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ABSTRACT:

The evolution of warm-bloodedness among fossil vertebrates has previously
been tentatively reconstructed by use of anatomy and paleoecology. Here this
problem is studied by another available and completely independent tool: the
histological structure of fossil bone, which is functionally interpreted by
comparison with bone histology of living forms. Comparative histology of bone
tissues among living tetrapods can be functionally interpreted in connection
with various physiological, morphological, adaptive and other characteristics,
and hence affords a wide and firm approach to bone histophysiology. More
precisely, functional interpretation of the taxonomic distribution of bone
tissues among living tetrapods points to a gross relationship between bone
histology and the patterns of growth and metabolism. Those histophysiological
conclusions, stemming from a wide comparative and functional interpretation
of bone tissues, are extensively discussed.

With this in mind, extensive examination of bone histology among fossil
tetrapods, especially stegocephalian Amphibia and synapsid and archosaurian
Reptilia, has been performed. The distribution of the various bone tissue
patterns among those groups demonstrates occurence of an active metabolism
among advanced mammal-like reptiles (therapsids) and among many Mesozoic
archosaurs, including dinosaurs. Endothermy among tetrapods is as old as
the Permian.

Those conclusions are checked against other relevant evidence and
extensively discussed from the histophysiological and various paleontological
points of view.

RÉSUMÉ:

L'évolution de la physiologie thermique chez les tétrapodes fossiles a
déja fait l'objet d'essais fondés sur des études anatomiques et paléoécologiques.
Ce problème est abordé ici grâce à des arguments tout à fait indépendants qui
demeurent disponibles pour le paléontologiste: ceux tirés de l'étude
histologique des tissus osseux fossilisés. Leurs structures recoivent une
interprétation fonctionnelle par comparaison avec l'histophysiologie des
formes actuelles. En effet, l'histologie comparée des tétrapodes vivants peut
être interprétée en fonctions de leurs diverses caractéristiques physiologiques,
morphologiques, adaptatives. . et elle fournit alors une base large et
solide pour l'interprétation histophysiologique des tissus osseux. Il s'avère
en particulier que la répartition taxinomique des types de tissus osseux met
en évidence une relation entre types histologiques, type de croissance et
métabolisme. Ces conclusions histophysiologiques, issues d'une large
interprétation comparative des tissus osseux chez l'actuel, sont discutées
en détail.

Ceci posé, on a procédé a l'analyse comparée des tissus osseux chez les
tétrapodes fossiles, Amphibiens stégocéphales et Reptiles synapsidés et
archosauriens, tout particulièrement. La répartition taxinomique des types

de tissus osseux semble montrer que les thérapsides ainsi que de nombreux archosauriens du secondaire, dinosaures en particulier, avaient un métabolisme actif. Dans ces conditions, l'endothermie chez les tétrapodes remonterait au moins au permien.

Ces conclusions sont confrontées à d'autres types d'approche du problème et sont largement discutées a la fois dans des perspectives histophysiologiques et paléontologiques diverses.

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Introduction

During recent decades, attention has been repeatedly focused by vertebrate paleontologists on the problem of the history of thermoregulation. With the major anatomical steps of skeletal evolution among tetrapods established, it becomes clear that at least some knowledge of related fields, such as ecology, behavior and even physiology are now needed to get a deeper insight into major evolutionary processes and trends among fossil vertebrates. This is obviously a difficult goal, as the chain of processes linking the available fossils to the living populations from which they come is long and biased (Olson, 1971). In such circumstances, every kind of information that a fossil might still contain about its once living body should be welcome. Until now, however, nearly all the information pertaining to fossils as remnants of integrated living organisms came from two distinct "levels of organization", the ecological level on the one hand and the anatomical level on the other. This is especially true in tetrapod paleontology, where most of the paleobiological inferences are derived from skeletal anatomy. The problem of the evolution of thermoregulation is a good example of this. Most of the facts and functional hypotheses dealing with the rise of endothermy, especially among therapsids and dinosaurs, stem from gross anatomical data (e.g. Schuh, 1951; Brink, 1956, 1967; Russell, 1965; Ostrom, 1969), and to a far lesser degree from ecological data and ichnological and taphonomic data that bear on behavior (Bakker, 1971b, 1972; Brink 1955, 1958).

This same problem has been studied here from completely different data. My evidence comes from another available "level of organization", the histological structure of bone in fossil tetrapods (de Ricqlès, 1968a, 1969a, 1969b, 1972b, 1972c, 1972d and unpublished thesis). The histology of hard tissues is usually well preserved in fossil material. This opportunity is well taken into account in paleobotany, invertebrate paleontology and, among vertebrates, specialists on fishes, but until now very little has been done with bone histology of fossil tetrapods in paleobiology, through functional and histophysiological interpretations, in spite of the extremely accurate and thought-provoking descriptive studies that have been available for a long time (e.g. Seitz, 1907; Gross, 1934; Enlow and Brown, 1956, 57, 58).

On the other side, many fields relevant to paleobiological interests are blossoming. Examples are the histophysiology of modern bone tissues (Frost, 1964; Bourne, 1971-73) and the comparative physiology of thermoregulation and study of metabolic rates in various modern tetrapods (Prosser and Brown, 1961; Whittow, 1970-73).

For some years now, it has been my aim, starting from descriptive and comparative paleohistology (de Ricqlès, 1968a, 1968b, 1969b, 1972b) to try to correlate the various data stemming from those discrete fields and hence to reach a functional interpretation in which they are all meaningful and useful to each other (de Ricqlès, 1972c, d).

The tentative conclusions presented here may be partially inadequate but it is important to promote a new tool. Comparative paleohistology, with a functional interpretation, is a kind of a bridge from the field of structures and morphology to that of functions and physiology. Hence a "paleophysiology" will be forged, which is a necessary background for a mature paleobiology, one that is able to demonstrate and explain the evolution of form-function relationships through time.

This paper, which summarizes a part of the author's still unpublished thesis (de Ricqlès, 1973), first reviews and discusses the functional interpretation of comparative histological data among living animals and their bearings on temperature physiology. Afterwards, corresponding paleo-histological data are used to try to reconstruct the history of endothermy among various lineages of fossil vertebrates.

Histophysiological Meaning of Cortical Primary Bone Tissues

Comparative studies of bone histology show that primary bone tissues of periosteal origin, which often form the bulk of the long bone shafts, have extensive structural variations which can be easily classified by their patterns of vascularization (Enlow and Brown, 1956; de Ricqlès, 1973). The many structural patterns so obtained can be arranged into more comprehensive categories by the organization of the intrinsic collagenous fibers of compact bone. I have proposed to group under two basic patterns of organization the periosteal bone tissues most commonly met in the long bones of tetrapods (de Ricqlès, 1972c, 1973). They are 1) the lamellar-zonal and 2) the fibro-lamellar patterns of organization. In the first, periosteal deposition is grossly lamellar or parallel-fibered, and vascularization is rather scattered and can be completely lacking (Fig. 1). In the fibro-lamellar pattern, on the other hand, periosteal deposition is fibrous or woven, vascularization is dense, and blood vessels are encased in numerous primary osteons which are made of finely lamellated, centripetally deposited, bone substance (Fig. 2).

Extensive examination of the conditions of bone deposition demonstrates that lamellar-zonal patterns are always associated with a low rate of growth, while fibro-lamellar tissues are always deposited when growth is sustained and active (Amprino, 1947; Enlow, 1966). This relationship between histological pattern and speed of deposition can be easily explained by the diversity of histogenetic circumstances induced by the speed of growth.

In a region of a bone experiencing a low rate of growth (or in a whole skeleton submitted to such a condition), periosteal bone is formed by the mineralization of fine collagenous fibers which are completely formed in situ shortly before mineralization. Those fibers are densely coated and superimposed one above the other, thus giving a more or less regular lamellar structure to the thick periosteal deposit, and few blood vessels from the periosteum are entrapped in the hard forming tissue during the process. If growth stops, a circumferential "rest line" is deposited until growth starts again. Regular superposition of such structures within the cortex often suggests a cyclical pattern of growth in many vertebrates (see below). If, on the other hand, bone deposition occurs very quickly and continuously, the ossification process spreads within the external fibrous layer of the periosteum, where numerous pre-existing collagenous fibers are entrapped within the mineralizing substance. This ossification process continuously jumps farther and farther into the neighbouring fibrous layers, and the resulting bone tissue is a fine cancellous bone with an irregular, fibrous matrix. The numerous vascular cavities left within the rapidly forming fibrous bone are ultimately filled up by centripetal
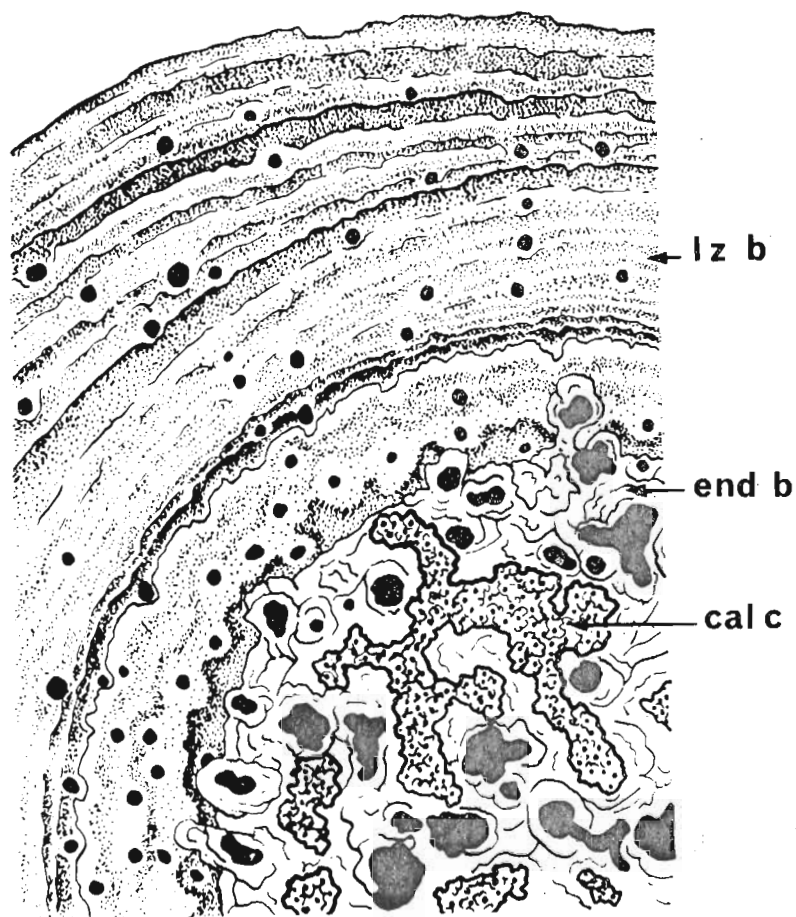
Figure 1. The lamellar-zonal pattern. Periosteal bone tissue is mainly formed by more or less thick, regular, appositional lamellae, concentrically and centrifugally deposited around the shaft. Vascularization is rather scattered and the primary vascular canals, here with a longitudinal course, have not experienced centripetal deposition at their margin, and hence are not here primary osteons proper. Drawn from a rib of a lower Permian mesosaur (where, incidentally, the inner portion of the shaft is built by endosteal compaction between remanent islands of calcified globular cartilage, a feature often met among aquatic tetrapods with pachyostotic bones).

    l.z.b.: Lamellar-zonal pattern of periosteal bone.
    Cal. c.: Calcified cartilage.
    End. b.: Endosteal bone.

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deposition of primary osteons of fine lamellar structure; the fibro-lamellar pattern is then completed (Fig. 2, Fig. 3) (see, e.g., Petersen, 1930; Pritchard in Bourne, 1971).

    Fibrous bone would be more quickly deposited than periosteal lamellar bone because it is largely formed by metaplastic ossification of previously available collagenous fibers. On the contrary, lamellar bone would be the result of a far more complete de novo formation neoplasy (Pritchard, 1961; in Bourne, 1971). "Pseudolamellar" or "parallel-fibered" bones would be more or less intermediate between the other patterns with respect to the rate of deposition (Enlow, 1969).
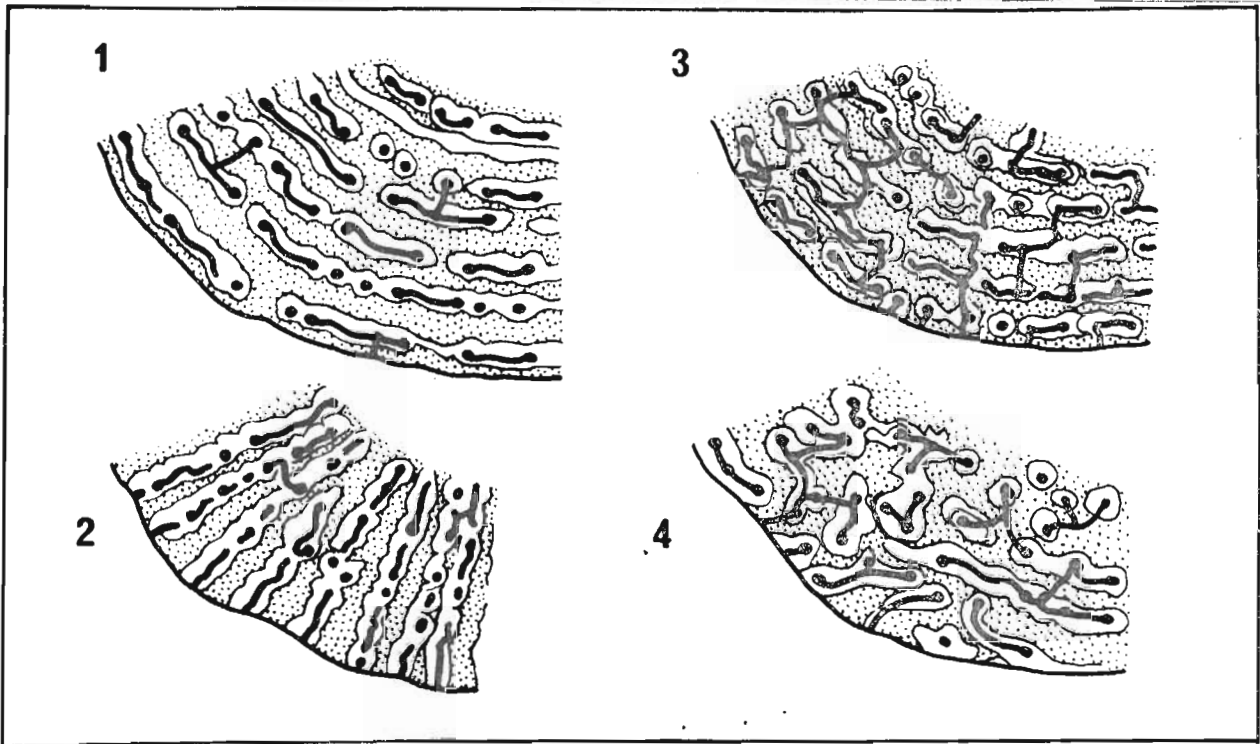
Figure 2. The fibro-lamellar pattern. Some diagrammatic instances of
variations in the vascular orientation within the general pattern of
fibro-lamellar periosteal bone tissues.
Stippled areas: fibrous periostial tissue centrifugally deposited.
White areas: fine lamellar bone of the primary osteons, centripetally deposited.
Black: vascular canals.
1: Laminar tissue, 2: Radiating tissue, 3: Plexiform tissue, 4: Reticular tissue
(From de Ricqlès, 1973, to be published).

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     While the interpretation of Haversian remodeling has given rise to much
work (see below), it is surprising that the histophysiological meaning of the
variety of primary periosteal tissues has been more or less neglected, as noted
by Currey (1962). However, the pattern of primary periosteal bone is diagnostic
for a functional interpretation of bone tissues. The constant antagonism
between the circumstances of deposition of the lamellar-zonal and fibro-lamellar
patterns of periosteal bone tissues seems to be the expression of a constant
general factor which underlies those circumstances. It is remarkable that
contrasting circumstances of deposition: within a given bone, among the
various bones of a skeleton, among the various stages of growth of an individual,
among individuals of the same species that differ in their rate of growth, or
even among different species or supraspecific taxa that differ in growth rate;
give a result which is always the same. This constancy of histological response
to different rates of growth, whatever the organizational level considered,
means that a common underlying factor expresses itself always in the same way.
This factor seems to be the absolute intensity of metabolism associated with
periosteal osteogenesis.
     It is clear that the absolute intensity of metabolism must be higher for a
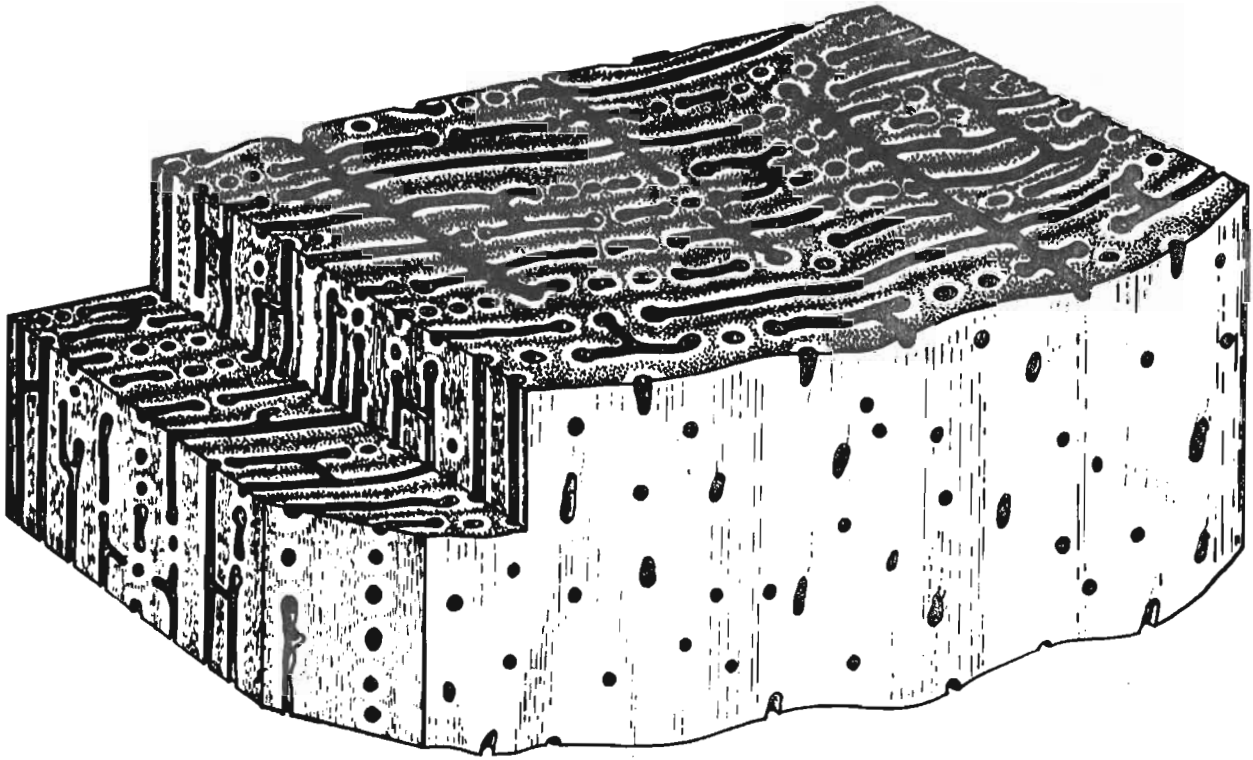fast-growing organism, reaching quickly a great size, than for a slower-growing

Figure 3. The fibro-lamellar pattern. Schematic three-dimensional picture
of the plexiform bone tissue, as found in the shafts of a mid-Jurassic sauropod,
Bothriospondylus. The fibrous periosteal tissue (stippled) is rapidly expanding
outwards while the very regular, dense, three-dimensional network of primary
vascular channels is surrounded by primary osteons (white)(from de Ricqlès, 1968a).

        *   *   *

one. Constant parallelism between this obvious necessity and the deposition
of a fibro-lamellar pattern in the one case, and of a lamellar-zonal pattern
in the other, strongly suggests a causal relationship between gross metabolic
activity and the general form of periosteal bone deposition.

A European salamander (Salamandra salamandra) needs four years to reach
adulthood and weighs at this age only about twenty grams. Many mammals take
two years to reach adulthood and weigh hundreds of kilograms at the time.
Differences in bone tissue histology between the two are largely the expression
of the tremendous differences of rates of increment involved and of the under-
lying differences in metabolical activity. These points are basic for a
meaningful comparative interpretation of bone histology.

Rings of Growth

Among bony fishes, the use of scale structures to assess individual age is
a current practice. In many species, bones as well show distinct bands more or
less similar to the growth rings of the scales (Castanet et al., 1970). It is
generally agreed that the cyclical bursts of growth of chondrosteans and
teleosts depend on cyclical environmental or physiological variations of a
yearly period. Such a line of reasoning obviously affords the possibility of
evaluating individual age among ectotherms if cyclical bandings in scales and
bones are indeed annual. Both extensive (Peabody, 1961; Warren, 1963) and
intensive (Petter-Rousseaux, 1953; Castanet, 1974) surveys have demonstrated
that the same kind of growth rings as those met in fish bones are also

frequently seen in the bony skeleton of ectothermic tetrapods, even if it is difficult to use them directly as an index of individual age. In the lamellar-zonal pattern of periosteal bone so commonly encountered among ectothermic tetrapods, "rings of growth" are often narrow circumferential avascular sheets of bone, the <u>annuli</u>, sandwiched within larger, vascularized sheets, the "zones". Those contrasting structures are more or less regularly superimposed on each other several times through the whole thickness of the cortex, giving it an overall stratified appearance.

Such regularly deposited annuli and zones are not met often, if at all, in bones of mammals and birds (Warren, 1963; Enlow, 1966, 1969). Within the thickness of a cortex circumferential "rest lines" may often be present, but repetitive, cyclical superposition of such structures is not very frequent. Among mammals, circumferential lines of this kind, when met, often turn out to be "reversal" or "tide" lines linked with a local aspect of growth remodeling (Enlow, 1963) rather than demonstrating a cyclical (annual) increment. The circumstances are different, of course, in ectodermal derivatives (horns, claws and other keratinous structures) and even in teeth of mammals where, as is well known, cyclical (annual) increments are not infrequently met (Peabody, 1961; Low and Cowan, 1963). This is especially true among water-dwelling species experiencing extensive cyclical (annual) changes in ecology and behavior, such as pinnipeds (Laws, 1962).

Again, even among mammals experiencing annual osteogenesis of a special kind, such as growth of the antlers of deer, intensive osteogenesis of the antlers is linked with Haversian substitution rather than with cyclical "rest lines" in other parts of the skeleton (Hilman et al., 1973). Only in mammals of small size growing slowly during many years under climates showing severe annual variations (arctic to cold temperate), would annual zonation of periosteal deposits be present as a rule, and then only in the outermost cortex (Klevezal, 1972). Cyclical annuli and zones seem completely unknown from the bones of any birds (Warren, 1963; Enlow, 1966).

To conclude, if only primary bone tissue is taken into account, a broad comparative survey of living animals shows that, among ectotherms, cyclical apposition of periosteal bone is extensively met, while this pattern of bone deposition is rare among endotherms, where the skeleton is often made of the fibro-lamellar type of periosteal bone which gives little evidence, if any, of rings of cyclical growth.

Substitution in Compact and Spongy Bone Tissues

In spite of the extraordinarily high number of studies devoted to haversian substitution in compact bone, it seems that there is still no general agreement regarding the meaning of this process. Many workers have for long suspected, for instance, that Haversian substitution in compact bone was an adaptive response of the tissues to mechanical stresses. More recently, it has been argued that Haversian substitution would be the result of physiological necrosis of osteocytes (Enlow, 1962), or of metabolic starvation resulting from damages to the vascular system of primary compact bone (Currey, 1964). For a variety of reasons which need not be dealt with here, those explanations, and others, seem to me unlikely, and could at best account for some haversian substitution, without indicating the basic significance of the process as a whole.

A wider histophysiological interpretation of Haversian substitution seems to me available (e.g. Amprino, 1967): Haversian substitution would be an histological expression of phosphocalcic metabolism. The skeleton would act

as a reservoir, freeing or fixing phosphocalcic salts according to the
various physiological requirements and diet availability, and hence allowing
homeostatic regulation. By this interpretation, Haversian substitution
would have to be more frequent in animals with high metabolism (endotherms)
than in ectotherms. A wide comparative analysis of bone tissues among
modern tetrapods shows that this is indeed the case, especially if animals
of medium to large size are taken into account. (Histological data are in
the papers of Amprino and Godina, 1947; Enlow and Brown 1956, 1957, 1958.)

Substitution within cancellous bone tissue is more difficult to assess
than in compact bone, without elaborate techniques. It has been often shown,
however, that substitution in spongy bone can account for an even greater part
of the phosphocalcic salt exchanges than Haversian substitution in compact
bone itself (Amprino, 1967). Again, comparative histology is adequate to
test a supposed relationship between this kind of substitution and the
intensity of metabolism and indeed, among modern tetrapods, remodeling and
substitution in cancellous bone seem much more active and wide spread among
endotherms than among ectotherms. (Data are in the papers of Haines, 1942;
Enlow, 1969.).

Among birds, a well known instance of skeletal involvement in calcium
homeostasis is what is called medullary bone, which acts as a specialized
labile store, available for the calcification of egg shell (see, e.g.,
Taylor and Bellanger, 1969). It is noteworthy that very extensive and fast
changes in bone histology associated with deposition or remobilization of
medullary bone occur in birds, which are endotherms with a very active
metabolism. Among living reptiles which lay calcified egg shells (e.g.
tortoises, gekkonid lizards and crocodiles), extensive mobilization of
medullary bone has not been described but rather "most areas of the cancellous
medulla appear to have retained their original plan of structural arrangement
. . . in mature individuals" (Enlow, 1969, p. 54).

To conclude, only dense Haversian bone is generally taken into account
for histophysiological interpretations of compact bone tissues. On the
contrary, it seems that the full array of facts stemming from comparative
bone histology points towards a common and coherent histophysiological meaning
for both primary (periosteal) and secondary (Haversian) bone, as well as for
compact and cancellous bone tissues. The whole histological structure of the
skeleton is associated with the basic metabolic pattern of the whole organism.
Everything else being equal, animals with a comparatively low metabolism will
generally have at the same time patterns of growth, thermal physiology, and
bone histology different from those of animals with a comparatively high
metabolism. Conversely, bone histology could be used to assess at least
general patterns of growth and the gross metabolic level of the animal studied.
I shall now proceed to express those points of view in more detail and to
discuss them.

Histological Discussion

Metabolic factors underlying histological diversity of bone tissues have
been stressed in previous sections because they are of basic importance in the
functional interpretation of bone histology pertinent to the problem of the
history of thermoregulation. It is obvious, however, that many other factors
underlie histological diversity, and a comparative approach can demonstrate
them. I will not deal here with those various factors but will mention some of
them briefly, to indicate that they have not been overlooked in this functional
interpretation of bone tissues (de Ricqlès, 1973).

First of all, it is clear that anatomical and topographical factors are basic for a meaningful interpretation of histological diversity (Enlow, 1963, 1966). Many structural peculiarities which can be observed in routine histological sections are linked to such factors, especially among higher vertebrates. As the conditions of growth (speed of deposition, intensity of growth remodeling, and so on) are different for each bone of a skeleton, each part of a bone, each spot of a section, and for each period of individual life, a comparison that would not take into account those factors would have indeed little meaning. However, when the influence of such anatomical and topographical circumstances is acknowledged and integrated, it becomes possible to interpret more general, systematic histological variations demonstrated by comparative histology, in functionally comparable parts of the skeleton among various vertebrates.

In the same way, histological diversity, as revealed by comparative studies, is more or less directly linked with such other factors as body size, mechanical influences, or basic adaptive situation. For instance, land-dwelling vertebrates of rather large size have shafts where outer cortical bone is compact. This sharply contrasts with the cancellous bone of the inner medullary region, which can be poorly developed or even lacking. On the contrary, water-dwelling forms of roughly the same size have a cancellous rather than compact outer core of bone which merges very gradually into an extensively developed spongiosa in the medullary region.(See e.g. Seitz, 1907; Gross, 1934; Nopcsa and Heidsieck, 1934; for descriptive data). This can be observed in unrelated groups sharing the same kind of gross adaptation, such as ichthyosaurs and cetaceans, and shows clear examples of histological parallelism under similar adaptive circumstances.

General factors such as basic adaptive condition or phyletic situation are sometimes presented, when evolution of hard tissues is discussed, as key factors which can directly "explain" the histological patterns of the hard tissues found in a given bone. Those general factors, in my opinion, are rather less significant than direct, ontogenetic factors (topographic localization, rate og growth, patterns of bone remodeling, longevity) in explaining histological diversity. For instance, two factors of great interest in understanding histological diversity are body size and longevity. Everything else being equal, secondary osteons are always more numerous in bones from animals of large body size and great individual age (Amprino and Godina, 1947).

It is only after the influence of such ontogenetic factors on bone histology is taken into account that factors of a more general kind, such as adaptive and phylogenetic situations, can be used to explain histological diversity.

If all the various ontogenetic, adaptive and phylogenetic factors of bone diversity are taken into account, it nevertheless remains that metabolic factors play also a leading role that could explain the peculiar taxonomic distribution of various histological patterns of bone tissues (de Bonis et al., 1972; de Ricqlès, 1972c, d). Well vascularized fibro-lamellar tissues, dense Haversian bone, and extensivelyremodeled cancellous bone are features so commonly met in bones of mammals that they are widely--and incorrectly--accepted as the "standard pattern" of any bone tissues, a quite misleading assumption as, in the modern world, they are commonly and extensively met in large endotherms only. Conversely, lamellar-zonal tissues, often marked by annuli and zones of cyclical increment, poor vascularization, infrequent Haversian substitutions, and discrete remodeling of cancellous tissues, are most commonly encountered among modern ectothermic tetrapods. Therefore, it seems to me that, among living tetrapods, there is a gross relationship between bone histology and basic thermal physiology. This relationship can be understood if bone histology

and thermal physiology are both considered as by-products of the pattern of animal metabolism. The correlation is obvious, of course, between the rate of metabolism and the general pattern of thermal physiology (see e.g. Prosser and Brown, 1961; Whittow, 1970-73). The relation between rate of metabolism and bone histology seems less obvious at first sight but can be understood through the study of the growth process. For the pattern of growth is linked with the pattern of metabolism on the one hand (cyclical growth all during life for ectothermic tetrapods, continuous growth with a high rate but only during a specialized period of early life for endotherms), and also linked with the type of bone histology, on the other, as it has been already shown above.

It must be stressed that a relationship between primary bone tissue histology and a general kind of thermal physiology is only indirect but commonly exists because it is realized through the pattern of growth. Admittedly if, in an ectotherm, one selects only those parts of the skeleton which have to grow far more quickly than most others, for morphogenetic reasons, it is likely that those regions will also show fibro-lamellar patterns, if often associated here with annuli (Castanet, 1974). Similarly it is possible to select among endothermic mammals, even of great size, regions of the skeleton which have to grow more slowly than most other parts of it; those slow-growing regions will be made of lamellar-zonal tissues and sometimes even grow in cyclic (annual) increments (Klevezal, 1972). The observations do not contradict the thesis of a general relationship between bone histology and patterns of metabolism, but they indeed show that patterns of bone histology are only indirectly, not directly, associated with endo- or ectothermy.

Again, an endotherm specialized in very small body size, will not generally show in its skeletal histology any clear evidence of its very high metabolism because its overall growth rate will be low. This can be seen in bone structures of some small mammals (shrews, small rodents) and birds (passerines) (Enlow and Brown, 1957, '58). Of course, endotherms are not obliged to get big (even if they nearly always grow fast), but in such circumstances they simply afford little histological evidence of endothermy. Only bones from medium-sized to large animals can show histological features pertaining to their pattern of thermal physiology and metabolic activity.

Now, if indeed an ectotherm could maintain a very high rate of continuous growth and develop into a large animal as quickly as an endotherm does, both could have exactly the same kind of bone tissues in such circumstances. In the modern world, such a situation is unlikely, however, because ectotherms have a low intensity of metabolism and, after a short early period of rapid increase, are obliged to rely on low rates of growth, often cyclical, for the rest of their lives even if they eventually become large. Only large sea turtles can sustain rather high rates of growth during early life (A. d'A. Bellairs, 1969), and they have an incipient endothermy probably caused by continuous muscular activity required for active swimming (Frair et al., 1972). It is indeed noteworthy that, among living reptiles, those big turtles have the most elaborate bone tissues, with fair vascularization in some places (Foote, 1916) and even some extensive Haversian substitution in old, large individuals (Amprino and Godina, 1947). Tunas and swordfishes are among the largest teleosts, fast moving and possessing a kind of endothermy (see e.g. Fry et al., in Whittow, 1970). Again, tunas show a very distinct pattern of bone tissue with a well vascularized primary bone and rather

extensive Haversian substitution (Stephan, 1900; Amprino and Godina, 1956),
in clear contrast to most other teleosts (Enlow and Brown, 1956) ([1]).

So I believe that there is a general functional relationship between
bone histology, pattern of growth, intensity of metabolism and gross thermal
physiology (de Ricqlès, 1972c, d). In other words, comparative histological
examination, if used within adequate critical limitations such as those
outlined above (see also Enlow, 1966), is a tool available to demonstrate the
pattern of thermal physiology in many circumstances. Evidence for this relies
on facts available from living vertebrates, where both histology and physiology
can be studied. Now we can investigate in turn fossil vertebrates, where
only bone histology is available, and hence try to assess their thermal
physiology.

Some Comments on Definitions and Terminology

As justifiably noticed recently by Feduccia (1973) and Bennett and
Dalzell (1973), among others, some works dealing with the history of thermo-
regulation are plagued by an inadequate use of biothermal terminology.
Following previous studies (de Ricqlès, 1972c, d), I shall use here at the
same time the words ecto- and endotherms, homeo- and poikilotherms both in
opposition and in combination.

One is accustomed to use "homeotherms" sensu lato as a synonym of
"warm-blooded animals", which are typically the birds and mammals in our
modern world. Conversely, poikilotherms are supposed to be the "cold-blooded"
amphibians and reptiles, among tetrapods. It must be stressed at once that
those approximations are inadequate and would only have, at best, some
pedagogical value. In fact, as they "freeze" the whole problem, they tend to
hide the much more complicated, gradual, picture that is emerging from modern
comparative physiology (see e.g. Whittow, 1970-73).

Both mammals and birds have (generally) at the same time a high body
temperature which remains constant, a high metabolic rate, and insulation
(fur or feathers), and so they can be properly described as "endothermic
homeotherms". Conversely, most modern amphibians and reptiles show the
opposite situation and are best described as "ectothermic poikilotherms"
(de Ricqlès, 1972c, d, 1973). Even in the modern world, there are many
instances where those conditions are not typically met. Hibernating mammals
are not typical homeotherms; conversely, many amphibians and reptiles can
attain a surprising level of "ectothermic homeothermy" thanks to behavioral
and ecological mechanisms (see e.g. Brattstrom, Templeton in Whittow, 1970).
Others show at least an incipient endothermy (sea turtles, varanid lizards,
boid snakes) in some circumstances, being kinds of "endothermic poikilotherms",
a situation more or less met also among teleosts (tunas) and even sharks
(see Fry et al. in Whittow, 1970).
                *   *   *

([1]). Modern holosteans have sometimes been thought to possess dense
Haversian bone, but published data (Stephens, 1900; Enlow and Brown, 1956)
show that the compact bone is formed by a periosteal tissue, thickly lamellated,
with extensive regions of growth annuli and very poor vascularization, thus
conforming with the lamellar-zonal pattern. Haversian substitution, while
extensive, is mainly restricted to cancellous endosteal bone containing marrow
cavities, a situation which is common in large bones of mature animals both
ectotherms and endotherms. Moreover, bone tissue of holosteans possesses
peculiar histological specializations (lepidosteoid tubules) which are never
found in bone tissues of endotherms. As a whole, holostean bone fits well in
the structural pattern of large, long-lived ectotherms.

Obviously, our usual and sharp distinctions between "warm-" and "cold-blooded" animals must be tempered. A proper qualification of a given case can best be reached by the simultaneous use of the endo/ecto and homeo/poikilo couples of adjectives. So subtle and various are the conditions in the modern world regarding thermal physiology that it must be suspected at once that the conditions were equally complex among fossil forms. One cannot look just for a clear-cut occurrence of "warm-" _versus_ "cold-blooded" animals among fossil vertebrates. Again, it must be realized that if the origins of perfect "warm-bloodedness" (endo- _and_ homeothermy) are looked for among the primitive representatives of lineages of warm-blooded modern vertebrates, one cannot ask for a sudden appearance among them of all the associated features that one can find among living, modern, warm-blooded animals. On the contrary, some intermediate states of development of "warm-bloodedness" are to be sought for. It has been repeatedly stated, for instance, that sauropods were ectothermic homeotherms (Colbert et al., 1946; Spotila et al.,1973). On the other hand, some therapsids have been understood as endothermic poikilotherms (Heath, 1968), while some pelycosaurs have been interpreted as ectothermic homeotherms (_inter alia_ Bramwell et al., 1973), according to the present terminology.

Such unfamiliar situations, and others, may have arisen repeatedly in various lineages, as indeed they still do in the modern living world. However, it seems to me that the most meaningful advance towards "warm-bloodedness" of modern mammals and birds is the acquisition of endothermy, the ability to produce one's own heat thanks to high metabolic rates.

We shall now proceed to see how comparative paleohistological data are adequate to demonstrate this achievement among various lineages of fossil tetrapods.

Paleohistological and Comparative Data:
Taxonomic Distribution of Bone Tissues among Fossil Vertebrates

As a first approximation, we can hypothesize that, among fossil tetrapods, those which have the same histological patterns as modern "cold-" or "warm-blooded" animals, had more or less the corresponding kind of basic physiological level of organization. My comparative studies in paleohistology (de Ricqlès, 1968a, b; 1969b; 1972b; 1974), which are still in part unpublished, as well as the numerous data already available in the literature (e.g. Seitz, 1907; Gross, 1934; Enlow and Brown, 1956-58; Currey, 1962) give a reasonable knowledge of the spectrum of variation in bone histology among the whole array of fossil amphibians and reptiles.

Among amphibians, the temnospondyl stegocephalians have been intensively studied (Gross, 1934; Enlow and Brown, 1956; de Ricqlès, unpublished works). The more advanced forms (stereospondyls and neo-rachitomes) have more or less specialized bone patterns related to their water habits. Permian rachitomes are perhaps more generalized histologically. All those stegocephalians clearly show a lamellar-zonal pattern of bone tissues, with extensive instances of protracted and cyclical increment. Other stegocephalians (Ichthyostegalia, Anthracosauria, and especially Embolomeri and Seymouriamorpha) have also been studied but to a lesser extent, owing to the scarcity of available material. As far as they are known, however, they show the same basic lamellar-zonal pattern of bone tissues as in temnospondyls. This is also the same for the few lepospondyls investigated. Among reptiles, various cotylosaurians have been histologically investigated (Enlow and Brown, 1957; Peabody, 1961; Enlow, 1969; de Ricqlès, unpublished work). While mesosaurs are highly specialized, and not unlike some advanced stereospondyls regarding histology

(Fig. 1), more typical forms (including captorhinomorphs, diadectids, pareiasaurs and procolophonids) obviously possess a lamellar-zonal pattern of primary bone tissues with instances of cyclical zones of increment.

"Reptilian" synapsids have been intensively studied (Enlow and Brown, 1957; de Ricqlès, 1969b, 1972b, 1974). Non-ophiacodont pelycosaurs have a lamellar-zonal pattern of bone histology, very similar to what is found among cotylosaurs and rachitomous Stegocephalia. Ophiacodon has a puzzling bone histology, which is reminiscent at first sight of the structure found among some therapsids (see below) because of dense vascularization of periosteal bone, but which is in fact more probably related to a rather aquatic habit. Histological studies of aquatic reptiles (plesiosaurs and marine crocodiles [mesosuchians]; see e.g. Seitz, 1907; Gross, 1934; Nopcsa and Heidsieck, 1934) have shown that vascularization of cortical bone can be very extensive, with many vascular canals oriented parallel to the long axis of the bones. It is probably such a condition which is found in Ophiacodon in an incipient form. Early, primitive members of the therapsid radiation, eotheriodonts and titanosuchids, have bone patterns which clearly diverge from those of sphenacodont pelycosaurs. Here, extremely dense vascularization of the cortex is met and Haversian substitution is extensive in some cases. Nevertheless, the periosteal deposition of cortical bone remains grossly lamellar and instances of cyclical accretion are known. More advanced therapsids: herbivorous anomodonts (deinocephalians, dicynodonts, kannemeyeriids and the like) as well as more or less primitive or advanced carnivorous theriodonts (gorgonopsians, therocephalians, bauriamorphs, cynodonts) decidedly show a fibro-lamellar pattern of primary bone tissues, not possible to distinguish, in fact, from those of any Cenozoic or living therian of roughly the same size (de Ricqlès, 1969b, 1972b and unpublished studies). Among gorgonopsians and cynodonts, as well as dicynodonts sensu lato, which have been rather more extensively studied than other groups, various patterns of fibro-lamellar tissues have been found, which match almost exactly the tissues found in analogous carnivorous and herbivorous modern mammals. Again, Haversian substitution may be plentiful, at least in some part of the skeleton, while rings of cyclical growth seem to be completely missing, at least among theriodonts.

Among archosaurs, preliminary studies of early thecodonts (proterosuchians) and more advanced ones, and more extensive examination of various dinosaurs, have been performed (Seitz, 1907; Gross, 1934; Enlow and Brown, 1957; Currey, 1962; de Ricqlès, 1968a, b, and unpublished work). It seems that some lineages (at least Parasuchia, Mesosuchia, Eusuchia) retained a more or less lamellar-zonal pattern, perhaps associated with aquatic specialization. On the other hand, advanced thecodonts (Ornithosuchia) and even some very early and primitive forms (erythrosuchid Proterosuchia) already had a surprisingly dinosaur-like bone histology, with extensive occurrence of very well vascularized fibro-lamellar primary tissues (Gross, 1934; de Ricqlès, 1968b). As for dinosaurs, it has long been known that, in clear contrast with the more typical reptilian condition, bone tissue is either composed of very well vascularized fibro-lamellar primary tissues (Fig. 3) or is extensively changed into dense Haversian (secondary) bone (inter alia Seitz, 1907; Gross, 1934). And pterosaurs seem to share with large birds a very well vascularized fibro-lamellar bone tissue (Gross, 1934; Enlow and Brown, 1957).

That at least a part of the taxonomic distribution of bone tissues among fossil and recent tetrapods as presented above relies on hard facts has been shown recently by computer studies (de Bonis et al., 1972 and unpublished works). When the relevant paleohistological data available in the literature (excluding those presented by this writer to prevent possible self-biasing of the data) are treated by factor analysis, they indeed reproduce the characteristic taxonomic distribution presented above.

Functional Interpretation of Paleohistological Findings (Fig. 4)

From the above, it seems that histological data point to an almost certain ectothermic-poikilothermic physiology among stegocephalians and most (if not all) cotylosaurs. Those data also suggest that pelycosaurs had the same basic patterns of thermal physiology, possibly refined, in some cases, by a crude homeothermy, thanks to the dorsal "sail" supported by the elongated neural spines (see inter alia Bramwell et al., 1973). In accordance with a now generally held opinion, it seems to me that this very early trend towards thermal control among ectotherms, if perhaps awkward and crude in some respects, nevertheless is very significant as it was developed several times in the lineage which was to give rise ultimately to much more advanced homeotherms, namely the mammals.

In clear contrast to the pelycosaurs, every advanced mammal-like reptile (therapsids), and even perhaps some transitional forms (eotheriodonts)
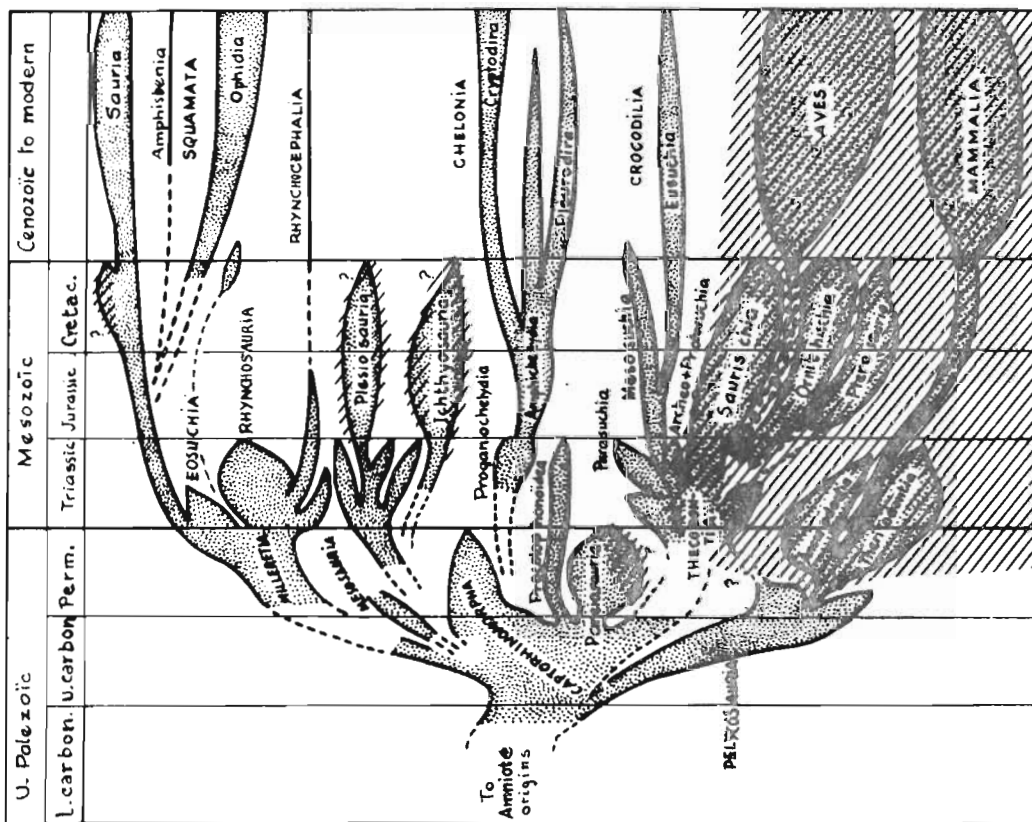

Figure 4. A pictorial family tree of amniote vertebrates, with delineation of endothermic lineages (dashed), as suggested by paleohistological data. Delineation within thecodonts is provisional and the status of some pareiasaurs, ichthyosaurs, plesiosaurs and mosasaurs regarding endothermy is completely conjectural.

between sphenacodont pelycosaurs and therapsids, have a decidedly mammal-like bone histology. Among large, primitive forms (e.g. titanosuchians), a peculiar, primitive condition of endothermic poikilothermy was probably present, as well as among some dicynodonts sensu lato. Theriodonts, including gorgonopsians, had very likely an endothermy associated with a more or less well established homeothermy, a condition which at any rate may not have been unlike what is found among living Monotremata.

Among archosaurs, where my personal descriptive studies are not as extensive as among synapsids, there seems to have been a very early dichotomy between lineages with a rather "conservative" thermal physiology of the general ectothermic-poikilothermic type on one hand, and others which have experienced a surprisingly fast and early advance towards endothermy, on the other. Among the former are water or swamp dwellers: perhaps the chasmatosaurid proterosuchians, certainly the Parasuchia and most of the Crocodilia sensu lato. It is quite possible that an early trend towards endothermy, perhaps linked to the very roots of the archosaurian lineage as a whole, has been lost or kept unchanged in some of those lineages of semi-aquatic archosaurs. On the other hand, erythrosuchid proterosuchians, at least some pseudosuchians, pterosaurs and all the investigated dinosaurs (including carnosaurs, prosauropods, sauropods and ornithopods, just to quote only those forms studied by the present writer) definitely show indications of very high rates of continuous (not cyclic) growth and extensive bone turn-over, which are met, in modern living tetrapods, only among endotherms. Consequently, it is this writer's opinion that they had a well developed endothermy at least by the mid Triassic, most probably rooted in earlier times.

For both synapsids and archosaurs, histological data point to an origin of endothermy during late Paleozoic time. It is tempting to accept the hypothesis that Permian glaciations played a part in the initiation of endothermy.

It is quite possible that some endothermy (associated or not with some kind of homeothermy), at least in an incipient state, was developed in some lineages of euryapsids (plesiosaurs), "parapsids" or more properly ichthyopterygians (ichthyosaurs) and even among some lepidosaurians (Platynota: Mosasauria). The whole range of those aquatic tetrapods demonstrates extensive histological specialization linked with their mode of life. They have to be studied further at the histological level before conclusions can be drawn about their kind of physiology. On the other hand, available histological data (Seitz, 1907; Gross, 1934; Enlow and Brown, 1957) are completely accordent with the presence of endothermy among pterosaurs (Fig. 4).

Paleontological Discussion

Many papers have dealt, at length or incidentally, with the possible origin, evolution or implications of warm-bloodedness among various groups of fossil tetrapods, especially therapsids (inter alia Brink, 1956, 1967; Olson, 1959; Van Valen, 1960; Reed, 1960; Geist, 1972; Hopson, 1973) and some Mesozoic archosaurs, including dinosaurs (Colbert et al., 1946; Schuh, 1951; Russell, 1965; Ostrom, 1969; Bakker, 1961 b, 1972) and pterosaurs (Seeley, 1901; Broili, 1941; Schuh, 1951). Now, each of these works are so rich and interesting that they deserve extensive detailed discussion, which has been in part attempted elsewhere (de Ricqlès, 1973). Of course, they do not give an unanimous picture of the history of thermal physiology. Only the broadest currents of thoughts will be briefly recalled here and compared with the interpretation of the histological data presented above.

Prominent studies about the evolution of endothermy rely on a correlation between an upright gait (parasagittality) and an active metabolism (endothermy) (Schuh, 1951; Heath, 1968; Ostrom, 1969; Bakker, 1971 b), an opinion which has been rather vividly contested recently (Bennett and Dalzell, 1973; Feduccia, 1973). First of all, it is obvious that my interpretation of the histological data is relevant to a discussion of this topic. If, on the one hand, early archosaurs (erythrosuchids) as well as more or less primitive therapsids (titanosuchids sensu lato, gorgonopsians, therocephalians, anomodonts)were already endothermic, as I believe, there would be no correlation among them between endothermy and parasagittality, as they were all sprawlers or at best semi-erect animals. On the other hand, it is obvious that, in the modern world, there are still endothermic sprawlers (Monotremata and others) and, on the contrary, all really erect, parasagittal tetrapods are endotherms: there are no parasagittal ectotherms. Then, there seems to be at least some kind of relationship between gait and thermal physiology among terrestrial tetrapods. It is clear that parasagittality affords, perhaps but not necessarily at higher metabolical cost, a generally more effective locomotion on land than that afforded by a sprawling gait, especially among rather large animals. Now, is endothermy a necessary causal factor for the acquisition of a parasagittal gait (Ostrom, 1969), or, on the contrary, is it this advanced gait which has been the starting point of endothermy (Heath, 1968)?

In my point of view, it is among early, already more or less endothermic tetrapods which still had a sprawling or semi-erect gait that were laid the physiological bases for further anatomical evolution towards more effective locomotion and active (if possibly stereotyped) behavior, through the progressive acquisition of a parasagittal gait. It seems that such a gait was acquired much more completely and quickly among some lineages of archosaurs than among synapsids during the Triassic. In turn, this upright gait could indeed account for the success of those archosaurs during the Mesozoic, as advocated by Bakker (1971 b), along with other factors (Robinson, 1971). On the contrary, I disagree with Bakker (1971 b) and then would agree with Bennett and Dalzell (1973) and Feduccia (1973) about the geologic time of appearance of endothermy among archosaurs. Histological data point to a very early (Permian) origin of endothermy, both among synapsids and archosaurs, while the climatic evolution during the early Mesozoic (say, the mid-Triassic: Robinson, 1971) does not seem to have any bearing on the initiation of endothermy among archosaurs. But if endothermy was already present among some archosaurs during this period, it could have been easily maintained as a relatively inexpensive condition under a hot, equable climate and, in turn, could even have led rather quickly towards new adaptive niches exemplified by pterosaurs and ultimately birds. At the same time, an upright gait could have been a preadaptive basis for niches exploiting very large body size, as exemplified by dinosaurs (see below).

Parasagittality and possible correlative adaptations towards large size, fast movement, and more active behavior on land seem retrospectively linked with endothermy, but occurrence of an upright gait in a given lineage can give little clue about the time of origin of endothermy in the lineage. In the modern world, large varanid lizards which are sprawlers or at best have a semi-erect gait are able, in hot climates, to raise their inner temperature through active moving (see, inter alia, Bakker, 1971 b). This incipient endothermy has possibly occurred many times in various lineages of extinct tetrapods, and thus endothermy may have been present before any obvious anatomical progress more or less linked with it, such as parasagittality, subsequently developed (de Ricqlès, 1972 c, d).

Now, a relationship between size and gait seems acknowledged by every student in the field (Ostrom, 1969; Bakker, 1971 b; Bennett and Dalzell, 1973;

Feduccia, 1973). For any terrestrial animal, really large size can be
reached only by the acquisition of an upright gait, for obvious mechanical
reasons. Large size can be achieved by sprawlers only if they become
amphibious or aquatic. If we turn now to early (Permian) endotherms neither
the limb anatomy nor the gait was changed, at the beginning, from the primitive
terrestrial sprawling gait, but the occurrence of endothermy offered now the
evolutionary possibility of active and extensive growth towards larger body
size. This in turn, for mechanical reasons, would have created a strong
pressure towards the evolution of more and more upright, semi-erect, then
fully erect limbs. Those transitional stages would be demonstrated by such
forms as, among others, titanosuchians, deinocephalians and erythrosuchids.
Extensive pachyosteosis (2) of such forms, which are the first really large
terrestrial tetrapods, is most probably linked to high rates of growth
combined with retention of primitive bone morphology (de Ricqlès, 1972 c, d,
1973). Once the mechanically efficient erect posture was acquired (especially
among various archosaurs, and to a far lesser extent among theriodonts),
further evolution of the growth fields (Enlow, 1968) that modulate bone
morphogenesis would in turn have favored more and more slender and elongate
bone morphology, well suited to rapid motions. Such advanced morphology,
again, requires many histological refinements: more precise spatial
organization and much higher rates of differentiation of the chondrocytes in
epiphyseal plates, and more extensive growth remodeling in metaphyseal regions,
which are both costly for the metabolic budget. Growth remodeling and the
intensive turnover of phosphocalcic salts associated with rapid growth would
have favored a more and more intensive Haversian substitution, already
favored by an expansion of highly vascularized fibro-lamellar primary tissues.
Spongy bone, also experiencing extensive growth and metabolic remodeling,
would thus have gained the opportunity to adapt itself more precisely to
heavy mechanical requirements during individual growth. All those improvements
in locomotion ability would have been in turn functionally associated with a
more and more active life, itself permitted by a more active metabolism
(de Ricqlès, 1972 c, d, 1973) (Fig. 5).

Endothermy, growth patterns, gait, bone bone morphology and histology have
been functionally linked. In various archosaurian lineages, occurrence of
an upright gait, even of bipedalism, of elongated limb bones, large body size,
fibro-lamellar cortical apposition, intensive Haversian substitution, and
rapid, continuous growth have been phyletically linked with the development
of a more and more active metabolism. In my view, these anatomical, histological
and physiological characteristics are at least partially interrelated, as they
are all consequences, and expressions, of endothermy. As far as archosaurs
are concerned, this interpretation of the histological data agrees, at least
on some fundamental points, with other studies based on anatomy and paleoecology
(Schuh, 1951; Russell, 1965; Ostrom, 1969; Bakker, 1971 a, b, 1972). More
recently, however, discordant opinions have been brought into the picture
(Bennett and Dalzell, 1973; Feduccia, 1973; Spotila et al., 1973; Thulborn,
1973). In spite of the fact that those works make no mention of the

                   *   *   *

(2). Pachyosteosis among titanosuchians and deinocephalians should not
be confused with morphological and histological peculiarities often found
among aquatic tetrapods (see Fig. 1) which are also named pachyosteosis but
which in fact have a quite different significance (see Nopcsa and Heidsieck,
1934). Of course, the pachyosteosis associated with adaptation to aquatic
life is neither linked with lamellar-zonal or fibro-lamellar patterns of
periosteal bone, nor with endothermy or ectothermy, occurring both among
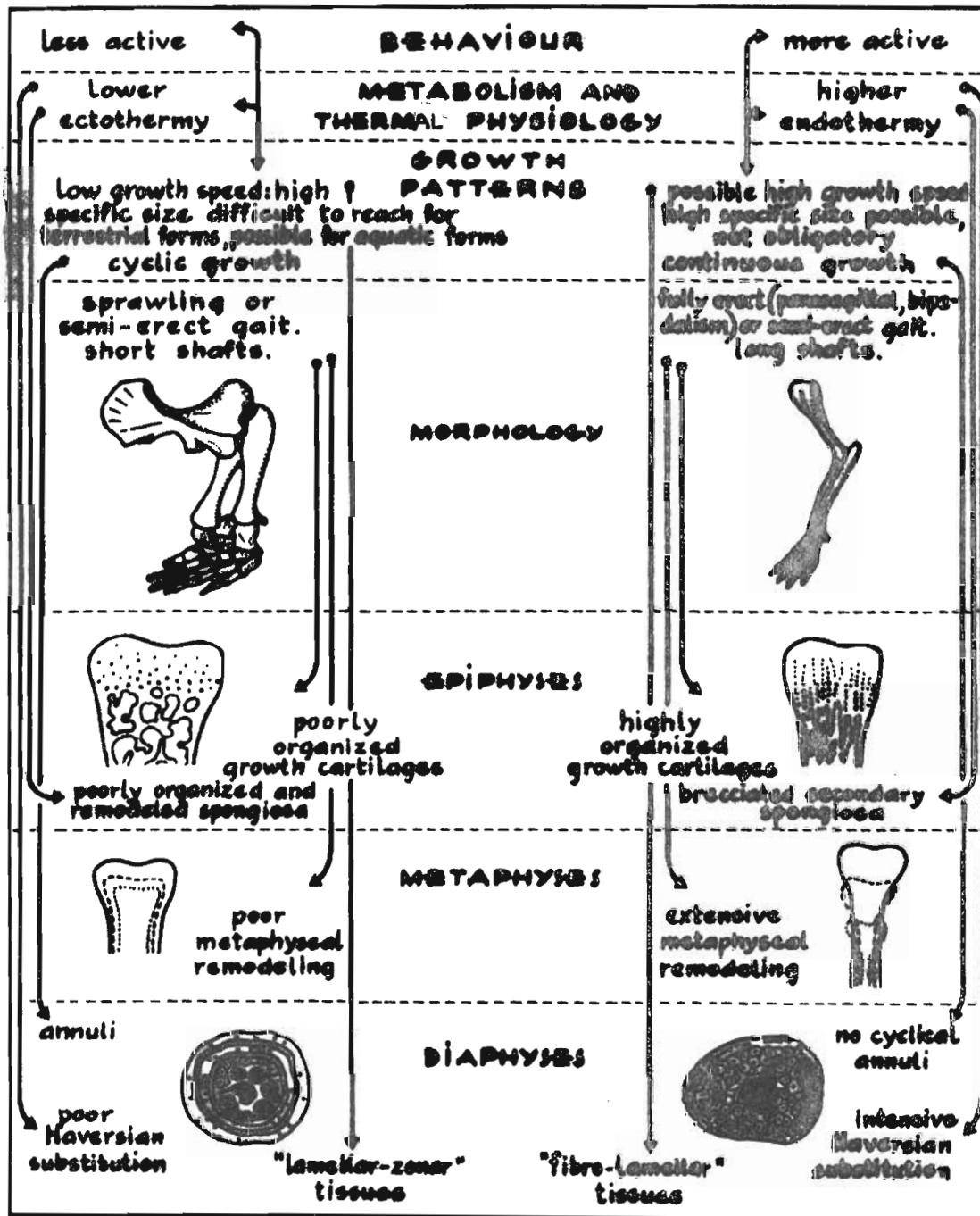ectotherms and endotherms.

A. de RICQLÈS

Figure 5. An attempt to visualize gross functional relationships between bone histology, morphology, and thermal physiology among terrestrial tetrapod vertebrates. Typical primitive ectothermic pattern is shown on the left, typical advanced endothermic pattern on the right of the picture. Many groups of tetrapods may of course show various intermediate conditions, for one or several factors involved, and hence should be placed at or near the middle of the picture. Modified from de Ricqlès, 1972 d.

histological data, they all offer interesting challenges to the interpretation of dinosaur endothermy. As exemplified by those recent studies, nearly the whole argument about the thermal physiology of Mesozoic archosaurs is based on various interpretations of supposed functional relationships among body temperature, energy metabolism, size and gait. Supposed relationships between endothermy and an upright, parasagittal gait are of course a special bone of contention about which this writer has given above his own point of view.

Now, as paleohistological data are most obviously related to body size and rate of growth, it is from this point of view, the meaning of large size relative to other, anatomical, physiological and behavioral factors, that I wish to discuss the problem.

If, for a moment, therapsids, dinosaurs and even some thecodonts are put out of the mind as "reptiles", one is compelled to notice that most other tetrapods of the Mesozoic and late Paleozoic, including stegocephalians, had body sizes of the same order of magnitude as modern, living, reptiles. The biggest non-therapsid, non-archosaurian reptiles were all water-dwelling forms, for which the problems linked with growth are very different from those of land dwellers, and whose thermal physiology and energy metabolism are still open questions anyway. Thanks to optimal climatic conditions, it is likely that the sizes of the biggest crocodiles (Sarcosuchus, Phobosuchus), plesiosaurs (Kronosaurus), and mosasaurs (Tylosaurus) were not far from the ultimate limits to which ectotherms could grow, with length (if not bulk) approximating those of the biggest sharks (Rhincodon), which, admittedly, can get large at lower metabolical expense, thanks to the use of cartilage instead of bone for skeletal construction. From the point of view of size alone, therapsids, various thecodonts and obviously dinosaurs are exceptions among terrestrial reptiles, with dimensions and weights of the same order of magnitude as those of the biggest Cenozoic and living birds and mammals. It seems unlikely that optimal climatic conditions alone (see below) could have induced such patterns of growth among ectothermic therapsids and dinosaurs only, as other contemporaneous land-dwelling reptiles had sizes approaching those of modern reptiles. It seems to me probable that the peculiar patterns of growth commonly met among therapsids and archosaurs were instigated by some physiological peculiarities, the most likely being rather high metabolic rates and consequent endothermy. This would in turn help to solve another problem, that of individual longevity among large dinosaurs.

If the data on dinosaur weights computed by Colbert (1962) are accepted, it would seem that, using known rates of growth of large modern ectotherm reptiles (see Bellairs, 1969), longevities of at least two centuries and probably many more would be needed for the adult weights of dinosaurs to be reached (de Ricqlès, 1972 c, d). This is perhaps not an impossible situation but the principle of uniformitarianism invites us to seek another explanation, as no longevities of such magnitude are known for living animals. On the contrary, if the rates of growth of large modern mammals are used, as indeed suggested by the complete similarity of bone histology in the two groups, the scale of weight of dinosaurs would be reached within few decades. This is a reasonable assumption that fits well with the known longevities of large animals today.

If only uniformitarianism is to be taken into account, one would be compelled to use known rates of growth of big modern endotherms to reach the computed weights of dinosaurs within known scales of longevity (de Ricqlès, 1972 c, d, 1973). This would afford, I believe, another presumption for endothermy among dinosaurs, because a large ectotherm, with its lower rate of metabolism, just could not have sustained its growth at the necessary rate.

Until now, I have relied on the uniformitarianism principle to hypothesize similar situations in living and fossil animals, as well as similar external circumstances, but it could be argued that bone tissues apparently associated with endotherms in the modern world could have pertained to ectotherms during the Mesozoic, as environmental conditions were more favorable at the time for ectotherms: in such a case, bone histology would not indicate the thermal physiology of extinct forms. The widespread occurrence of hot or warm, equable climates during the Jurassic and Cretaceous (Axelrod and Bailey, 1968; Robinson, 1971) could have favoured an optimal ontogenetic development among ectotherms as well as a phylogenetic trend in the same direction, but these lines of reasoning are not as compelling as they may look.

First of all, in the modern world, most tetrapods, especially ectotherms living in hot climates, have often developed behavior not for getting more heat from an external origin but, on the contrary, to conceal themselves against overheating (see for instance Templeton in Whittow, 1970, who gives numerous references on this subject). Much higher temperatures than those of the present day tropics would be harmful, both for animals and plant life. As enzymes and other proteins are prone to destruction from even slight overheating, I think it unlikely that the whole living world of the Mesozoic was adapted to much higher temperatures than those which are still found in our hottest regions. Consequently, I do not think it likely that young Mesozoic reptiles could have faced much higher external temperatures than those of our tropics, or could have taken much advantage of them anyway to get large. On the other hand, one does not get a larger ectotherm just by offering it a hotter environment; each species has its own optimal requirements. It is perhaps as easy to think that dinosaurs were already endotherms than to hypothesize that they were ectotherms with enzymatic systems nevertheless specialized to work at a very high, constant, body temperature exclusively obtained from external origin in very hot climates.

Finally, the occurrence of bone tissues which are common among modern endotherms extends over many geological periods, each of which experienced extensive climatic changes and various temperature ranges. If the plexiform tissue (Enlow and Brown, 1956; de Ricqlès, 1968 a, b, 1973) of a supposedly ectothermic mid-Jurassic sauropod (Fig. 3) is also found--as is indeed the case--in the bones of an upper Permian supposedly ectothermic therapsid, this would mean that in both cases this variety of the fibro-lamellar pattern, which is adapted to a rapid and massive bone deposition, was associated with the same hot, equable climate that would have favored extensive growth among "reptilian" ectotherms in both cases. However, it is a well known fact that climates were quite different in these different periods (Robinson, 1971). I do not believe, consequently, that the bone tissues just reflect the same opportunities of optimal growth for ectotherms, restulting from the same optimal external circumstances. Rather, they demonstrate that, in spite of varied external circumstances, there was the same inner physiological basis in each case to induce the same patterns of active growth.

In an interesting paper, Spotila et al. (1973) have recently tried to quantify body temperatures of large reptiles, following the lines of earlier work by Colbert et al. (1946), in which dinosaurs are understood as ectothermic homeotherms. That the bulk of large dinosaurs prevented quick changes in body temperature and hence afforded practically a state of homeothermy seems indeed unquestionable and I fully agree with this opinion, but much more controversial remains the question of endothermy among dinosaurs. Spotila et al. would favour an ectothermic-homeothermic model for dinosaurs. I can agree with those authors when they state (1973: 400) "that it is unlikely that (dinosaurs) . . . would have evolved a high metabolic rate for thermoregulation only",

and, later on: "There is no need to postulate any but reptilian physiological characteristics to these giants for thermoregulatory purposes," but the hypothesis of endothermy among dinosaurs is helpful in understanding other aspects of their biology than thermoregulation (Ostrom, 1969; Bakker, 1971 a, b; 1972). Endothermy seems to me useful to explain very high rates of sustained growth experienced by young dinosaurs, as is demonstrated both by histology (see above and de Ricqlès, 1968 a) and the structure of populations (Richmond, 1965). One is not obliged, on the other hand, to imagine for the dinosaurs a metabolism as active as those of modern birds or even modern Theria. Obviously, there are all possible transitions in metabolic activity between a typical "reptilian" level and those of modern endotherms. Where the exact position of dinosaurs is along this scale is difficult to demonstrate unequivocally. Moreover, it is quite possible, and even likely, that the rate of metabolism was different among various groups of dinosaurs themselves, but we now have no evidence to assess such differences.

In the "ectothermic–homeothermy" hypothesis, young dinosaurs would have experienced a typical reptilian thermal physiology and then shifted to mass homeothermy when a sufficient bulk was subsequently achieved. Even Spotila et al. are obliged to concede that the survival of the young "may have required some thermoregulatory behavior. . . that was not evident in adults" (1973:400). It is perhaps easier to understand high speed of continuous growth, high bone turn-over and anatomical adaptations to active terrestrial life by a common background of endothermy both for youngs and adults. Admittedly, this would have been completed and refined by mass homeothermy during long adulthood and by possible behavioral homeothermy in the young. It seems to me that the position of Spotila et al. is paradoxical when they accept as a "typical reptilian physiology" animals with "high, constant body temperature". . . "possibly in the typical mammalian range", coupled at the same time with a low metabolic rate. How and why could the metabolism be kept so low with such a high, constant body temperature? In my opinion it remains that big dinosaurs had a peculiar physiology by any standards, one which can hardly be regarded as "typically reptilian" but must be better understood as something of its own.

It is often argued that sauropods could not have been endotherms because the high metabolic cost of endothermy could not have been afforded by such huge animals, with relatively small mouths and weak teeth, but the argument can be turned around. First, endothermy is likely to have been associated with a very active enzymatic apparatus working at a high, constant temperature and allowing a very efficient anabolism, exactly as among modern birds. Secondly, because they were so large, sauropods may have reached true endothermy (associated, of course, with mass homeothermy, which seems now perfectly clear) at relatively low metabolic cost, especially under warm climates. Surface-to-volume ratios demonstrate that it costs relatively less to be a large, rather than a small, endotherm.

Now the supposed combination of small size, lack of insulation and endothermy in young dinosaurs seems "lethal" to Thulborn (1973), but very little is known, in fact, of their ecology and behavior. It is not at all impossible, after all, that such a kind of physiology was indeed very efficient under warm, equable climates such as reconstructed for the Mesozoic (Axelrod and Bailey, 1968). Even hatchling ostriches are active at once (Berlioz, 1950) and their down covering seems to have a poor insulative capacity. All we actually know about young dinosaurs, thanks to histology, is that they enjoyed a very active, continuous, sustained growth, which seems to me easier to understand associated with a rather active metabolism. On the other hand, there is no evidence whatsoever for or against the presence of fatty or insulative organs in very

young, small dinosaurs, but this question has some intriguing aspects.
Criticizing Bakker's suggestions (1971 b) of air sacs in dinosaurs, Feduccia
(1973:168) is led to admit that small endothermic dinosaurs would have had
to have insulatory coverings. Contrary to his belief, however, there are
some indications that this could well have been the case (Broili, 1941;
Jensen, 1969; Stoll, 1971; Maderson, 1972; see also earlier works of Lowe,
e.g. 1928, 1935). Bird feathers are such complex and specialized anatomical
and histological structures that it is unlikely that they appeared all at
once, say in a "pre-Archaeopteryx" stage. On the contrary, it seems likely
that "pre-feathers" progressively evolved for a long time among "pro-aves".
Moreover, it is generally agreed that the effective presence of hair or
feathers must be considered as definite evidence of endothermy (Cowles,
1958)--the converse proposition not being correct, of course--and it is thus
very clear that those "pro-aves", whatever they were phyletically, were in
turn true endotherms. Now, recent anatomical reappraisals point to a very
close coelurosaurian-avian relationship (Ostrom, 1974) which would mean, in
turn, that endothermic pro-aves are to be looked for among small saurischian
dinosaurs. Indeed, we already have some evidence, if still slight, that
some "reptilian" archosaurs had a hairy or "pre-feathery" cover (Duerden,
1922; Broili, 1941; Jensen, 1969; Stoll, 1971; Maderson, 1972 a, b; Sharov,
1970; Ellenberger, 1974). A hairy covering seems now an unquestionably well
established fact among pterosaurs (Broili, 1941; Schuh, 1951, who gives earlier
references; Sharov, 1971). All in all, those lines of evidence and of
reasoning point towards the effective occurrence of endothermy among Mesozoic
archosaurs, including at least some lineages of dinosaurs.

Feduccia's comments (1973) on the low ratio of brain to body size among
dinosaurs which, in his opinion, prevents the possibility of endothermy
among dinosaurs, may not deserve as much weight as it seems. First of all,
Feduccia does not explain or demonstrate any functional relationship between
endothermy and brain-to-body ratios. Advanced, presumably endothermic,
therapsids still had a relatively small brain (Hopson, 1969). On the other
hand, the ratios are biased "against" dinosaurs simply because they are
(generally) very large animals with consequently poor brain-weight indices
anyway. But, even with this, the ratio of brain to body weight seems
roughly the same in ornithomimid dinosaurs and in good endotherms like
ostriches (Russell, 1972). It seems that one is always impressed by the
dinosaur's small brain relative to body size, ignoring the meaning of the
absolute volume of the brain itself. A Tyrannosaurus neurocranial cavity of
530 cc. could contain a brain of at least 250 cc. (Osborn, 1912). If the
volume of individual cells was roughly the same as in modern crocodiles, and
if the architectonics were at least of a similar general pattern (which is
again a conservative assumption, the architectonic pattern being in all
probability at an intermediate stage between crocodiles and birds), this
volume is in itself obviously quite enough to house a highly complex brain,
able to control an active, if stereotyped, behavior, associated with a rather
high metabolism. After all, such a brain would fall, in absolute weight,
within the range of those of living lions and grizzlies (Crile and Quiring,
1940) and would be more than six time the weight of an ostrich's brain, the
largest modern endotherm of archosaurian lineage.

Both Bennett and Dalzell (1973:170) and Feduccia (1973:166) seem doubtful
about the very presence of an upright gait associated with parasagittal
locomotion in dinosaurs. However, anatomical and ichnological evidences have
been compelling for a long time that this was indeed the case. The older
concept of dinosaurs as aquatic sprawlers should not be revived again.

Another comment of doubtful value is made by Feduccia (1973:167) about dinosaurian epiphyseal structures, which he believes to be less complex than in mammals and (implicitly) unable to have supported active endotherms on land. Indeed, dinosaurian long bones lack independently ossified epiphyses, but everybody acquainted with their long bones will agree that they have well-formed, fully efficient joint structures, well suited to an active, fully terrestrial life. The thick cartilagineous epiphyseal surfaces of sauropods are an adaptation to active growth and heavy weight (de Ricqlès, 1968 a, 1972 a). Above all, modern lepidosaurs have, like mammals, fully independently ossified epiphyses (Haines, 1942, 1969) and are nevertheless (as a rule) good ectothermic sprawlers. On the contrary, birds are endotherms with an upright gait and are nevertheless nearly completely deprived of any kind of independent epiphyses (Haines, 1942), exactly like their dinosaur close relatives. Obviously, there is no correlation between presence or lack of independently ossified epiphyses, sprawling or erect gait, and endo- or ectothermic physiology. Independent epiphyses have been separately acquired during presumably Jurassic times both by synapsids and lepidosaurs and may have nothing to do with thermal physiology. Advanced, probably endothermic, therapsids still had typically reptilian epiphyseal mechanisms (Haines, 1938; de Ricqlès, 1972 a; 1973) and at best a semi-erect gait (see Jenkins, 1971, for cynodonts). It is interesting that long bone evolution among synapsids has been of the mosaic type, with advanced features (histology of diaphyses in therapsids) associated with conservative ones, such as epiphyseal mechanisms. This last peculiarity seems clearly linked, in turn, to a rather conservative gait and bone morphology in some instances (dicynodonts). In more advanced endotherms (mammals), definitive epiphyseal stabilization during adulthood may have evolved as a refinement used to stop growth and hence allows the exploitation of ecological niches linked to small or moderate body size, in spite of the very high rates of growth available through the intensity of metabolism, and which, otherwise, would spontaneously lead towards larger body size (3). It is worthy of note that both lepidosaurs and synapsids evolved independent epiphyses when they were forced towards small size during the Jurassic, as a result of the competition with big archosaurs.

To sum up, recent comments (Feduccia, 1973; Spotila et al., 1973; Bennett and Dalzell, 1973; Thulborn, 1973) on the thermal physiology of extinct forms, notably dinosaurs, afford interesting and sometimes very useful challenges to earlier works (inter alia Schuh, 1951; de Ricqlès, 1969, 1972 c, d; Ostrom, 1969; Bakker, 1971 a, b; 1972) on the subject, but they nevertheless fail to refute the basic thesis of an early, active, not typically "reptilian" pattern of physiology among various lineages of "infra-mammalian" and infra-avian" tetrapods, which is now supported by a large array of facts stemming from ecology, anatomy and histology.

Concluding Remarks

It seems likely that studies permitting a better understanding of thermic physiology and an appreciation of gross physiological levels of organization among fossil vertebrates will receive more and more attention in the future, and will allow a more meaningful reconstruction of tetrapod evolution. It is clear however that the intricate development of endothermy and of bone histology among tetrapods represent very complicated evolutionary processes. I am fully conscious that this contribution may have oversimplified the subject, its

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(3). During the Cenozoic and especially in the Pleistocene, rodents and insectivores which inhabited islands in the Mediterannean region have repeatedly and quickly evolved towards large body size, thanks to the lack of large predators in those isolated areas (see e.g. Thaler, 1973).

main objective being to draw attention towards paleohistology as a tool in vertebrate paleobiology. However, this may be, it is necessary to review some topics which have special bearing on the evolution of endothermy as it has been understood here.

Archosaurs and synapsids have had extensive evolutionary interactions all during their history, with alternate phases of success and shadow for each lineage. A better understanding of the history of endothermy is basic for a more meaningful explanation of the various factors involved in this story.

The great problem of extinctions, of the therapsids at, or near, the top of the Triassic, of the dinosaurs and many others at the end of the Cretaceous, exemplifies events of special interest. It is nearly certain that at least the problem of late Mesozoic extinction is directly related to the nature of thermal physiology in some of the lineages involved (Russell, 1965; Axelrod, and Bailey, 1968).

Finally, evidence for endothermy in various lineages of Mesozoic tetrapods generally accepted as members of the class Reptilia, once more raises questions about the validity and usefulness of this systematic assemblage. More generally, this invites a critical reappraisal of the meaning of our systematic tools and of the concepts underlying them. If such forms as therapsids, some thecodonts, pterosaurs and dinosaurs were endotherms, if some of them, at least, had hairy or feather-like coverings, it becomes nearly impossible to propose any reasonably concise definition of a class Reptilia that would encompass all the forms currently and classically recognized as reptiles.

Amniotes may well turn to be a monophyletic, natural, group and hence Reptilia sensu lato may well turn to be a natural assemblage, at least at the beginning of their history. This possible acceptance of the formal validity of reptiles as a natural group would thus be acknowledged, however, within the frame of vertical, cladistic, thinking, but of course the class Reptilia was formalized within horizontal, gradistic, thinking. In fact, all the great traditional classes are inherited from a fixist period of scientific thinking, when paleontology had little to do with formalized systematics. For this reason, they always more or less cover horizontal organizational levels, as promoted by Schaeffer (1965), or grades. But now, do the reptiles sensu lato form a real organizational level or grade of their own? From the above, it is clear that reptiles may well turn out to be a good clade but that they certainly encompass more than one grade (de Ricqlès, 1972 d).

If definition of a class Reptilia must be kept within its historical frame with horizontal, gradistic thinking, it seems necessary that the endothermic therapsids and dinosaurs, among others, should be excluded from it. Together with other problems, this has prompted various comments about the best boundaries of the class Reptilia (e.g. Van Valen, 1960; Reed, 1960; Brink, 1967; Hopson, 1969; de Ricqlès, 1972 c, among many others). Most recently, however, Bakker and Galton (1974) have proposed a new approach to this problem, as far as archosaurs are concerned, and it is their proposal that I wish to discuss now.

Bakker and Galton propose to group some endothermic archosaurs in a class Dinosauria that would encompass some endothermic dinosaur-like thecodonts, saurischians, ornithischians and birds. I think that such a systematic assemblage should not be accepted at once as 1°/ it uses as a systematic tool a characteristic of doubtful practical systematic value, 2°/, it does not use this same characteristic in the same way for the various groups involved and hence is a system with dubious inner logic and rationality, and 3°/, it invites confusion between cladistic and gradistic systematic categories. Let me quickly review these three points.

First, an important inadequacy of the classification proposed by Bakker and Galton is the formal use of endothermy as a key characteristic in systematics. I think that in spite of their obvious biological interest, physiological characteristics are not very good tools in formalized systematics and should best be avoided because they are necessarily at best hypothetical and at worst controversial in paleontology. Above all, they are not "all or nothing" characteristics and thus cannot help to draw clear-cut boundaries between formal systematic assemblages. For instance, regarding the class Dinosauria sensu Bakker and Galton (1974), it is now, as far as I know, impossible to draw definite boundaries, on histological grounds, between all definitely ectothermic (reptilian) and endothermic ("dinosaurian") archosaurs: lack of data is still enormous. In the same way, it is still difficult, and perhaps of little meaning, to draw sharp boundaries, on histological or other grounds, between ectothermic (reptilian) synapsids (pelycosaurs) and endothermic mammals sensu Van Valen (1960) (including therapsids); see also the above section on definition and terminology. Physiological characteristics are basic to an adequate understanding of fossil vertebrates as animals, but they are even more controversial and difficult to handle than are anatomical characteristics in formalizing boundaries in systematics.

Secondly, Bakker and Galton include birds in their new class but at the same time they exclude pterosaurs. However, we have at least as good reasons to accept endothermy for pterosaurs as for dinosaurs (Saurischia and Ornithischia). If the boundary of the new "class Dinosauria" is mainly drawn on the possession of endothermy, I do not understand why pterosaurs should not be included in this class, as they are also most probably descendants of early endothermic thecodonts. In the same way, at least some thecodonts themselves were probably endotherms and not far from the roots, if not necessarily at the roots themselves, of endothermic dinosaurs. Why should they be excluded from the new "class Dinosauria"?

Thirdly, we have already noticed that the classical concept of a class Reptilia (sensu lato) is somewhat unnatural in that it encompasses more than one great structural level of organization or grade. The same objection can be raised against Bakker and Galton's concept of a class Dinosauria. Even if I fully agree with an extremely close functional and phyletical relationship between "higher" endothermic archosaurs (Saurischia, for instance) and birds, nevertheless, I am not ready to accept them all as only one structural organizational level or grade. In horizontal, gradistic systematics, a formal distinction must be kept between birds, which obviously form a good grade of their own, and a "supra-reptilian" but nevertheless still "infra-avian" grade which, in my opinion, is filled by endothermic thecodonts, dinosaurs (saurischians and ornithischians) and pterosaurs. Hence, the class Dinosauria sensu Bakker and Galton (1974) is obviously a cladistic, not a gradistic, assemblage, but it has been noted above that vertebrate classes, from their very conceptual and historical roots, are, and should perhaps remain, good, horizontal, gradistic, systematic assemblages. The new "class Dinosauria" is more like an incomplete, arbitrarily delineated clade, than a formal class.

If one thinks it absolutely necessary to formalize in a gradistic classification the interrelationships of archosaurs, one could perhaps propose a class Dinosauria with endothermic thecodonts, pterosaurs, saurischians, and ornithischians as included orders. Such a class Dinosauria would be a good grade, contrasting with the class Reptilia sensu stricto (ectothermic archosaurs and all other ectothermic amniotes) on the one hand, and against the class Aves, on the other hand. In the same way, it is possible, as sometimes advocated, to erect a class Therapsida between (ectothermic) reptiles and the class Mammalia.

In this writer's opinion, however, it is now much more useful to realize in ones mind that the familiar concept of the great class Reptilia encompasses more than one structural level of organization or grade, rather than to gamble on the erection of new formal gradistic categories, or to try to find new "natural" boundaries in what are obviously phylogenetic lineages.

Acknowledgments

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While this paper was in press, other works dealing with topics discussed
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