing oblique bundles. Some of the vascular canals have a thin halo of non-fibrous bone, forming very simple primary osteons. Transverse banding and vague traces of zonation are seen in places. Near the external surface, this bone is coated with irregularly lamellated tissue, with complications due to the presence of a nodular external ornament. A thin and more uniform covering of this tissue continues across the basal surface. Parts of the interior show replacement of the primary tissue by compact secondary osteons, which form dense Haversian bone in places, and in one part this grades into a patch of reconstructed cancellous bone.

This material thus shows osteoblastic and probably metaplastic tissues as both occurring in dinosaurian osteoderms, with different roles in different cases and with metaplasia possibly beginning their formation in all cases. In particular, the pattern of interwoven ossified fiber bundles seen in, for example, *Polacanthus* is very similar to patterns of interwoven fiber bundles in some crocodile hides, suggesting origin by ossification of parts of a similar hide. If so, osteoderms may sometimes preserve the structure of dinosaurian skin, even if this is not preserved as such, and the hide of *Ceratosaurus* would also seem to have differed from that of *Polacanthus*. By analogy with Ferguson's (1984) alligator findings, the contrast between the *Sauropelta* and other ankylosaur samples could be due to a difference in age, sex, or both.

17. OTHER SPECIAL TISSUES

Pachycephalosaur skull caps can show numerous closely spaced radial vascular canals, which open at the external surface. In deeper parts, approaching the braincase, they may show enlargement by resorption or pass into spaces in cancellous bone. In a sample from *Stegoceras*, a tangential section near the surface showed them enclosed within cylindrical primary osteons, set in a matrix of woven bone. The tissue thus has the character of fibro-lamellar bone, but it is not a normal member of the fibro-lamellar complex and has no known counterpart in other forms. Its high vascularity is also more suggestive of a heat-exchanging organ than of the head-butting habits ascribed to these animals.

Hatchling tissues have yet to be reported from dinosaurs but are likely to follow patterns known from other forms. Any showing post-juvenile fibro-lamellar bone will probably show a cancellous juvenile variant, built either entirely from woven bone or with partly formed primary osteons enclosing wide vascular lumina.

Bone of this type, persisting in a partly grown juvenile, is known from the hadrosaur *Procheneosaurus* (Nopcsa and Heidsieck, 1933, as "*Tetragonosaurus*").

18. PATHOLOGICAL TISSUES (FIGS. 68–72)

Pathological bone tissues may be summarized briefly as mostly produced by departures from normal patterns of ossification or reconstruction, some of which reflect genetic defects, or by various types of reaction to injury, inflammation, infection, metastasis, or combined factors. Aging effects and true bone cancers also occur. Post-traumatic conditions can be due to bones being bruised, bent, twisted, broken, or bitten, with infection sometimes following, especially in the two last cases. Various types of fractures reflect their causes and the types of bone affected.

Palaeopathology is the study of lesions seen in fossil bones and seeks to establish their natures. This is often far from easy. Fractures usually present no problems, except when they might be taphonomic (i.e., postmortem), but most diagnoses of disease involve working from bone only, with no knowledge of associated soft parts or infective agents or of physiological or genetic abnormalities. Recently, Rothschild and Turnbull (1987) claimed serological evidence of a treponemal infection, but their material was only 11,500 years old, and it has yet to be shown that such data can be had from substantially older bones. Hence, diagnosis largely has to be based on comparison with similar modern lesions, which could be misleading. Some fossil lesions also have no exact modern counterparts, and some past infective agents may no longer exist. The latter possibility is likely to increase with geological age and to be greatest in long-extinct forms with no descendants. Further complications are that different conditions can have similar effects, and different authors can reach different conclusions. A dinosaurian lesion, for instance, ascribed by Swinton (1934) to periosteal sarcoma was reinterpreted by Campbell (1966) as reflecting a viral infection, and Martin and Rothschild (1989) described Moodie's (1923) diagnoses as mostly mistaken. The treponemal infection claimed by Rothschild and Turnbull (1987) was thought more probably fungal or tubercular by Neiburger (1988).

Accordingly, this section simply shows some examples of conditions seen in dinosaurs, with no attempt at comprehensive coverage. Figure 68 shows osteoporotic bone from an *Apatosaurus* scapula (C-LQ 114), and this condition is also known to the writer from a *Camarasaurus* limb bone. Normally compact bone has been converted into finely cancellous bone by secondary enlargement of primary vascular canals and by replacement of primary bone by incompletely formed Haversian systems (secondary osteons). Although not demonstrably sex-linked, the condition shows the same loss of balance between bone resorption and

bone replacement as in human osteoporosis, of which it seems to be a dinosaurian equivalent. Bone loss has not gone as far as in advanced human cases, but the limb bones of such massive animals would almost certainly collapse long before that state was reached. Figure 69 shows abnormal secondary osteons, which seem to have been formed along stress cracks in a bone from a small theropod. Figure 70 shows a splinter of periosteal bone imbedded in part of a massive cancellous exostosis formed on a broken *Allosaurus* rib (C-LQ 116) and undergoing replacement along parts of its lower edge. Features seen in these two figures show that damage occurred during life and was not taphonomic. Figure 71 shows cancellous reactive tissue of the disputed Swinton-Campbell tumor growing out from a surface formed by normal compact bone, also showing internal cavitation in parts (cf. Campbell, 1966, Figs. 1–3). The dinosaur represented, thought by Campbell to be *Mochlodon*, could in fact be the hadrosaur *Orthomerus*, in which the writer has found similar lesions. Finally, Figure 72 shows material from a cavernous sauropod vertebra in which the cavernous spaces were infilled by a cancellous reactive growth, and the original inter-cavernous plates were progressively destroyed by irregular internal cavitation. Reactive tissue is seen at the top and at the bottom, with the "ghost" of a largely destroyed inter-cavernous plate running transversely between them. What caused this condition is unknown, but some form of infection or a cancerous metastasis are possible.

19. BONE AND PHYSIOLOGY

Physiological assessment of fossil animals is not a normal aim of bone histology, but various bone tissues have been claimed to throw light on the thermal physiology of dinosaurs. In the writer's opinion, there is reasonable evidence from bone that they differed physiologically from all modern reptiles but no certain evidence of how much they differed.

First, it needs to be realized that none of the tissues that are normal constituents of tetrapod bones can be used to distinguish between ectotherms and endotherms because all occur in both. Both show all fibrillar types from lamellar bone to woven bone; both form periosteal and endosteal bone, of the same primary and secondary types; and both may show minor developments of metaplastic bone. In both, periosteal bone ranges from uniform and lamellated tissues to fibro-lamellar bone, with annual cyclicity sometimes added to produce zonal patterns. Overall, the two groups do show contrasting general styles of bone histology in that typical zonal patterns are seen chiefly in ectotherms, whereas continuous growth, fibro-lamellar bone, and extensive Haversian reconstruction are known mainly from endotherms; but exceptions

occur in all these cases, and bones of very small forms often show no hint of different physiologies.

Second, whereas modern ectotherms and endotherms show contrasting general styles of bone histology, this contrast has no certain significance in fossils because we do not know the stage in physiological evolution at which the "endothermic" style originated. What needs to be known, but is not known, is the thermal physiology of the oldest forms to show "endothermic" patterns because, unless these were endotherms themselves, such bone is not evidence of endothermy. This is why the writer (Reid, 1987, 1990) has emphasized that the earliest synapsids to show endotherm-like bone were not advanced forms close to mammals, but primitive therapsids showing no other signs of being endotherms (Kemp, 1982). In such therapsids it does not seem to mark endothermy but only some earlier step in physiological evolution, which could also have had to be taken for endotherms to start to evolve. One can only guess at what this could have been; but a possible answer is the advent of complete "double-pump" circulation, with the systemic and pulmonary circulations fully separated, allowing endotherm-like growth and the start of a move toward endothermy (Reid, 1987).

Of tissues supposed to throw light on physiology, Haversian bone has been known to be extensive in some dinosaurs since the pioneer studies of Seitz (1907) and was cited as evidence of high metabolic rates by both Bakker (1972) and de Ricqlès (1974, 1976), although on rather different grounds. For Bakker, this followed from its high vascularity, held to indicate high levels of calcium and phosphate exchange between bone and body fluids; and he also ascribed the same significance to laminar fibro-lamellar bone, which can be even more vascular (Currey, 1960). De Ricqlès, in contrast, placed his emphasis on the repeated gross exchanges between bone and body fluids in the production of dense Haversian bone, in which bone is resorbed and redeposited repeatedly, and bracketed this with repeated reconstruction in "Haversian" cancellous bone. Their arguments are thus complementary but not identical. Both arguments are reasonable, but both involve various problems.

First, as was seen by Bouvier (1977), Haversian bone is not unknown in modern kinds of reptiles, and, though dense Haversian bone is rare, the writer (Reid, 1987) has figured it from the tortoise *Geochelone triserrata*, in a specimen showing it developed as extensively as in humans. Second, even in endotherms it is mainly a feature of medium-sized and large forms and is characteristically absent in the smallest, despite metabolic rates being highest in the smallest forms and lowest in the largest. This shows size as a factor reversing what would be expected if levels of Haversian reconstruction were simply controlled by metabolic levels, and hence rules out a

causal connection between them (McNab, 1978). Indeed, because the relationship between size and basic metabolic rates follows parallel patterns in ectotherms and endotherms, small lizards without Haversian bone can have higher mass-specific metabolic rates than large mammals that show it extensively (cf. Reid, 1987, Fig. 4). Third, delayed reconstruction in some species again rules out a simple relationship between it and metabolic levels. Currey (1960), for instance, reported cats as not starting to form Haversian bone until well after sexual maturity, while Ferguson (1984) found reconstruction in alligator scutes to begin at about 6–8 years of age, although the metabolic rates of these animals fall progressively as they grow (Coulson and Hernandez, 1983, Table 2.1). From a survey of mammals, Ruth (1953) concluded that the age at which reconstruction starts and the rate at which it then proceeds are both controlled genetically. Fourth, the association of extensive Haversian reconstruction with large sizes suggests the mechanical stresses produced by heavy weights as a causal factor, especially in animals that walk upright, and some authors (e.g., Ostrom, 1980) have seen this as accounting for extensive reconstruction in large dinosaurs. Fifth, Enlow (1962a) identified other non-metabolic factors that lead to local Haversian reconstruction, and some of these can be recognized as also affecting dinosaurs. This applies, for instance, to the radial blocks of dense Haversian bone seen under certain muscle scars in *Iguanodon* (Reid, 1984a, Figs. 19, 22) and probably to comparable features seen in some Cleveland-Lloyd *Allosaurus* bones (e.g., femora C-LQ 096 and 112; tibia C-LQ 104). In the *Iguanodon* case, the trigger factor may have been cellular necrosis in avascular metaplastic bone (see section 15 above). Sixth, whereas general reconstruction in dinosaurian diaphyses may be as total as in some mammals, it may also be as limited as is usual in crocodiles in even forms as large as *Allosaurus* and *Iguanodon* (see section 7 above). This is not a problem if one follows Bakker's (1972) argument, since the primary tissues were highly vascular, but it does not fit that of de Ricqlès (1974, 1976), from which extensive Haversian reconstruction should be usual in large forms with high metabolic rates. On the other hand, it also conflicts with the concept of weight as a causal factor, except at still larger sizes.

To these problems must be added the contention of some authors (e.g., Hotton, 1980) that extensive reconstruction in large forms could reflect the effects of large sizes combined with those of homoiothermy based on bulk instead of endothermy. Two decades ago, Spotila and others (1973) used a mathematical model to show that a dinosaur with a 1 m diameter body, a 5 cm insulating layer of subcutaneous fat, and an alligator-like physiology could have maintained a core temperature varying only between 28.5°–29.6°C in air temperatures cycling daily between

22°–32°C and that the time taken for 63.7% of the change between any two equilibrium temperatures (their "time constant") would have been 48 hours. Many dinosaurs were of this size or larger, and some were much larger. Such stabilization of temperature by bulk, termed mass or inertial homoiothermy, could also have been supplemented by the thermal conductance of the skin being lower than that of mammals above 100 kg weight, as in modern reptiles (McNab and Auffenberg, 1976), and by control of heat exchanges through the skin by contraction or dilation of superficial blood vessels (Regal and Gans, 1980). In addition, the larger such animals grew, the more their bodies would retain the heat produced by activity, and, in large herbivores, bacterial fermentation of gut contents could have been a substantial heat source (Farlow, 1987) involving no expenditure of energy by the animals themselves. Along with heavy weights, high constant temperatures maintained in these ways and boosting metabolic levels correspondingly could potentially be the basis of extensive reconstruction in large and presumably long-lived animals, without any approach to endothermic metabolic levels and with results that could not be distinguished from those seen in true endotherms.

Because of these problems, no certain physiological significance can yet be assigned to Haversian bone in dinosaurs; but de Ricqlès (1974, 1976) also based an alternative argument on fibro-lamellar bone. This has the advantage of being a primary tissue that shows how dinosaurs grew, and so allows comparison with growth patterns seen in modern forms. As he realized, many dinosaurs could form fibro-lamellar bone continuously up to large and very large sizes. Not all the records he relied on (de Ricqlès, 1980, Table 1) show histological details, some only showing periosteal bone as non-zonal, but verified examples are known from all the main groups of dinosaurs and in forms up to the size of *Brachiosaurus* (Gross, 1934). As de Ricqlès emphasized, such bone is strictly only evidence of continuous growth at rates comparable with those of large fast-growing mammals and birds, but since such growth is now only seen in endotherms, it can be thought only possible for endotherms. Again, this argument is reasonable, but it has two major flaws. First, when de Ricqlès used it he was under the impression that zonal patterns, now typical of ectotherms, do not occur in dinosaurs, and he abandoned it in favor of the influence of mass effects when examples were found in two sauropods (Reid, 1981; de Ricqlès, 1983). Zonal bone is now known to be widely distributed in dinosaurs, although less common than non-zonal tissues (Reid, 1990). It seems to show them as still close enough to typical reptiles physiologically to have retained a capacity for the same style of growth and is evidence against dinosaurian endothermy unless similar tissues can be found in ecologically comparable endotherms.

Second, and more seriously, de Ricqlès (1974, 1976) only used the term fibro-lamellar for tissues of this type formed continuously and did not apply it to identical tissues found by Enlow (1969) to be formed by both turtles and crocodiles during periodic rapid growth. These have the obvious implication that the simple formation of such bone does not require higher metabolic rates than these animals experience when growing most rapidly. Paul (1991) tried to avoid this conclusion by claiming that no modern reptiles can grow quickly in the wild, but, in material supplied to the writer by Professor N. W. J. Ferguson, good fibro-lamellar bone is seen in young wild American alligators from North Carolina, where these animals are at the northern limit of their range and can be subject to freezing conditions in winter. And, at 28°C, above the range (23.5°–27°C) in which Joanen and McNeese (1976) were able to double wild alligator growth rates, the mass-specific standard metabolic rate for 7 kg specimens was determined by Coulson and Hernandez (1983, Table 2.1) as only one-twentieth of that of a comparable (10 kg) dog (0.40 liters O^2 per kg per day, compared with 8.0 liters). In that light, claiming fibro-lamellar bone as implying endothermic metabolic rates is not realistic.

The ability of dinosaurs to grow quickly and continuously to large sizes, implied by non-zonal fibro-lamellar bone, remains good evidence that they did differ physiologically from all modern reptiles; but, in the writer's opinion, the only certain inference to be drawn from it is the possession of cardiovascular and hemal systems able to support such growth. Tetrapods can be programmed genetically to grow more slowly than they could, but none can grow faster than a maximum potential rate determined by the rate at which substrates and energy can be supplied to growing tissues. A high efficiency in these respects is implicit for dinosaurs, which could not otherwise have grown quickly to large sizes, and would almost certainly have been based on the complete double-pump circulation thought necessary by Seymour (1976) and Ostrom (1980) on hemodynamic grounds. Factors involved would be the rate at which blood could be pumped through capillaries supplying growing bone, the number of capillaries traversing a given amount of growing tissue, and the capacity of the blood for carrying and delivering needed substrates and oxygen. The oxygen-carrying capacity of the blood could have been higher than that of modern reptiles, among which that of, for example, alligators is only 40% that of mammals (Coulson, 1984). To these factors would need to be added a capacity for maintaining needed flow rates against increasing frictional resistance to blood flow as vessels lengthened during growth. Increasing resistance with growth was seen by Coulson and Hernandez (1983) as a reason for progressive circulatory slowing in alligators, which in turn is a probable reason for

growth slowing progressively, and proportionate changes that they noted are probably also involved. Comparing examples weighing 1.6 and 99 kg, they found that, relative to body weight, the heart of the larger individual weighed less than half that of the smaller, whereas its aorta had relatively less than one-sixth of the diameter. The circulatory systems of dinosaurs, in contrast, must have kept pace with growth in a manner that allowed the essentially constant rates of bone formation seen in even massively large forms.

If this picture is correct, the primary basis of fast continuous growth in dinosaurs was not high metabolic rates, but high circulatory efficiency. Efficient circulation would presumably lead to a rise in metabolic rates, to above those seen in modern reptiles; but how far they would rise is not predictable. It must also be remembered that mammalian and avian endothermy is not just a matter of high metabolic rates, but of ability to maintain homoiothermy, independently of bulk and activity, by means of precise physiologically controlled balances between heat production and heat losses. There is no way in which bone histology can show dinosaurs as having this ability.

POSTSCRIPT

In a recent development, Baretto and others (1993) have claimed that what they term avian-type growth plates in the long bones of young maiasaurs imply both high metabolic rates and determinate growth, besides also supporting the view that birds are dinosaurs. By growth plates they mean the zones of calcified cartilage under which new endochondral bone is formed as long bones grow in length. The notion that epiphysial structure could throw light on physiology is new, but the arguments it is based on are faulty (a) in restricting comparison with modern ectothermic reptiles to lizards, which have calcified epiphyses and sub-epiphysial growth plates, (b) in ignoring the work of Wheeler Haines (1938, 1942) on epiphysial evolution, and (c) in assuming necessary connections between fast growth, high metabolic rates, and determinate growth. That fast growth need not imply a high metabolic rate has been shown above, but the other points need further comment.

First, it is true that the growth plates of most bird long bones are sub-articular, as in dinosaurs (section 8 above); but so are those of turtles and crocodiles among modern reptiles (e.g., Haines, 1938, Figs. 3–6; 1969, Figs. 2–7), and, in fossil groups, those of, for example, "thecodontians," plesiosaurs, ichthyosaurs, synapsids, cotylosaurs, and labyrinthodonts. This condition is thus not "avian" or a "shared derived character," common only to dinosaurs and birds, but, as seen by Haines (1938), simply the primitive tetrapod pattern from which derived conditions with separately calcified epiphyses have been evolved iteratively (cf. Haines, 1942, Figs. 1, 5). Further, neither a high metabolic rate nor determinate growth can be inferred from a condition shared with turtles and crocodiles, and, though growth is determinate in birds, such growth cannot be inferred from any juvenile tissue but only from adult bones showing evidence of active growth ceasing before death (section 6d above). Thus, though the structures figured by Baretto and others (1993) are consistent with young maiasaurs growing quickly, the rest of their contentions do not follow from their evidence.

Second, it also is possible that the sub-articular pattern seen in birds, although primitive morphologically, may be secondary phylogenetically (Haines, 1938, 1942). This possibility arises from (a) the presence of a calcified epiphysis at the top of the tibia, (b) the appearance of calcified epiphyses in other bones in conditions of induced chondrodystrophy (Landauer, 1931), and (c) the presence in juvenile bird epiphyses of cartilage canals, which are otherwise seen only in forms that have calcified epiphyses (lizards, mammals). As seen by Haines, Landauer's findings point to reactivation of genes that are normally "switched off"; and, as he also saw, a secondary suppression of epiphysial calcification could be due to the pneumaticization of metaphyses. If this is so, sub-articular endochondral growth must be atavistic in birds, whereas nothing suggests that it is anything but primitive in dinosaurs.

It can hence still be asserted that no type of bone has yielded evidence of dinosaurs having had endothermic (or, avian) metabolic rates. It does not, of course, follow that they cannot have had high metabolic rates; but, if any did, the evidence for this will need to come from some other source.

APPENDIX A: HISTORICAL BACKGROUND

Although a detailed history of bone histology would take more space than can be justified here, it is useful to have an outline picture of how current perspectives were evolved and how various concepts that are used in text above were introduced. This will in turn provide a basis for understanding various deviant and obsolete usages.

Nomenclature used today has its most distant root in lectures given by Clopton Havers to the Royal Society of London in 1690, later published in his *Osteologia Nova* of 1691. These contained the first descriptions of the vascular canals of compact bone, which later came to be called canals of Havers, and, later, Haversian canals. Havers himself did not understand their vascular character, supposing instead that they carried an oil, which "mollified" (i.e., softened, or conditioned) the bone and also lubricated joints. Enlow (1962a) cites Albinus (1757) as having first shown their vascular character by injecting colored

dyestuffs into blood vessels leading into bones. Transfer of the term Haversian to bone itself began in 1846, when Todd and Bowman described concentrically structured cross sections of what are now called secondary osteons as "Haversian systems." The origin of these structures by resorption and redeposition was then recognized by Tomes and de Morgan (1853), who introduced the term Haversian spaces for the resorption spaces within which secondary osteons are formed. The term Haversian was first used systematically for whole tissues by Foote (1916), but only one of four types to which he applied it is Haversian in the current sense, due to Enlow and Brown (1956).

In other early developments, osteocyte lacunae were first recorded by Deutsch and Purkinje (1834), and first called by that name by Todd and Bowman (1846). The first reports of their occurrence in dinosaurs, as "bone cells," were by Quekett (1849) from bones of Iguanodon and by Mantell (1850) from a humerus of Pelorosaurus, from which Mantell also gave the first report of dinosaurian "Haversian" canals. Tomes and de Morgan (1853) gave early descriptions of the growth of periosteal and endochondral bone, but they did not use these terms and wrongly thought it normal for chondrocytes to transform into osteocytes. This only happens in metaplastic ossification of cartilage. Fossil endochondral bone was figured under that name by Hasse (1878) from vertebrae of two ichthyosaurs, a nothosaur, a plesiosaur, and a supposed Thecodontosaurus vertebra. Detailed studies of bone from ichthyosaurs and plesiosaurs were next published by Kiprijanoff (1881, 1882), who was also first to illustrate the cones of endochondral bone that these animals often show in limb bones. These structures were termed epiphyses by Lydekker (1889), thus wrongly equating them with the ossified epiphyses of mammals, and only later identified correctly by Moodie (1908), who also noted ossified epiphyses as lacking in theropods. Seitz (1907) published studies of bone in fossil reptiles including twelve dinosaurs, among which were the Morrison genera Allosaurus, Apatosaurus, Camarasaurus, Diplodocus, Haplocanthosaurus, and Stegosaurus. His work is notable for making the first clear distinction between primary and secondary sorts of "Haversian" (vascular) canals and for giving the first illustrations of "growth rings" from dinosaurs, from Allosaurus and Stegosaurus. Besides describing the gross structure of tissues, he gave details of the form and arrangement of osteocyte lacunae and canaliculi, also noting examples of fungal enlargement, mineral filling, and loss in fossilization.

The next work needing attention is that of Foote (1916), which, while having some value, has been a major source of confusion in nomenclature. At a time when medical dogma held bone to be built from "Haversian systems," due to their prevalence in human compact bone, Foote recognized that many kinds of tetrapods show compact

bone not built in this manner. In his view, compact bone could be built from three types of gross structural units called lamellae, laminae, and Haversian systems, and could hence be referred to three main types called First, Second, and Third, or lamellar, laminar, and Haversian. In this usage, lamellar, based on gross structure, applies to bone described as "lamellated" by the writer and not to the lamellar bone of modern fibrillar nomenclature. It also takes in lamellations called "laminae" by Tomes and de Morgan (1853), which, in turn, are not Foote's "laminae," defined by the presence of successive concentric vascular networks. In modern terms, his "laminar" type was vascular zonal bone in, for example, Alligator mississipiensis, but was laminar fibro-lamellar bone in mammals, in which he held his "laminar" type to be most fully developed. His "Haversian systems" were described as "completely" or "incompletely differentiated," according to the presence or absence of sharp peripheral boundaries, and thus included both primary and secondary osteons, whose different origins he did not understand. His "Third" or "Haversian" group of tissues was divided correspondingly into subtypes III, I, and III, C, for tissues thought to have "Haversian systems" incompletely and completely differentiated; type III, I, was subdivided further into Ia, Ib, and Ic, according to what he saw as their level of differentiation. Of these tissues, only Type III, C, is Haversian bone in the modern sense, built from secondary osteons. His figures drawn to illustrate types III, Ia, and Ib show periosteal bone sensu lato, with primary osteons in a matrix of uniform or lamellated bone (1916, Pl. A, Figs. K, L), whereas his type III, Ic, found only in birds, appears to be fibro-lamellar bone with densely packed primary osteons (Pl. A, Fig. M) like that figured by the writer (Reid, 1984b) from Struthio.

In other developments, more relevant to modern usage, the term osteon was introduced by Biedermann (1913), and Weidenreich's monumental studies of fibrillar structure appeared ten years later (1923). At first distinguishing only "Faserknochen" and "Schalenknochen" (literally, fiber-bone and shell-bone) as broad types, comprising coarsely and finely bundled tissues, his classification assumed the form translated by Pritchard (1956) in a textbook article of 1930. Gross (1934) next applied Weidenreich's methods, plus some others of his own, to a study of bone from fossil reptiles and amphibians, referring their compact bone to three types that translate as zonal periosteal bone (zonare Periostknochen), laminar periosteal bone (laminare Periostknochen), and secondary osteon-bone (sekundare Osteonknochen). In introductory text, he made the first clear distinction between primary and secondary osteons, describing their different origins correctly. His zonal type included the writer's lamellated and restricted zonal types, thus corresponding with the later "lamellar-zonal" type of

de Ricqlès (1974). A vascular zonal type seen in *Nothosaurus* was held to be specially typical. His laminar type, in contrast, was laminar fibro-lamellar bone, with concentric vascular networks and circumferential osteons, which he found in the therapsid *Kannemeyeria,* the "thecodontian" *Erythrosuchus,* and the dinosaurs *Plateosaurus* and *Brachiosaurus,* as well as in a juvenile mammoth and "numerous ungulates." This usage restricts the term laminar to only one of the two types called laminar by Foote (1916), the other as seen in, for example, alligators being classified as zonal. The third tissue, termed secondary osteon-bone, is the dense Haversian bone of current usage. A further tissue termed primary osteon-bone was noted as occurring in birds, but not clearly described or illustrated.

Regrettably, Gross ended his paper by equating his three types of compact bone with those distinguished earlier by Foote. These equations are wrong in all three cases and seem to have resulted from his relying on Foote's idealized figures (1916, Pl. B, Figs. 1–6) without understanding his text. First, the "lamellar" type of Foote took in endosteal tissues as well as periosteal bone, and some of Gross's zonal types are "laminar" in Foote's nomenclature (in, e.g., *Nothosaurus*). The "laminar" type of Foote includes both zonal and laminar types in Gross's sense, whereas only one of Foote's four "Haversian" types corresponds with Gross's secondary osteon-bone. The real relationship of these classifications is as stated in this paragraph and above.

The next significant work was a study of a wide range of modern and fossil vertebrates by Enlow and Brown (1956, 1957, 1958), who used a classification based essentially on gross structure and vascular patterns, without reference to fibrillar data. Much of their nomenclature is now obsolete, but they are notable for using the term Haversian bone in its current sense, as equivalent to Gross's secondary osteon-bone. Regrettably, they also introduced two divergences from Gross's usage. First, they applied the term laminar to vascular forms of zonal bone, instead of to laminar bone *sensu* Gross, which they renamed as plexiform bone. Second, they used the term primary osteon as meaning primary vascular canal, and described primary osteons *sensu* Gross as "protohaversian systems." Later Enlow (1969) switched to using "primary osteon" in Gross's sense, but continued using "laminar" as meaning vascular zonal bone. The term laminar bone thus came to be used in three confusingly different senses:

(1) *sensu* Foote (1916), as including both vascular zonal bone and laminar fibro-lamellar bone;

(2) *sensu* Gross (1934), as including only laminar fibro-lamellar bone; and

(3) *sensu* Enlow and Brown (1956) and Enlow (1969), as including only vascular zonal bone.
To this situation a further complication was then added by

de Ricqlès (1974), who applied both "plexiform" and "laminar" to forms of laminar bone *sensu* Gross, according to the presence or absence of radial vascular canals. Tissues showing these conditions are intergrading in practice, and whether radial canals are conspicuous in sections can depend on whether they lie in the plane of section.

At this point, it should be clear that considerable possibilities exist for confusion and misunderstanding when referring to past literature, if different usages are not understood and different authors are not recognized as following different usages. Especially, when the terms lamellar, laminar, and Haversian are encountered, it is important to be sure what is meant by the author concerned. Besides the cases noted above, the terms lamellae and laminae can also still be found used interchangeably in some medical literature.

Further understanding of the tissues now called fibro-lamellar bone (de Ricqlès, 1974) was next provided by Smith (1960), who recognized that the spaces in which primary osteons are formed can take the form of longitudinal tunnels, of an irregular network of passageways, or of radial or circumferential clefts. The resulting types of osteons were named cylindrical, irregular, radial, and circumferential, correspondingly, as in the writer's text. Such bone with circumferential osteons is the laminar bone of Gross (1934), whereas the other types characterize the tissue here called parallel osteoned, reticulate, and radiate, following de Ricqlès (1974). In the same year, a study of developing laminar bone by Currey (1960) confirmed an earlier description by Gross (1934). Both Currey and Smith confirmed Gross's view (1934) that the lamellar bone of primary osteons is not a replacive tissue, as held, for example, by Pritchard (1956). Neither author mentioned Gross's paper, but Smith used his term primary osteon, and Currey discussed illustrations that Enlow and Brown (1957) had copied from Gross and ascribed to him. Later, these papers formed the basis of de Ricqlès' treatment (1974, 1975) of these tissues as fibro-lamellar bone.

In other developments, a formal distinction between osteoblastic and metaplastic tissues was first introduced by Haines and Mohouiddin (1968), although implied in earlier work by Haines (1942). Enlow (1969) gave a still useful account of the bone of modern reptiles, with a classification based on various characters including fibrillar patterns. Most notably, in view of later physiological arguments, he recorded structurally fibro-lamellar bone as formed by both turtles and crocodiles during periods of rapid growth. A still more detailed classification, parts of which are followed here, was next given by de Ricqlès (1975), based chiefly on various aspects of gross structure, histology, and modes of origin.

From 1972, however, fossil bone became involved in "histo-physiological" speculations, outside bone histology

proper, in which certain tissues were claimed to give evidence of metabolic levels. Bakker (1972) and de Ricqlès (1974, 1975) both held extensive Haversian bone in dinosaurs to be evidence of high metabolic rates, though using different arguments. For Bakker, high rates of calcium and phosphate exchanges between bone and body fluids were implied by its high vascularity. For de Ricqlès, the same was implied by the resorption and redeposition involved in its formation. De Ricqlès (1974) also added a further argument based on periosteal growth patterns. Zonal bone *sensu* Gross (1934), renamed lamellar-zonal bone, was held to be characteristic of ectotherms, whereas fibro-lamellar bone, found extensively in dinosaurs, was now seen almost exclusively in endotherms. Strictly, fibro-lamellar bone in dinosaurs was only evidence of fast continuous growth at rates similar to those of large fast-growing endotherms, but, since such growth is now restricted to endotherms, it can be thought only possible for endotherms. Both these arguments are flawed in various ways, and de Ricqlès abandoned his former views in 1983 after both he (1983) and the writer (Reid, 1981) had found zonal tissues in dinosaurs. Bakker (1986) insisted that these finds were too few to be significant, but such bone has since been shown (Reid, 1990) to be widely distributed in dinosaurs and even seemingly normal in some genera, although less common than fibro-lamellar and related bone tissues. In the present paper, the writer can assign no sure significance to Haversian bone and sees fast growth to large sizes as strictly only evidence of cardiovascular and hemal systems able to support it.

In other minor developments involving dinosaurs, Nopcsa and Heidsieck (1933) compared bone tissues from ribs of juvenile and partly grown hadrosaurs (*Procheneosaurus*, as "*Tetragonosaurus*"; *Hypacrosaurus*) and noted differences in the form of osteocyte lacunae and canaliculi in periosteal bone s.s. and osteonic bone. The juvenile bone they figured (their Pl. 1, Fig. 2) is similar to bone from hatchling chickens, though not from a hatchling. De Lapparent (1947) gave figures showing lacunae and canaliculi in bone from *Rhabdodon*, including a drawing (his Fig. 6c) of part of the canalicular network. Isaacs and others (1963) recorded traces of collagen in a Triassic prosauropod, and Pawlicki and others (1966) gave the first transmission EM figures of dinosaurian osteocyte lacunae and collagen fibrils. Later, Pawlicki (1975) introduced the use of scanning EM methods; described and figured "osteocytes" (lacunae and canaliculi) from *Tarbosaurus* (1978), in which he also found mucopolysaccharide traces, concentrated around lacunae and vascular canals (1977), and discussed the physiological significance of dinosaurian lacunae and canaliculi (1984). The writer (Reid, 1981) added a new element to the physiological argument by showing that dinosaurian periosteal bone can follow zonal as well

as fibro-lamellar patterns. A review of dinosaurian bone tissues (Reid, 1984a), covering some of the same ground as the present work, included first records of a crocodilian style of endochondral ossification and of blocks of Haversian bone and intratendinous metaplastic bone related to muscular attachments. A juvenile tissue, resembling that of young birds and fetal mammals, has been identified by J. R. Horner but not yet published. Finally, various observations in the present work are new.

APPENDIX B: FURTHER PROBLEMS

In addition to examples noted already, there are various other cases in which terms used in the present study are used differently in medical literature, in ways that sometimes can be badly confusing if not understood. Conversely, readers with medical backgrounds may find terms used here in unfamiliar ways. This applies especially to usage of the terms primary and secondary, and to some extent to the term Haversian.

1. USAGE OF PRIMARY AND SECONDARY

In the present study, following, for example, Seitz (1907), Gross (1934), Smith (1960), and de Ricqlès (1975), the term primary is applied to bone tissues produced during growth, and the term secondary to those formed in internal reconstruction after preexisting bone has been resorbed. The same terms, however, have also been used in several different ways.

First, the term primary has been used in a structural sense, as meaning simplest. For Foote (1916), for instance, the lamellae of his "lamellar" type of bone were primary structures, since he regarded other structures ("laminae," "Haversian systems") as built from them. In another variation, the 1980 edition of *Gray's Anatomy* (Williams and Warwick, 1980) makes a distinction between circumferential or primary lamellae, and osteonic or secondary lamellae. In both cases, lamellae in bone lining medullary cavities, termed internal circumferential lamellae in traditional medical usage, are classed as primary, although as replacive lining bone they are secondary in the convention followed here. In the second, bone forming primary osteons is classed as secondary, despite being formed during growth without replacement of preexisting bone. But the same text also distinguishes between primary and secondary osteons, so that bone forming primary osteons is classed as both primary and secondary from different viewpoints. In addition, the distinction between primary and secondary osteons is based on age, without reference to whether or not they are replacive. This is because periosteal bone with primary osteons is typically not formed in humans beyond early infancy, after which there is a change to formation of sparsely vascular lamellated bone, said traditionally to form "external circumferential lamellae."

Haversian bone, in contrast, is first formed in infancy and then soon becomes the prevalent type of compact bone.

Second, because the primary osteons of human juvenile fibro-lamellar bone are formed after the periosteal framework, Pritchard (1979) described their formation as secondary ossification, and that of secondary osteons as tertiary ossification. He thus used secondary in two opposite senses in one text, since it refers to replacive bone in secondary osteon but to non-replacive bone in secondary ossification. This practice is not followed by the writer because the framework and osteons of fibro-lamellar tissues are normally formed in histological continuity, in the course of a single growth process, despite the switch from coarsely bundled to finely bundled bone.

2. HAVERSIAN BONE AND "HAVERSIAN SYSTEMS"

Differences between medical treatments of bone and this study are again due in part to the character of human bones, whose pattern is not typical of tetrapods in general. First, because of the prevalence of Haversian bone after infancy, many medical texts until recently have treated compact bone entirely in terms of Haversian bone, without mention of non-Haversian periosteal bone, and with some (e.g., Maximov and Bloom, 1957) describing Haversian systems (secondary osteons) as the structural units of compact bone. They are, of course, only the structural units of Haversian bone. The restriction of lamellated periosteal bone to "external circumferential lamellae" has also led to its being called "surface bone," as was done, for example, by Smith (1960) in the case of lamellae enclosed to form annuli, with some authors (e.g., Fawcett, 1942, p. 274) even treating these lamellae as formed after the Haversian tissue. In fact, the relation of Haversian to periosteal bone is always replacive, unless external bone resorption has locally truncated Haversian systems, which have then been overgrown by new periosteal lamellae.

Second, many older texts make no distinction between primary and secondary osteons, despite their different origins having been described by Tomes and de Morgan (1853), and their having done so also appears to have been widely forgotten. Gross (1934), for instance, made no mention of their paper when introducing the terms primary and secondary osteon, and Ruth (1953) only mentioned it to describe them incorrectly as having introduced the term Haversian system. After describing the process of resorption and redeposition (1953, p. 110–112) now called Haversian reconstruction (or replacement, or substitution) and the general structure of Haversian bone (p. 112–114), they also described a juvenile condition (p. 114–115) in which periosteal outgrowths, termed undulating laminae, united enclosing spaces that became "the seats of Haversian systems." This is plainly a description of the growth of juve-

nile fibro-lamellar bone with primary osteons. But, while pointing out such bone as different from adult Haversian bone (p. 114), they still called its osteons Haversian systems; this practice has persisted until recently, with restriction of the term to secondary osteons mostly following the work of Enlow and Brown (1956), Currey (1960), and Smith (1960). The terms atypical and typical Haversian system are also sometimes still used in place of primary and secondary osteon (see, e.g., Williams and Warwick, 1980).

Third, the modes of origin of the two types of osteons have also sometimes been confused. Ham and Cormack (1979, p. 438–439), for instance, treated osteons formed during post-juvenile growth as arising in tunnels formed initially as superficial grooves. Perhaps this sometimes happens, but young human bones sectioned by the writer show only typical internal reconstruction, with resorption spaces and secondary osteons first appearing within juvenile fibro-lamellar bone. The normal mode of origin of typical "Haversian systems" had also then been known for 126 years.

REFERENCES CITED

Albinus, B. B., 1757, not seen: cited from Enlow, D. H., 1962a.

Badi, N. H., 1972, Calcification and ossification of fibrocartilage in the attachment of the patellar ligament in the rat: Journal of Anatomy, v. 112, p. 415–421.

Bakker, R. T., 1972, Anatomical and ecological evidence of endothermy in dinosaurs: Nature, v. 238, p. 81–85.

Bakker, R. T., 1986, The dinosaur heresies: New theories unlocking the mystery of the dinosaurs and their extinction: New York, William Morrow, 482 p.

Barreto, C., Albrecht, R. M., Bjorling, D. E., Horner, J. R., and Wilsman, N. J., 1993, Evidence of the growth plate and the growth of long bones in juvenile dinosaurs: Science, v. 262, p. 2020–2023.

Biedermann, W., 1913, Physiologie der Stütz- und Skelettsubstanzen, XI, Das Knochengewebe, in Winterstein, H., ed., Handbuch der vergleichende Physiologie: Gustav Fischer Verlag Jena, p. 1085–1188.

Bouvier, M., 1977, Dinosaur Haversian bone and endothermy: Evolution, v. 31, p. 449–450.

Broili, F., 1922, Über den feineren Bau der "Verknöcherten Sehnen" (verknöcherten Muskeln) von *Trachadon*: Anatomischer Anzeiger, v. 55, p. 465–475.

Buffrenil, V. de, 1982, Données préliminaire sur la présence de lignes d'arrêt de croissance pèriostique dans la mandibule du marsouin commun, *Phocoena phocoena* (L.), et leur utilisation comme indicateur de l'âge: Journal canadien de Zoologie, v. 60, p. 2557–2567.

Buffrenil, V. de, Farlow, J. O. and Ricqlès, A. J. de, 1986, Growth and function of *Stegosaurus* plates: Evidence from bone histology: Paleobiology, v. 12, p. 459–473.

Buffrenil, V. de, Ricqlès, A. J. de, Ray, C. E., and Domning, D. P., 1990, Bone histology of the ribs of the Archaeocetes: Journal of Vertebrate Paleontology, v. 10, p. 455–466.

Campbell, J. G., 1966, A dinosaur bone lesion resembling avian osteoporosis with some remarks on the mode of development of the lesions: Journal of the Royal Microscopical Society, v. 85, p. 163–174.

Chinsamy, A., 1990, Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda): Palaeontologia Africana, v. 27, p. 77–82.

Coulson, R. A., 1984, How metabolic rate and anaerobic glycolysis determine the habits of reptiles, *in* Ferguson, M. W. J., ed., The structure, development and evolution of reptiles: Zoological Society of London Symposia 52: London, Academic Press, p. 425–441.

Coulson, R. A., and Hernandez, T., 1983, Alligator metabolism: Studies on chemical reactions in vivo: Comparative Biochemistry and Physiology, v. 74, p. i–iii, 1–182.

Currey, J. D., 1960, Differences in the blood-supply of bone of different histological types: Quarterly Journal of Microscopical Science, v. 101, p. 351–370.

Currey, J. D., 1962, The histology of the bone of a prosauropod dinosaur: Palaeontology, v. 5, p. 238–246.

Deutsch, C., and Purkinje, 1834, not seen: cited from Tomes and de Morgan, 1853, and Enlow, 1962a.

Enlow, D. H., 1962a, Functions of the Haversian system: American Journal of Anatomy, v. 110, p. 268–306.

Enlow, D. H., 1962b, A study of the post-natal growth and remodelling of bone: American Journal of Anatomy, v. 110, p. 79–102.

Enlow, D. H., 1969, The bone of reptiles, *in* Gans, C., and Bellairs, A. d'A., eds., Biology of the Reptilia: London and New York, Academic Press, v. 1, p. 45–80.

Enlow, D. H., and Brown, S. O., 1956, A comparative histological study of fossil and recent bone tissue, Part I: Texas Journal of Science, v. 8, p. 405–443.

Enlow, D. H., and Brown, S. O., 1957, A comparative histological study of fossil and Recent bone tissue, Part II: Texas Journal of Science, v. 9, p. 186–214.

Enlow, D. H., and Brown, S. O., 1958, A comparative histological study of fossil and Recent bone tissues, Part III: Texas Journal of Science, v. 10, p. 187–230.

Farlow, J. O., 1987, Speculations about the diet and digestive physiology of herbivorous dinosaurs: Paleobiology, v. 13, p. 60–72.

Fawcett, D. W., 1942, The amedullary bones of the Florida manatee (*Trichechus latirostris*): American Journal of Anatomy, v. 71, p. 271–303.

Ferguson, M. W. J., 1984, Craniofacial development in *Alligator mississipiensis*, *in* Ferguson, M. W. J., ed., The structure, development and evolution of reptiles: Zoological Society of London Symposia 52: London, Academic Press, p. 223–273.

Foote, J. S., 1916, A contribution to the comparative histology of the femur: Smithsonian Contributions to Knowledge, v. 35, p. 1–242.

Gross, W., 1934, Die Typen den mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien: Zeitschrift für Anatomie, v. 103, p. 731–764.

Haines, R. W., 1938, The primitive form of epiphysis in the long bones of tetrapods: Journal of Anatomy, v. 72, p. 323–343.

Haines, R. W., 1942, The evolution of epiphyses and of endochondral bone: Biological Reviews, v. 17, p. 267–292.

Haines, R. W., 1969, Epiphyses and Sesamoids, *in* Gans, C., and Bellairs, A. d'A., eds., Biology of the Reptilia: London and New York, Academic Press, v. 1, p. 81–115.

Haines, R. W., and Mohouiddin, A., 1968, Metaplastic bone: Journal of Anatomy, v. 103, p. 527–538.

Hall, B. K., 1984, Developmental processes underlying the evolution of cartilage and bone, *in* Ferguson, M. W. J., ed., The structure, development and evolution of reptiles: Zoological Society of London Symposia 52: London, Academic Press, p. 155–176.

Ham, A. W., and Cormack, D. H., 1979, Histology (8th ed.): Philadelphia, Lippincott, 966 p.

Hasse, C., 1878, Die fossilen Wirbel, Morphologische Studien, Die Histologie fossiler Reptilwirbeln: Morphologische Jahrbuch, v. 4, p. 480–502.

Havers, C., 1691, Osteologia Nova: London, Samuel Smith, 294 p.

Hotton, N., 1980, An alternative to dinosaur endothermy: The happy wanderers, *in* Thomas, R. D. K., and Olson, E. D., eds., A cold look at the warm-blooded dinosaurs: American Association for the Advancement of Science Selected Symposium 28: Boulder, Colorado, Westview Press, p. 311–350.

Isaacs, W. A., Little, K., Currey, J. D., and Tarlo, L. B. J., 1963, Collagen and a cellulose-like substance in fossil dentine and bone: Nature, v. 197, p. 192.

Janensch, W., 1947, Pneumatizität bei Wirbeln von Sauropoden und anderen Saurischiern: Palaeontographica, Supplement v. 7, p. 1–25.

Joanen, T., and McNeese, L., 1976, Culture of immature American alligators in controlled environmental chambers: Proceedings of the Annual Meeting of the World Maricultural Society, v. 7, p. 201–211.

Kemp, T. S., 1982, Mammal-like reptiles and the origin of mammals: London and New York, Academic Press, 363 p.

Kiprijanoff, A., 1881, Studien über die fossilen Reptilien Russlands: Mémoires de l'Acadèmie Impèriale des Sciences de St Petersbourg, ser. 7, v. 28, p. 97–103.

Kiprijanoff, A., 1882, Studien über die fossilen Reptilien Russlands: Mémoires de l'Acadèmie Impèriale des Sciences de St Petersbourg, ser. 7, v. 30, p. 52–55.

Klevezal, C. A., and Kleinenberg, S. E., 1969, Age determination of mammals from layered structures in teeth and bone: Jerusalem, Israel Program for Scientific Translations, 128 p.

Kölliker, A. von, 1889, Handbuch der Gewebelehre des Menschen: Leipzig, Engelmann, 409 p.

Landauer, W., 1931, Untersuchungen über das Kruperhuhn, II: Morphologie und Histologie des Skolets, imbesonders des skelets der langen Extremitätenknochen: Zeitschrift für mikroskopische–anatomische Forschung, v. 25, p. 115–141.

Lapparent, A. F. de, 1947, Les Dinosauriens du Crétacé supérieur du Midi de la France: Mémoirs de la Société géologique de France (Nouvelle Série), v. 56, p. 1–54.

Lydekker, R., 1889, Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), Part II: London, British Museum (Natural History), i–vi and 1–307.

Madsen, J. H. Jr., 1976, *Allosaurus fragilis*: A revised osteology: Utah Geological and Mineral Survey Bulletin, v. 109, p. i–xii, 1–163.

Mantell, G. A., 1850, on the *Pelorosaurus*, an undescribed gigantic terrestrial reptile, whose remains are associated with those of *Iguanodon* and other saurians in the strata of Tilgate Forest, Sussex: London, Philosophical Transactions of the Royal Society, v. 140, p. 379–390.

Martin, L. D., and Rothschild, B. M., 1989, Paleopathology and diving mosasaurs: American Scientist, v. 77, p. 460–467.

Maximov, A. A., and Bloom, W., 1957, A textbook of histology: Philadelphia, Saunders, 600 p.

McNab, B. K., 1978, The evolution of endothermy in the phylogeny of mammals: American Naturalist, v. 112, p. 1–21.

McNab, B. K., and Auffenberg, W., 1976, The effect of large body size on the temperature regulation of the Komodo monitor, *Varanus komodoensis*: Comparative Biochemistry and Physiology, v. 55A, p. 345–350.

Moodie, R. L., 1908, Reptilian epiphyses: American Journal of Anatomy, v. 7, p. 444–467.

Moodie, R. L., 1923, Paleopathology: Urbana, Illinois, University of Illinois Press, 567 p.

Moodie, R. L., 1928, The histological nature of ossified tendons found in dinosaurs: American Museum Novitates, no. 311, p. 1–15.

Moss, M. L., 1969, Comparative histology of dermal sclerifications in reptiles: Acta Anatomica, v. 73, p. 510–533.

Neiburger, R. J., 1988, Syphilis in a Pleistocene bear ? : Nature, v. 333, p. 603.

Nopcsa, F., 1917, Über Dinosaurier. 2. Die Riesenformen unter den Dinosauriern: Centralblatt fur Mineralogie, 1917, p. 332–348.

Nopcsa, F., 1923, Vorläufige Notiz über die Pachyostose und Osteosklerose einiger mariner Wirbeltiere: Anatomischer Anzeiger, v. 56, p. 353–359.

Nopcsa, F., and Heidsieck, E., 1933, On the histology of the ribs in immature and half grown trachodont dinosaurs: Proceedings of the Zoological Society of London, p. 221–227.

Ostrom, J. H., 1969, Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana: Peabody Museum of Natural History Bulletin, v. 30, p. 1–165.

Ostrom, J. H., 1980, The evidence for endothermy in dinosaurs, *in* Thomas, R. D. K., and Olson, E. C., eds., A cold look at the warm-blooded dinosaurs: American Association for the Advancement of Science Selected Symposium 28: Boulder, Colorado, Westview Press, p. 15–54.

Paul, G. S., 1991, The many myths, some old, some new, of dinosaurology: Modern Geology, v. 16, p. 69–99.

Pawlicki, R., 1975, Studies of the fossil dinosaur bone in the Scanning Electron Microscope: Zeitschrift fur mikroskopische und anatomische Forschung, v. 89, p. 393–398.

Pawlicki, R., 1977, Histochemical reactions for mucopolysaccarides in the dinosaur bone: Studies on Epon- and methylacrylate embedded semi-thin sections as well as isolated osteocytes and ground sections of bone: Acta Histochemica, v. 58, p. 75–78.

Pawlicki, R., 1978, Morphological differentiation of the fossil dinosaur bone cells: Light, transmission electron-, and scanning electron-microscope studies: Acta Anatomica, v. 100, p. 411–418.

Pawlicki, R., 1984, Metabolic pathways of the fossil dinosaur bone, IV: Modes of linkage between a variety of nexuses of osteocyte processes: Folia Histochemica et Cytobiologica, v. 22, p. 99–104.

Pawlicki, R., Korbel, A., and Kubiak, H., 1966, Cells, collagen fibrils, and vessels in dinosaur bone: Nature, v. 211, p. 655–657.

Pritchard, J. J., 1956, General anatomy and physiology of bone, *in* Bourne, G. H., ed., The biochemistry and physiology of bone: New York, Academic Press, p. 1–25.

Pritchard, J. J., 1972, General histology of bone, *in* Bourne, G. H., ed., The biochemistry and physiology of bone (2nd. ed.): New York, Academic Press, p. 1–20.

Pritchard, J. J., 1979, Bones: Burlington, North Carolina, Carolina Biological Supply Company, 16 p.

Quekett, J., 1849, On the intimate structure of bone, as comprising the skeleton in the four great classes of animals, viz, Mammals, Birds, Reptiles and Fishes, with some remarks on the great value of the knowledge of such structure in determining the affinities of minute fragments of organic remains: Transactions of the Microscopical Society of London, v. 2, p. 46–58.

Regal, P. J., and Gans, C., 1980, The revolution in thermal physiology, *in* Thomas, D. K., and Olson, E. C., eds., A cold look at the warm-blooded dinosaurs: American Association for the Advancement of Science Selected Symposium 28: Boulder, Colorado, Westview Press, p. 167–188.

Reid, R. E. H., 1981, Lamellar-zonal bone with zones and annuli in the pelvis of a sauropod dinosaur: Nature, v. 292, p. 49–51.

Reid, R. E. H., 1984a, The histology of dinosaurian bone, and its possible bearing on dinosaurian physiology, *in* Ferguson, M. W. J., ed., The structure, development and evolution of reptiles: Zoological Society of London Symposia 52: London, Academic Press, p. 629–663.

Reid, R. E. H., 1984b, Primary bone and dinosaurian physiology: Geological Magazine, v. 121, p. 589–598.

Reid, R. E. H., 1987, Bone and dinosaurian "endothermy": Modern Geology, v. 11, p. 133–154.

Reid, R. E. H., 1990, Zonal "growth rings" in dinosaurs: Modern Geology, v. 15, p. 19–48.

Reid, R. E. H., 1993, Apparent zonation and slowed late growth in a small Cretaceous theropod: Modern Geology, v. 18, p. 391–406.

Ricqlès, A. J. de, 1974, Evolution of endothermy: Histological evidence: Evolutionary Theory, v. 1, p. 51–80.

Ricqlès, A. J. de, 1975, Recherches paléohistologiques sur les os longs des tétrapodes, VII, sur la classification, la signification fonctionelle et l'histoire des tissus osseux des tétrapodes, Première partie: Structures: Annales de Paléontologie (Vertébrés), v. 61, p. 49–129.

Ricqlès, A. J. de, 1976, On bone histology of fossil and living reptiles, with comments on its functional and evolutionary significance, *in* Bellairs, A. d'A., and Cox, C. B., eds., Morphology and biology of reptiles: Linnean Society of London, Symposium Series 3: London, Academic Press, p. 123–150.

Ricqlès, A. J. de, 1980, Tissue structure of dinosaur bone: Functional significance and possible relationship to dinosaur physiology, *in* Thomas, R. D. K., and Olson, E. C., eds., A cold look at the warm-blooded dinosaurs: American Association for the Advancememt of Science Selected Symposium 28: Boulder, Colorado, Westview Press, p. 103–139.

Ricqlès, A. J. de, 1983, Cyclical growth in the long limb bones of a sauropod dinosaur: Acta Palaeontologia Polonica, v. 18, p. 225–232.

Romer, A. S., 1946, Vertebrate paleontology (2nd ed.): Chicago, Illinois, The University of Chicago Press, 687 p.

Rothschild, B. M., and Turnbull, W., 1987, Treponemal infection in a Pleistocene bear: Nature, v. 329, p. 61–62.

Ruth, E. B., 1953, Bone studies, II: An experimental study of the Haversian-type vascular channels: American Journal of Anatomy, v. 93, p. 429–455.

Seitz, A. L. L., 1907, Vergleichende Studien über den mikroskopischen Knochenbau fossiler und Rezenter Reptilien, und dessen Bedeutung für das Wachstum und Umbildung des Knochengewebes in allegemeinen: Abhandlungen der kaiserlichen Leopold-Carolignischen deutschen Akedemie der Naturforscher: Nova Acta, v. 87, p. 230–370.

Seymour, R. S., 1976, Dinosaurs, endothermy and blood pressure: Nature, v. 262, p. 207–208.

Smith, J. W., 1960, Collagen fibre patterns in mammalian bone: Journal of Anatomy, v. 94, p. 329–344.

Spotila, J. R., Lommen, P. W., Bakken, P. S., and Gates, D. M., 1973, A mathematical model for body temperatures in large reptiles: Implications for dinosaur ecology: American Naturalist, v. 107, p. 391–404.

Swinton, W. E., 1934, The dinosaurs: London, Thomas Murby, 233 p.

Todd, R. B., and Bowman, W., 1846, The physiological anatomy and physiology of man: Philadelphia, Blanchard and Lea, 448 p.

Tomes, J., and de Morgan, C., 1853, Observations on the structure and development of bone: London, Philosophical Transactions of the Royal Society, v. 143, p. 109–139.

Varricchio, D. J., 1993, Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*: Journal of Vertebrate Paleontology, v. 13, p. 99–104.

Weidenreich, F., 1923, Knochenstudien, I Teil, Über Aufbau und Entwicklung des Knochens und den Charakter des Knochengewebes: Zeitschrift für Anatomie und Entwicklungs-geschichte, v. 69, p. 382–466: II Teil, Über Sehnenverknöcherungen und Faktoren der Knochenbildung, p. 558–597.

Weidenreich, F., 1930, Das Knochengewebe, *in* Mollendorff, W. H. W. von, ed., Handbuch der mikroskopischen Anatomie des Menschen: Berlin, Springer-Verlag, v. 2, p. 391–520.

Williams, P. L., and Warwick, R., 1980, Gray's anatomy (36th ed.): Edinburgh, Churchill Livingstone, 1578 p.

Willis, R. A., 1962, The borderland between embryology and pathology: London, Butterworth.

(Note: Due to reorganization of this paper after photographic figures were mounted, text dealing with preservation in Cleveland-Lloyd bones, which Figures 1–5 illustrate, will now appear in a later part.)

Figure 1. Calcified cartilage, preserved at an articular surface, X64. Camptosaurus, *distal end of left humerus; C-LQ 105.*

Figure 2. Calcite filling the spaces between trabeculae in cancellous bone, X32. Ceratosaurus, *distal caudal vertebra; C-LQ 088.*

Figure 3. Finely crystalline gypsum in the medullary cavity of a Camptosaurus *humerus, X32. C-LQ 105.*

Figure 4. Coarser gypsum crystals in a crack through the cortex (compacta) of the same bone, X32.

Figure 5. A lens of chalcedony in the medullary cavity of the same bone, X21.

Figure 6. Osteocyte lacunae and canaliculi, as seen when infilled with dark material (here pyrite), X240. Undescribed carnosaur, rib; Wessex Formation (Wealden, Lower Cretaceous), Isle of Wight, England. None of the Cleveland-Lloyd sections show these features in such detail, due to lack of dark infilling. SM 5309.

Figure 7. A "Haversian system" (= a secondary osteon in cross section), as seen with crossed polarizers, showing the typical fine light and dark banding of lamellar bone, and the "axial cross" seen when it forms concentric structures; X100. Megalosaurus, *femur, OUM J.29753b; Bathonian (Middle Jurassic) near Oxford, England.*

Figure 8. Conspicuous fiber bundles in cancellous metaplastic bone from a dorsal plate of Stegosaurus, *X64; also illustrates a cancellous condition produced by resorption, implied by the truncation of fibers at cancelli. C-LQ 097.*

Figure 9. Fibro-lamellar bone showing the contrast in size and form of osteocyte lacunae in woven bone of the framework (dark trabeculae) and in parallel fibered and lamellar bone of the osteons (lighter bone surrounding vascular canals); X120. Sauropod indet. ("Cetiosaurus"), limb bone, OUM J.29835/p2; Bathonian (Middle Jurassic), near Oxford, England.
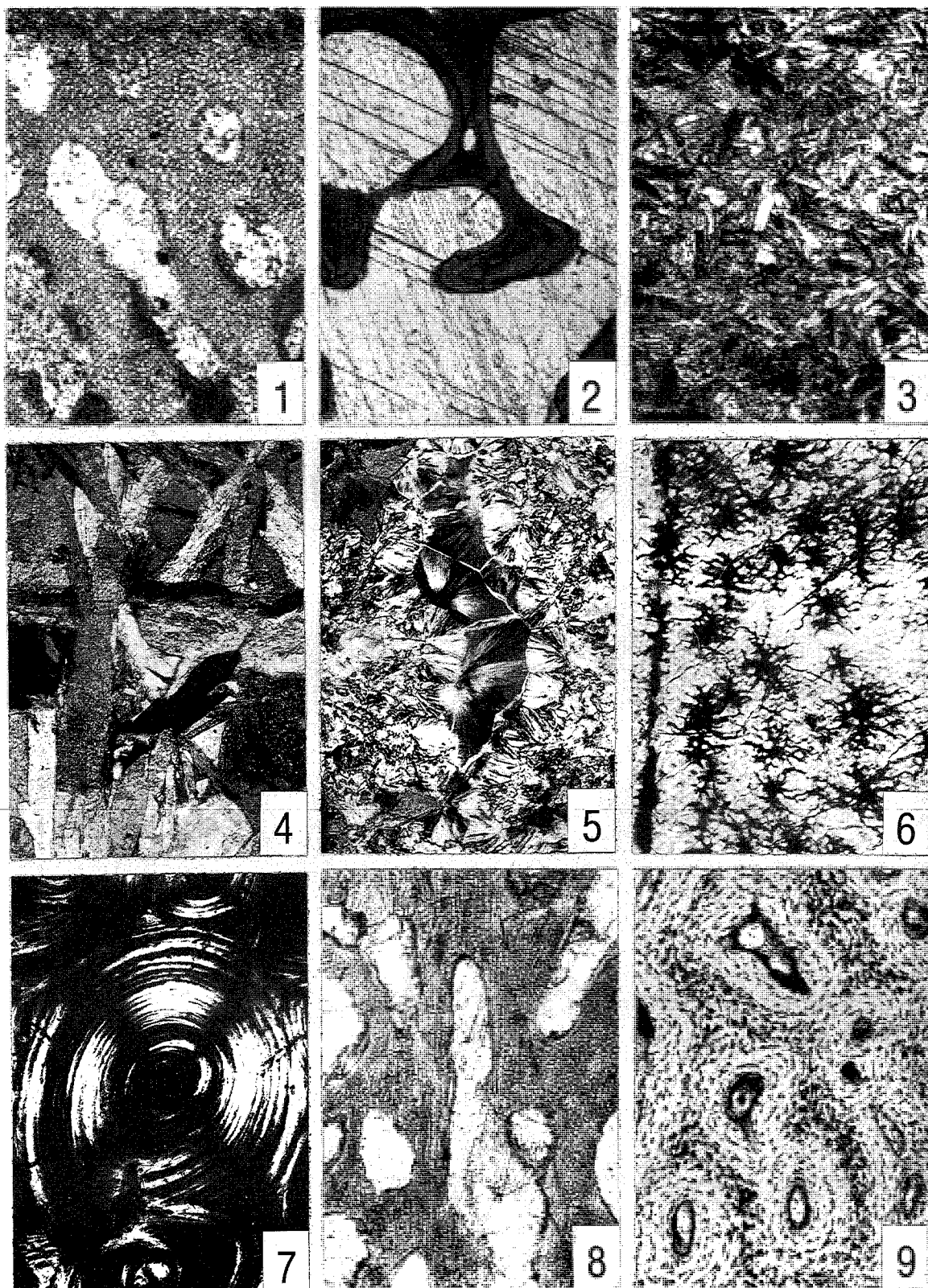
Figure 10. Apparent fibro-lamellar bone, seen in a transverse section of an Allosaurus femur, X64. This tissue resembles laminar fibro-lamellar bone (cf. figs. 31, 32), but lacks a distinct osteon system (see next figure). C-LQ 112.

Figure 11. The same tissue, as seen with crossed polarizers, X64. Some light and dark streaking and banding is seen, but clearly developed osteons are absent (cf. fig. 32). A longitudinal section of the same tissue shows total extinction at minimum transmission.

Figure 12. The same tissue, as seen in tangential section between vascular networks, X64. Osteocyte lacunae are variably oriented, with some aligned around radial vascular canals (Volkmann's canals).

Figure 13. The same area as seen with crossed polarizers, showing the patchy extinction pattern, X64.

Figure 14. Apparent fibro-lamellar bone with parallel cylindrical osteons, from an Allosaurus pubis; X64. Distinct osteons are obvious; but they do not appear to be formed from lamellar bone (see next figure). C-LQ 113.

Figure 15. The same tissue, as seen with crossed polarizers, X64. At minimum transmission, the osteons show total extinction, instead of the pattern that should be seen in lamellar bone (cf. figs. 7 and 30).

Figure 16. A laminar vascular network as seen in tangential section, from the bone shown in Figures 10–13, X64. C-LQ 112.

Figure 17. Avascular bone from an Allosaurus rib, X64. This tissue, developed locally, passes laterally into vascular bone, like that seen in Figure 14. C-LQ 081.

Figure 18. A plexiform vascular network as seen in radial section, X64. Allosaurus, distal caudal vertebra; C-LQ 087.
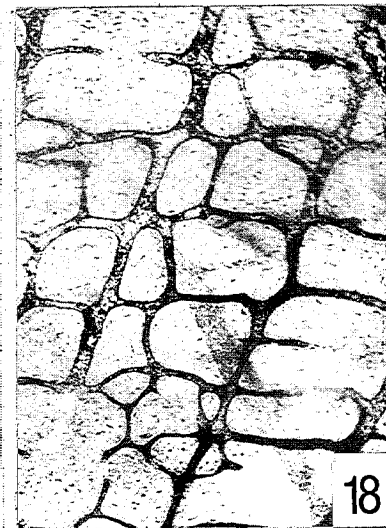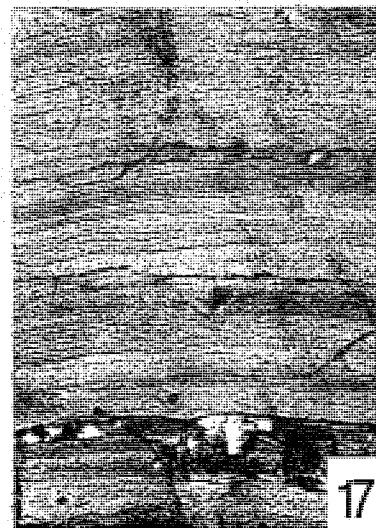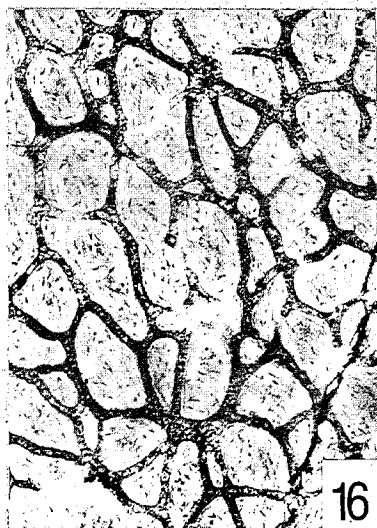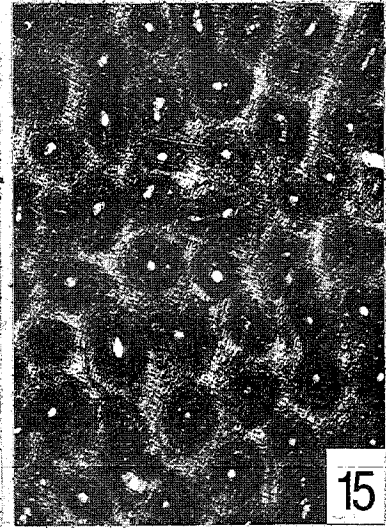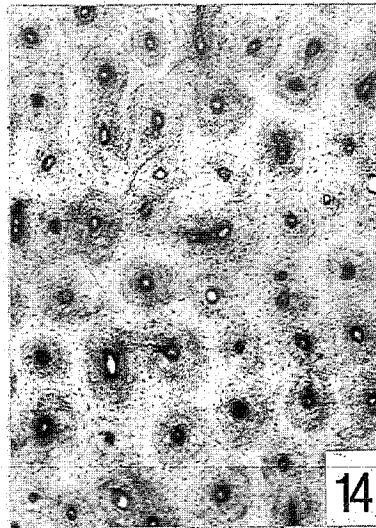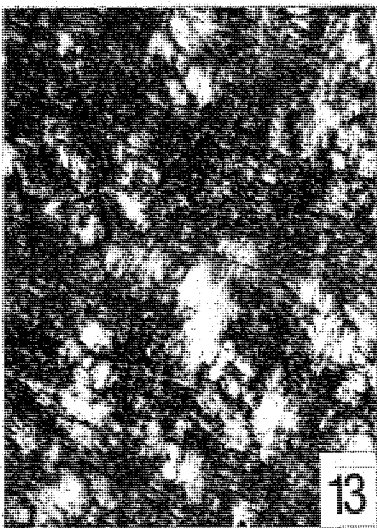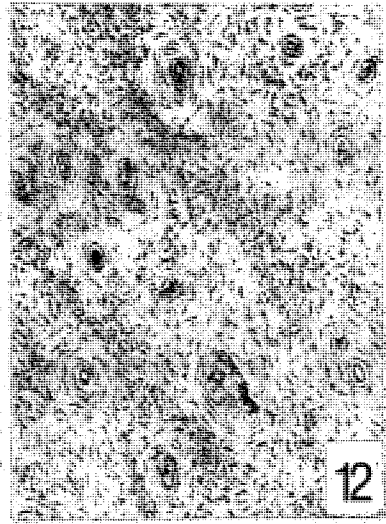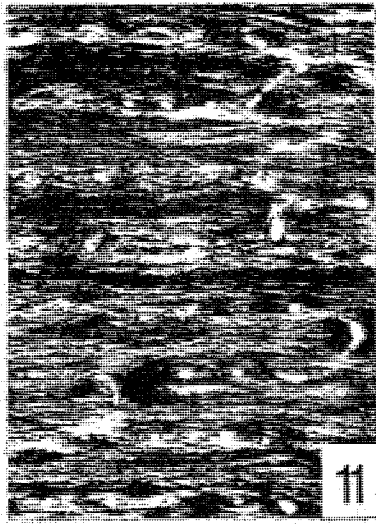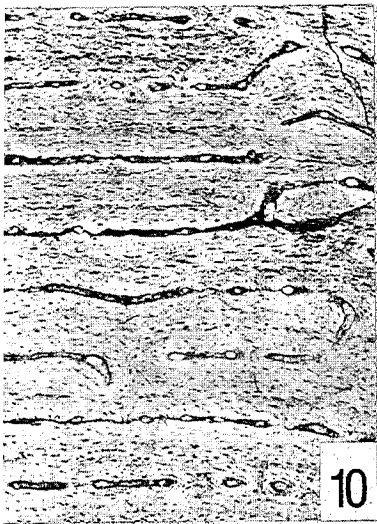
Figure 19. Non-fibrous cement forming clear cementing lines around "Haversian systems" in a Tyrannosaurus *rib, X64. Interstitial remnants of partly resorbed osteons can also be seen. Late Cretaceous, Glasgow, Montana; BM(NH) R.7995.*

Figure 20. Primary compact bone formed entirely from lamellated bone, seen in an Allosaurus *pubis, X64. In the lower part, a few "Haversian systems" have replaced the primary tissue. This example is from the same bone as tissue shown in fig. 14, into which it passes laterally. C-LQ 113.*

Figure 21. Lamellated bone forming annuli between non-lamellated vascular zones, X64. This tissue, developed locally in an Allosaurus *radius, passes laterally into bone in which only the top and bottom annuli persist. C-LQ 109.*

Figure 22. Late formation of lamellated bone (see top part) in a Ceratosaurus *limb bone, in which the compact bone is otherwise non-lamellated; X64. C-LQ 115.*

Figure 23. Zonal bone formed entirely from lamellated tissue, X30. Rhabdodon, *limb bone indet. (? ulna), BM(NH) R.3809; Maastrichtian, Szentpeterfalva, Romania.*

Figure 24. Irregular zonal bone, formed mainly from lamellated tissue, with some Haversian replacement in the lower (older) part, X32. Camarasaurus, *dentary; C-LQ 089.*

Figure 25. Zonal bone formed mainly from non-lamellated tissue, X64. Sauropod indet., rib; C-LQ 084.

Figure 26. Similar zonal bone from a chevron bone of Camarasaurus, *X32. C-LQ 060.*

Figure 27. Zonal bone grading outward (upward) into tissue with closely spaced resting lines, resembling lamellated bone, in an Allosaurus *ungual (manus); X64. C-LQ 077.*
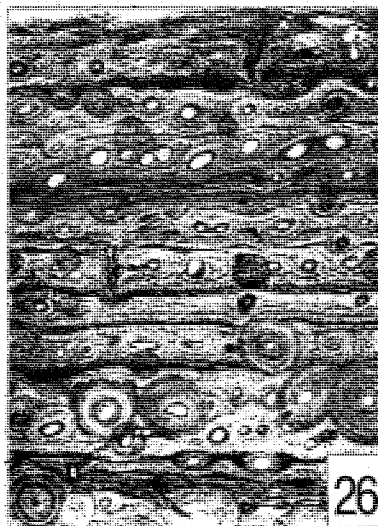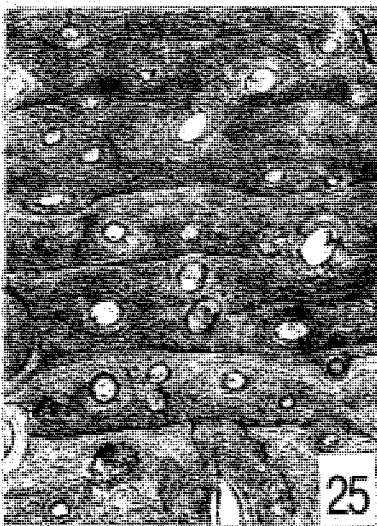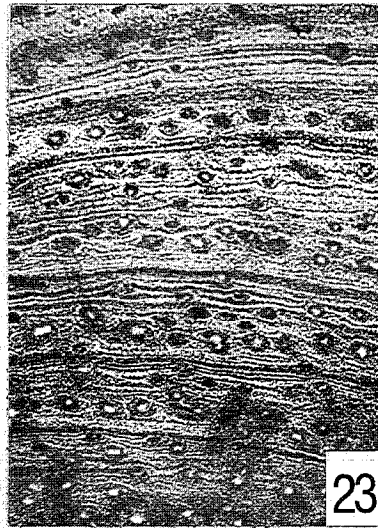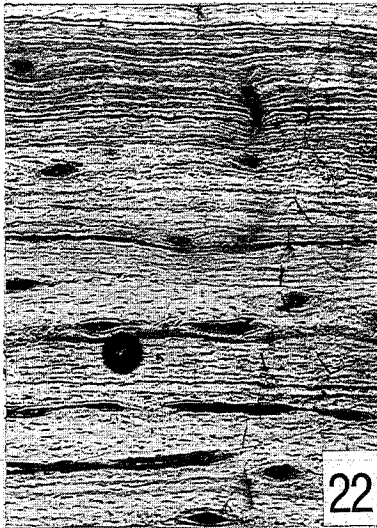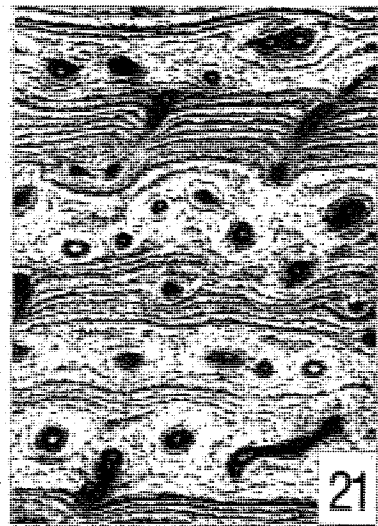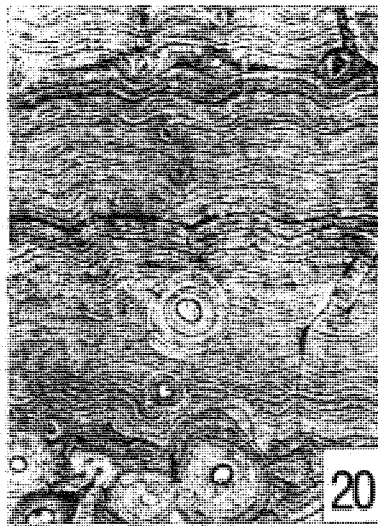
Figure 28. Fibro-lamellar bone with obvious primary osteons, which form the major part of the tissue, X64; see also fig. 9. Sauropod indet., limb bone, OUM J.29835/p2; Bathonian (Middle Jurassic), near Oxford, England.

Figure 29. Fibro-lamellar bone, in which osteons are only seen clearly when viewed with crossed polarizers; X75. Tyrannosaurus, rib, BM(NH) R.7995; late Cretaceous, Glasgow, Montana.

Figure 30. The same tissue as seen with crossed polarizers, X75. Each osteon has an inner part formed from lamellar bone, marked by an "axial cross," and a dark outer part formed from parallel-fibered bone. The netted lines running through the framework bone between osteons are optical extinction lines, which change position as the stage is rotated.

Figure 31. Regular laminar fibro-lamellar bone from a tibia of Iguanodon, X64. Author's collection; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England.

Figure 32. The same tissue as seen with crossed polarizers, showing more or less regular alternations of light lamellar and dark non-lamellar bone, and several boudin-like "pinches" between osteons; X64. The tissue also lacks the "bright lines" seen between osteon layers in mammalian laminar bone.

Figure 33. Accretionary bone (top) with resting lines, seen in an Iguanodon chevron bone; X64. BM(NH) R.5331; Wealden (Lower Cretaceous), England.

Figure 34. Haversian bone, as preserved in most Cleveland-Lloyd material, X64. Differential staining reflects original concentric structure, but few osteocyte lacunae are seen. Camarasaurus, dentary; C-LQ 089.

Figure 35. Haversian bone from an Iguanodon femur, showing osteocyte lacunae arranged concentrically around the central canal, X75. Author's collection; Wessex Formation (Wealden, Lower Cretaceous), Isle of Wight, England.

Figure 36. The start of Haversian reconstruction in an Allosaurus lachrymal, showing unreplaced primary bone (top), resorption spaces, and partly and fully formed secondary osteons ("Haversian systems"); X32. Primary bone is also still present interstitially in the lower parts of the figure. C-LQ 051.
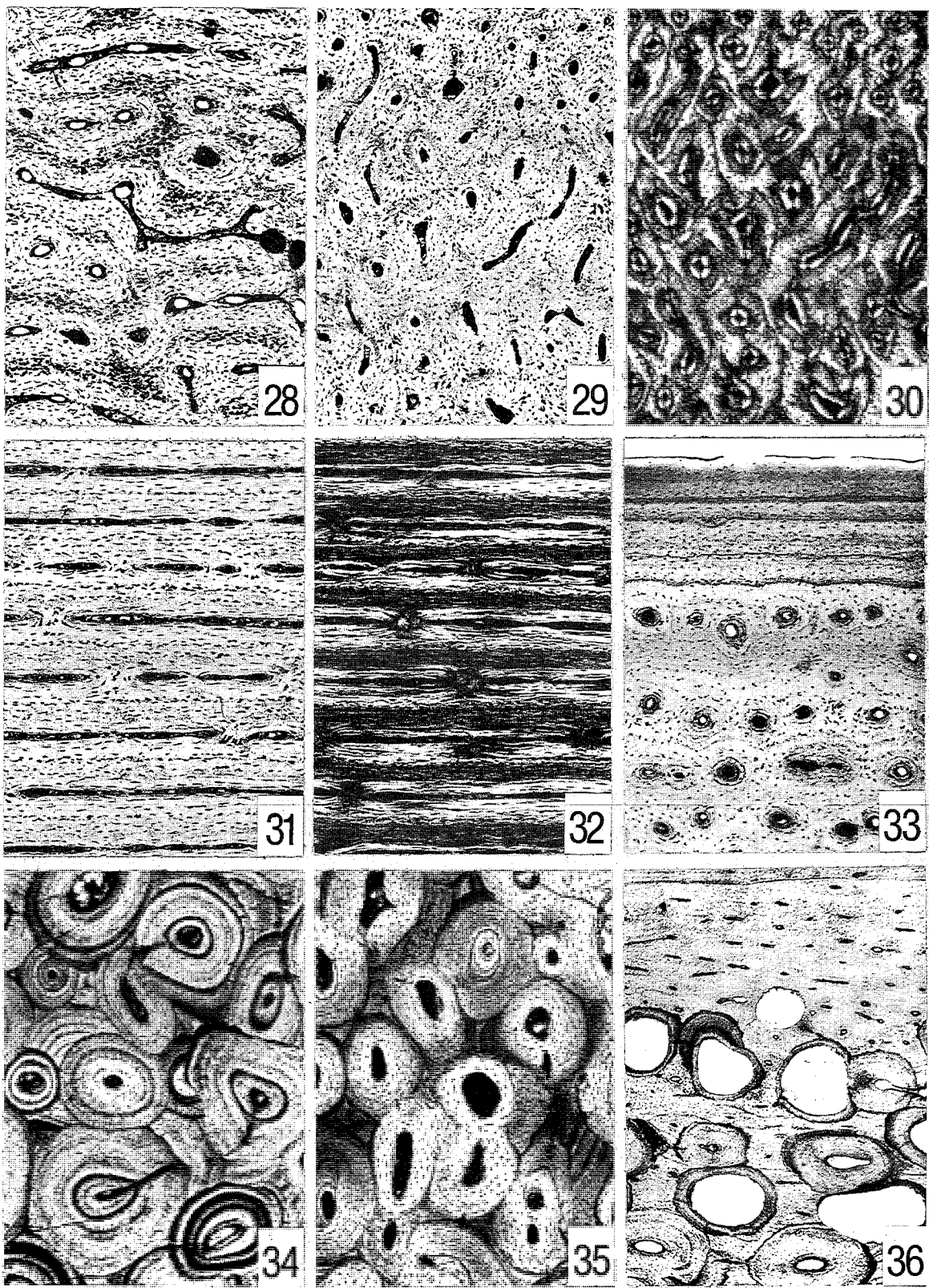
Figure 37. Longitudinal section of the head of an Allosaurus *femur, X3.5, showing endochondral trabeculae that extend to the articular surface. This pattern is usual in dinosaurian limb bones, which lacked the separately ossified bony epiphyses seen in mammals. C-LQ 111.*

Figure 38. Calcified hypertrophic cartilage from the articular surface of the same bone, X160, showing the characteristic rounded form and dense packing of the chondrocyte lacunae.

Figure 39. Endochondral ossification in the same bone, X64, showing dark endochondral bone forming on the walls of cavities excavated in calcified cartilage by marrow cells.

Figure 40. Cartilage "islands" in endochondral trabeculae in the same bone, X100.

Figure 41. Endochondral ossification in a humerus of Camptosaurus, *X64. The pattern is essentially the same as in* Allosaurus, *despite their wide taxonomic separation. C-LQ 105.*

Figure 42. A cartilage "island" in the same bone, X160, with bone infilling some chondrocyte lacunae.

Figure 43. Replacement of primary compact bone by secondary cancellous bone in an Allosaurus *ischium, X28. Thin-walled tubular osteons have been formed within large resorption spaces, and can also be seen to intergrade with smaller compact "Haversian systems." C-LQ 066.*

Figure 44. Secondary cancellous bone as seen with crossed polarizers, X64, showing brecciate structure resulting from continued reconstruction in the same bone.

Figure 45. Secondary cancellous bone replacing compact Haversian bone, X32. Allosaurus, pubis; C-LQ 113.
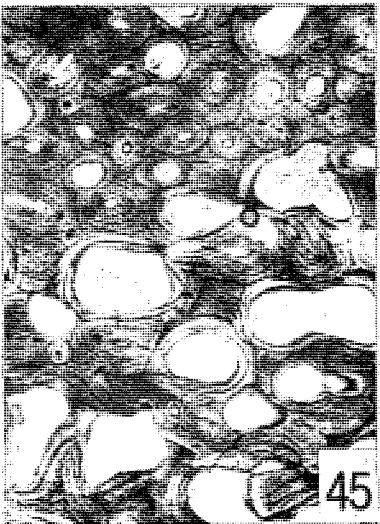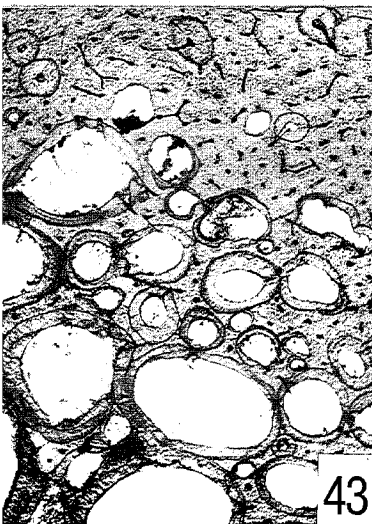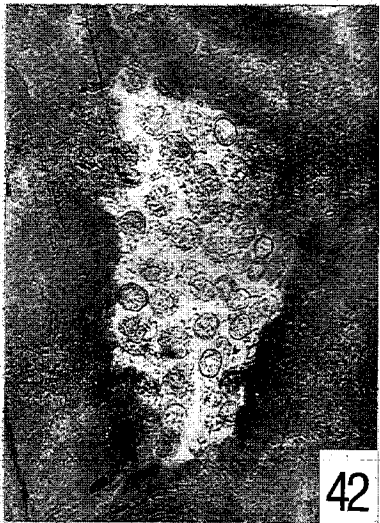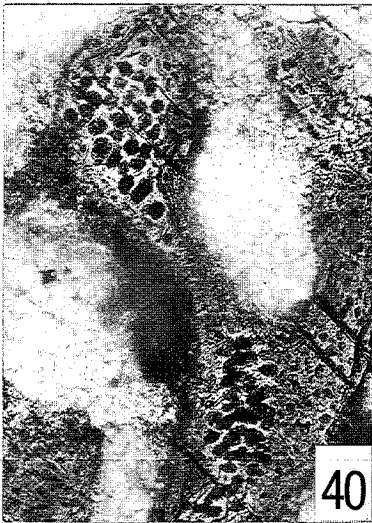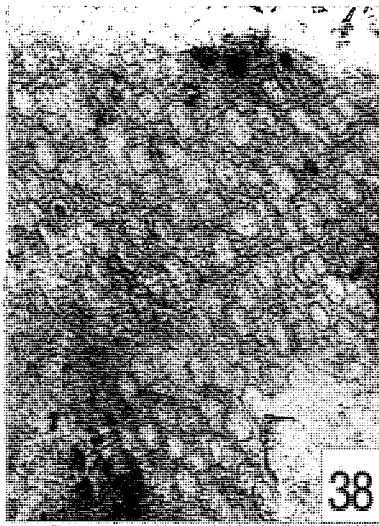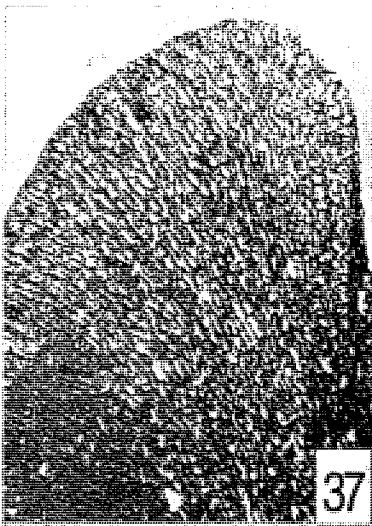
Figure 46. Compacted coarse cancellous bone, formed under an external resorption surface seen at top, X21. Allosaurus, distal part of pubis; C-LQ 090. The tissue compacted here is secondary cancellous bone; but similar compaction of primary endochondral bone can be seen in the lower parts of Figure 37.

Figure 47. The same tissue as in Figure 46, as seen with crossed polarizers; X21.

Figure 48. The effect of metaphyseal remodeling, seen in the distal part of an Allosaurus femur; X21. Primary compact bone, seen in the upper part, has overgrown compacted cancellous bone, formed under a resorption surface that now forms an internal reversal line. Some "Haversian systems" have also been formed in the compacted bone. C-LQ 092.

Figure 49. Endosteal lining bone, seen as a finely layered tissue at left, lining the medullary cavity of a limb bone; X80. Centrifugal resorption of vascular periosteal bone, seen at center and right, has been followed by centripetal growth of the endosteal tissue, with the limit of medullary resorption now forming a reversal line. Theropod indet., radius; C-LQ 130.

Figure 50. Part of a core section from a cavernous Allosaurus cervical, X5. Under an articular surface, seen at the top, compacted endochondral bone with several transverse bands of dense compaction passes down (= posteriorly) into dense bone forming the core of an internal plate between two large resorption spaces. Cleveland-Lloyd collection; no number.

Figure 51. Calcified cartilage and rapidly compacted endochondral bone, from the articular surface seen in Figure 50; X64.

Figure 52. Compacted cancellous bone forming coring bone between layers of lamellated lining bone (top, bottom), as seen with crossed polarizers in a cavernous sauropod vertebra; X64. Genus indet.; author's collection; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England.

Figure 53. "Haversian systems" in the core of an internal (intercavernous) plate, formed otherwise from lining bone with numerous resting lines; X32. Sauropod indet., cavernous vertebra; author's collection; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England.

Figure 54. Layered lining bone, showing a plumose arrangement of elongate osteocyte lacunae in the innermost layer (at right); X80. Sauropod indet., cavernous vertebra; author's collection; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England.
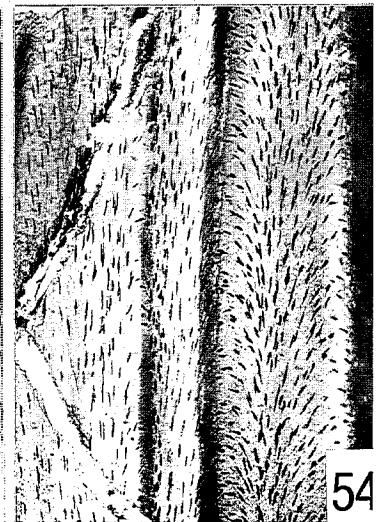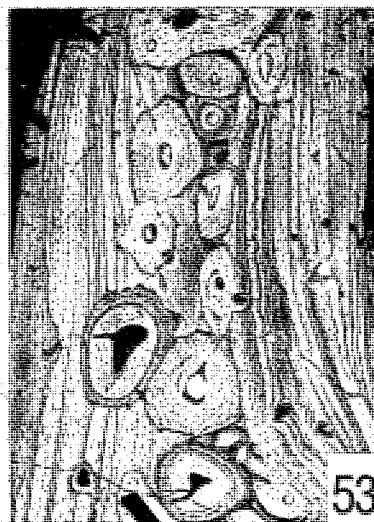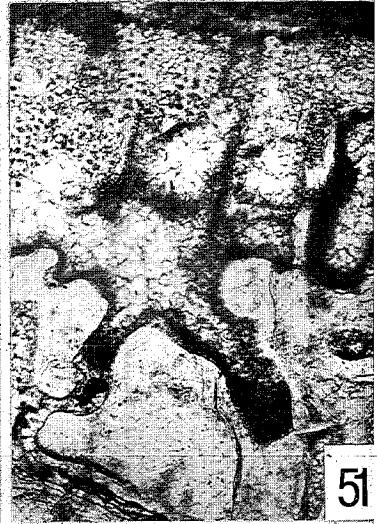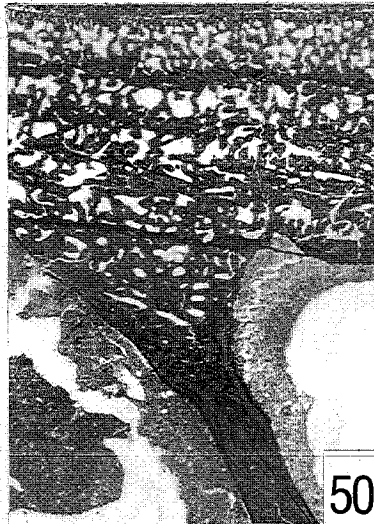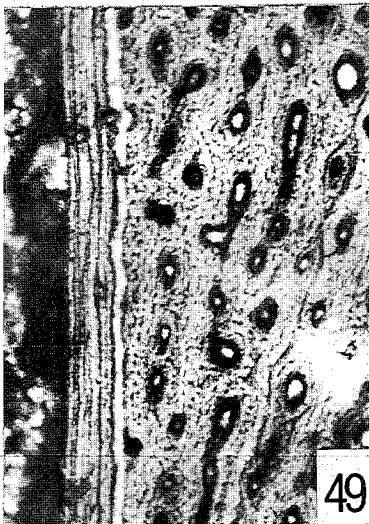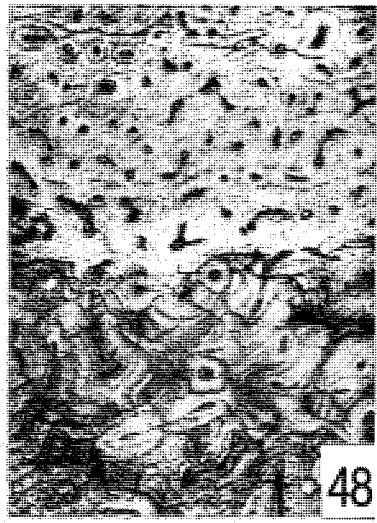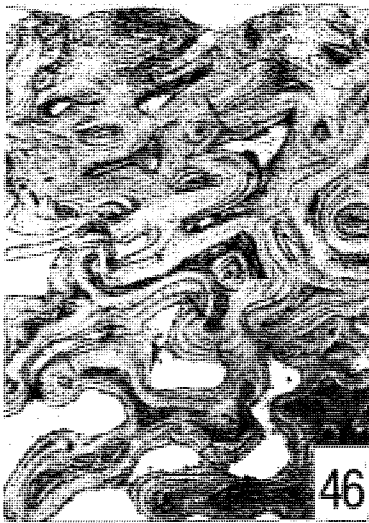
Figure 55. Cancellous alveolar bone (center and right) attached to the wall of the tooth-bearing groove in a Camarasaurus dentary, X32. The junction with Haversian bone of the dentary, seen at left, is a reversal (resorption) line, identified by cutting across several "Haversian systems." C-LQ 089.

Figure 56. Cancellous alveolar bone from the same dentary, showing its non-lamellar character; X32.

Figure 57. Intratendinous metaplastic bone, formed by ossification of the interspinous ligament in a sauropod, X64. The fiber bundles aligned vertically in the figure are horizontal and longitudinal in the specimen. Vague oblique transverse banding reflects variations in mineralization during growth. Haplocanthosaurus (?), neural spine of a mid caudal, horizontal section; C-LQ 110.

Figure 58. The same tissue as seen with crossed polarizers, showing differential mineral alteration along the lines of the fiber bundles; X64.

Figure 59. A tissue suggesting ossified fibro-cartilage, seen in the floor of the neural canal in an Allosaurus caudal, X80. C-LQ 087.

Figure 60. Tissue suggesting ossified fibro-cartilage, seen on both sides of the neuro-central suture in an Iguanodon caudal, and partly replaced by "Haversian systems"; X80. Author's collection; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England.

Figure 61. "Sharpey's fibers" in zonal bone from an Allosaurus phalange, X64. C-LQ 078.

Figure 62. Longitudinal section of bone from the outer part (see text) of an "ossified tendon" of Iguanodon, showing its fibrous character and elongate osteocyte lacunae; X120. Wealden (Lower Cretaceous), Isle of Wight, England; Sandown Museum, Isle of Wight (no number).

Figure 63. Transverse section of the same tissue, showing vascular canals, small primary osteons, and a canalicular network linking osteocyte lacunae; X120. These features show that this "ossified tendon" was not an ossified tendon in the literal sense.
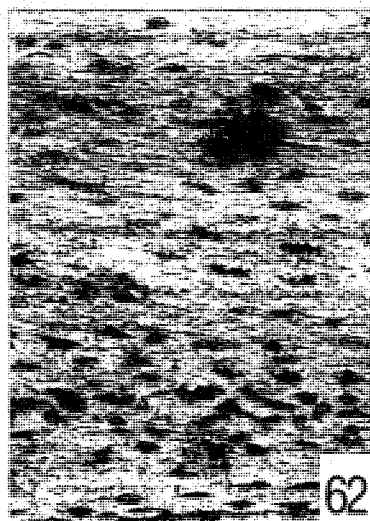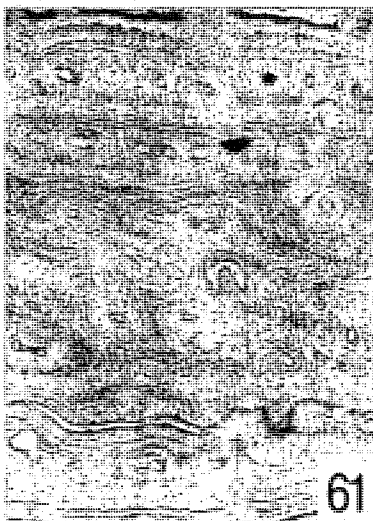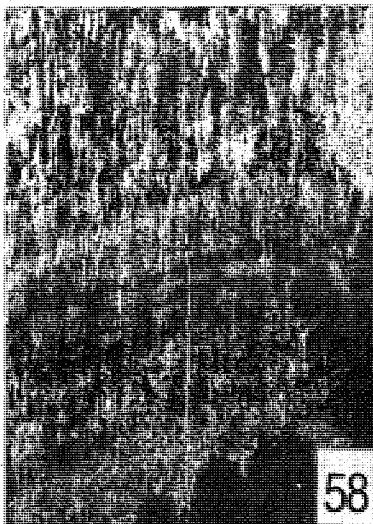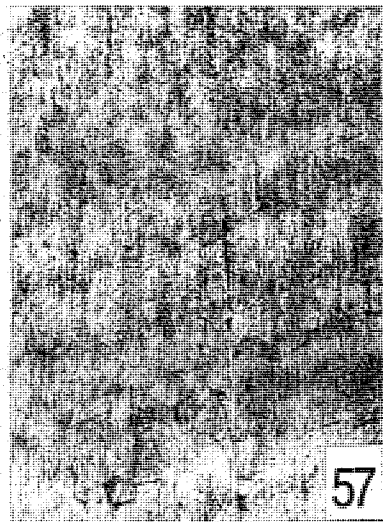
Figure 64. Radial section of a small dermal ossicle, supposedly of Stegosaurus, *X12. The ossicle is built mainly from tissue of the type seen in the next figure, but there are also scattered secondary osteons that run in various directions. C-LQ 128.*

Figure 65. Tangential section of the primary tissue of the same ossicle, as seen with crossed polarizers, showing interwoven bundles of densely fibrous bone; X32. The tissue has a similar appearance in radial sections.

Figure 66. Bone from the external part of an ossicle ascribed to Ceratosaurus, *showing the vascular internal tissue (see text), and an external crust of irregularly lamellated bone; X32. At higher magnifications, the internal tissue shows a finely fibrous texture, with fibers arranged radially except near the surface. C-LQ 100.*

Figure 67. Zonal bone from the crest of a dorsal plate of Stegosaurus, *undergoing replacement by "Haversian systems"; X32. C-LQ 085.*

Figure 68. Osteoporotic bone from an Apatosaurus *scapula, in which primary canals have been enlarged by internal bone resorption, and primary bone has largely been replaced by incompletely formed "Haversian systems"; X2.5. C-LQ 114.*

Figure 69. Abnormal secondary osteons with irregularly branching cross sections, developed along stress cracks in compact bone; X64. Dinosaur *indet. (? small theropod), limb bone; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England; author's collection.*

Figure 70. Splinter of periosteal bone (top left) imbedded in irregular cancellous bone of a massive exostosis, developed on a broken Allosaurus *rib; X32. The splinter is undergoing replacement along its lower edge. C-LQ 106.*

Figure 71. Reactive cancellous bone with radial trabeculae growing out from the surface of a dinosaurian limb bone; X32. Periosteal bone seen in the lower half of the figure is undergoing cavitation at bottom left. These features were attributed to periosteal sarcoma by Swinton (1934), but compared with the effects of avian (viral) osteopetrosis by Campbell (1966). Dinosaur indet. (? Mochlodon or Orthomerus); B.M.(N.H.) R.5505.

Figure 72. Pathological bone from a cavernous sauropod vertebra, in which cavernous spaces are infilled by a cancellous reactive growth (thin strips at top and bottom), and an intercavernous plate (middle two thirds, running transversely) has been extensively disrupted by irregular internal cavitation; X32. Sauropod indet.; author's collection; Wessex Formation (Lower Cretaceous, Wealden), Isle of Wight, England.
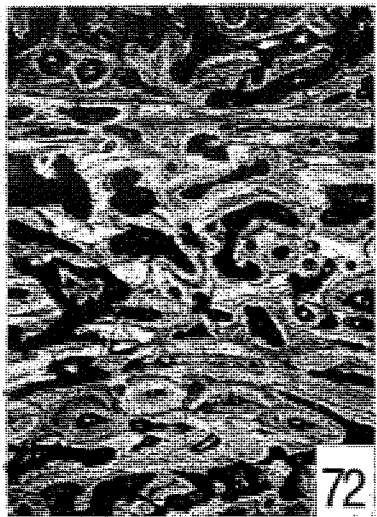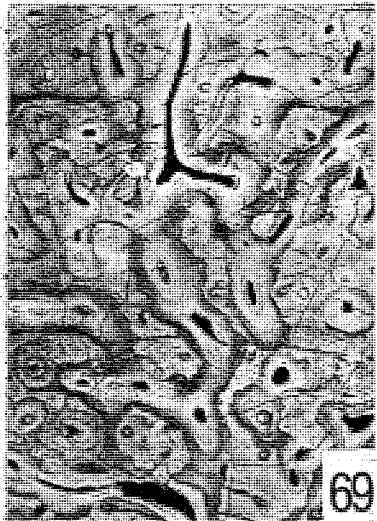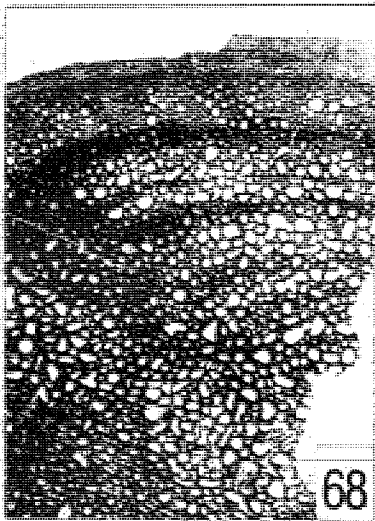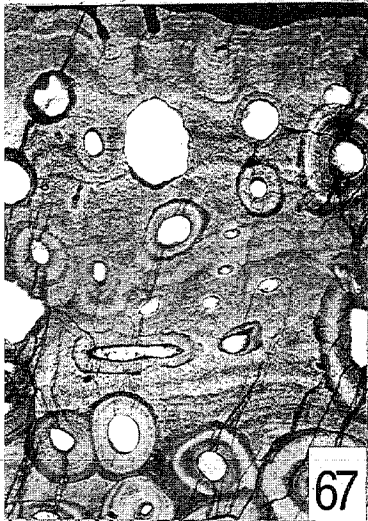
Figure 73. Vertical section through the centrum of a posterior cervical of Allosaurus, showing how the lateral pleurocoels open into cavernous internal spaces, in the manner of pneumatopores; X1. The irregular surface at the top follows the line of the neuro-central suture. C-LQ 095.

Figure 74. Transverse section of a rib of Ceratosaurus, a short distance below the section seen in the next figure; X1. The seeming medullary cavity is a downward extension of cavernous spaces extending through the capitulum and tuberculum. C-LQ 125.

Figure 75. Vertical section through the tuberculum of the same rib, showing the cavernous interior; X1.

Figure 76. Transverse section of an Allosaurus dentary, passing vertically through a socket from which the erupted tooth has been lost; X1. Left dentary, viewed from in front, with the medial (lingual) side at left. An immature (unerupted) tooth is seen on that side. Alveolar bone is limited to a thin lining only, except for a patch of cancellous bone at the base of the socket. C-LQ 133.

Figure 77. Vertical section through another socket of the same dentary, X1, with a more mature but displaced tooth seen at right. Due to lying obliquely, this tooth has no open base. On the lateral (right-hand) side the socket is thinly lined with alveolar bone for rather more than half its height, above which its wall is a resorption surface cut into Haversian bone. Two generations of alveolar bone, the older showing compaction, are seen in the deep part of the socket, with a curved reversal line between them. On the medial (left-hand) side, a tooth rudiment is seen above a shelf cut into alveolar bone. The canal seen under the lowest alveolar bone runs between the foramina noted by Madsen (1976, p. 29 and Pl. 9D, f).

Figure 78. Vertical section between two sockets in the same dentary, X1. Here the tooth-bearing groove is largely filled with alveolar bone, but is easily recognized by comparison with the two previous figures. At the top, part of a socket, sloping forward, extends into the plane of section, and two internal resorption spaces are seen lower down. On the medial (left-hand) side, alveolar bone extends upward as an interdental plate, whose base is arrowed. At least three generations of alveolar bone can be recognized in places.

Figure 79. Vertical section through a small right (?) dentary of Camarasaurus, passing through an empty socket; X1. The view is from in front, with the medial side at right. Alveolar bone is limited to a thin lining only except in the deepest parts. A rounded resorption surface is cut into it at left, below where an erupted tooth would have been, and an immature tooth seen at right lies in an ovate resorption space, suggesting the form of an enamel organ. C-LQ 089.

Figure 80. Transverse (horizontal) section through an interspinous ligament scar, in a posterior dorsal of Allosaurus; X2. The dark tissue seen under the irregular zigzag surface at left is intratendinous metaplastic bone, like that seen in Figures 57–58, in process of being replaced first by Haversian bone and then "Haversian" cancellous bone. Orientation of fiber bundles in the metaplastic bone is left to right. C-LQ 093.
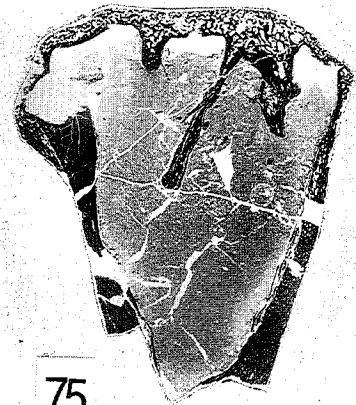
Figure 81. View of part of the junction of the "epiphyseal" and lateral surfaces of the distal end of a Camptosaurus humerus, X2. Compact bone just below the arrowed junction stands up slightly above the level of the "epiphyseal" surface, and could have been ossified partly from adjacent uncalcified cartilage. The "epiphyseal" surface shows the fine pores that are seen when marrow processes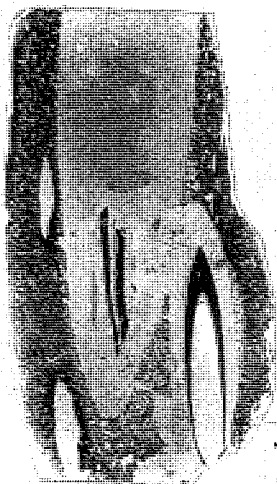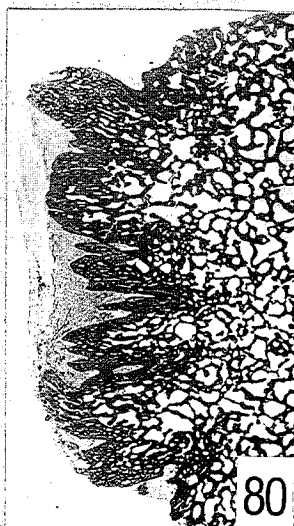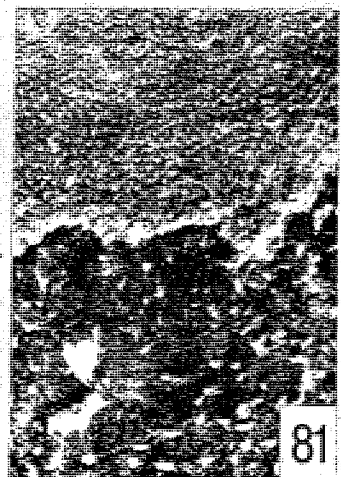 passed outward through the calcified cartilage. C-LQ 105.