Bone microstructure and growth patterns of early mammals

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We present results of the first studies of the bone microstructure of early mammals, based on the Early Jurassic *Morganucodon*, the Late Cretaceous multituberculates, *Kryptobaatar* and *Nemegtbaatar,* and the Late Cretaceous eutherians *Zalambdalestes* and *Barunlestes*. Our results show that the two eutherian taxa grew relatively slowly with periodic pauses in growth indicated by the presence of rest lines, while the multituberculates and *Morganucodon* had a faster rate of bone formation that suggests an overall rapid growth rate that slowed down later in ontogeny. Comparisons of the early mammalian bone microstructure with that of non-mammalian cynodonts, extant monotremes, and placentals are also made, and significant differences in the rate of osteogenesis in the various groups are documented. Our findings suggest differences in the growth rate between the multituberculates and the Mesozoic eutherians, and moreover, both groups appear to have slower growth rates as compared to modern monotremes and placentals. Our results further suggest that the determinate growth strategy typical of extant mammals evolved early in the evolution of the non-mammalian therapsids. We speculate that the sustained, uninterrupted bone formation among the multituberculates may have been an adaptive attribute prior to the K-T event, but that the flexible growth strategy of the early eutherians was more advantageous thereafter.

Key words: Mammalia, Morganucodonta, Multituberculata, Eutheria, Cynodontia, bone microstructure, growth rate, Jurassic, Cretaceous.

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Introduction

A notable bias in the fossil record is that few Mesozoic mammalian taxa are represented by skulls and postcrania. As a consequence, much of the early evolutionary history of mammals presents an enigma since most of what is known is limited largely to tooth and jaw morphology (Lillegraven et al. 1979; Kielan-Jaworowska et al. 2004). Within these limitations, the phylogeny of early mammals is reasonably well understood (Luo et al. 2002). In contrast, however, the biology of Mesozoic mammals is poorly known (e.g., Kielan-Jaworowska 1970, 1979; Jenkins 1990; Novacek et al. 1997). Furthermore, although the morphological evolution of mammals from the non-mammalian cynodonts is reasonably well-documented, the physiological changes associated with this transition remain more elusive. For example, exactly when endothermy evolved in the mammalian lineage is uncertain, although there have been several suggestions that it evolved among the cynodont ancestors of mammals (e.g., Kemp 1982). Indeed, evidence for respiratory turbinals in the nasal cavities of Late Permian nonmammalian therapsids has been documented, and may be indicative of high ventilatory rates associated with endothermy in these taxa (Hillenius 1994).

Although bone microstructure has been studied to assess growth patterns in a diverse range of extinct vertebrates (e.g., Chinsamy 1997, 2002; Ricqlès et al. 2000; Sander 2000; Erickson et al. 2004; Ray and Chinsamy 2004), the microscopic structure of Mesozoic mammals has remained undocumented. The reason for this is probably the lack of adequate materials since Mesozoic mammals (except for those from the Late Cretaceous of the Gobi Desert and Early Cretaceous of China) are generally known only from teeth or fragments of jaws with teeth. The current study examines the bone microstructure of five early mammalian taxa, *Morganucodon*, two multituberculates (*Kryptobaatar* and *Nemegtbaatar*), and two eutherians (*Barunlestes* and *Zalambdalestes*) (see Kielan-Jaworowska et al. 2000, and Kielan-Jaworowska et al. 2004 for recent reviews), to deduce aspects of their growth and biology. The bone histology of these early mammals is compared with previous studies of nonmammalian cynodonts (e.g., Ricqlès 1969; Botha and Chinsamy 2000; Ray et al. 2004), as well as with a range of extant and extinct mammals (Enlow and Brown 1958; Klevezal and Kleinenberg 1969). For comparative purposes the bone microstructure of the Early Jurassic pleurodont lepidosaur, *Gephyrosaurus,* the nonmammalian cynodont, *Tritylodon,* an extant monotreme, *Ornithorhyn-*

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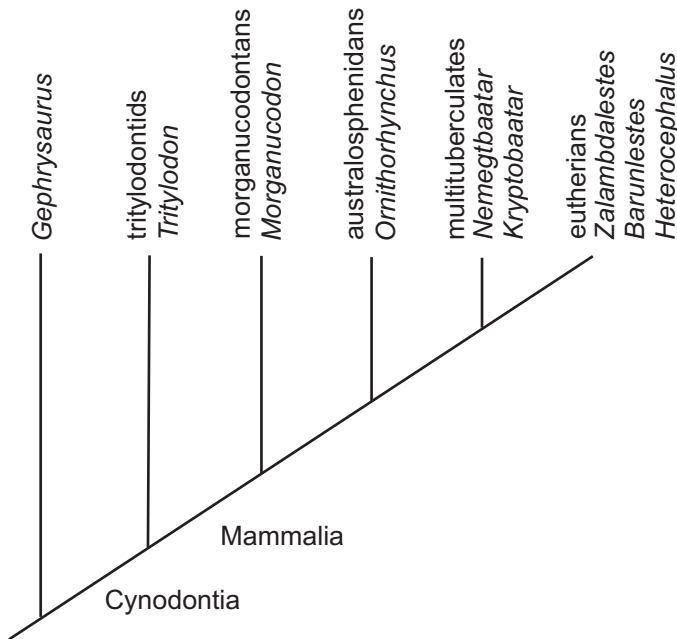
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Fig. 1. Cladogram showing the phylogenetic relationship of the taxa studied (simplified from Kielan-Jaworowska et al. 2004).

chus, and the extant eutherian *Heterocephalus* is also described. The cladogram (Fig. 1) illustrates the postulated phylogenetic relationship of the taxa studied.

Institutional abbreviations.—BPI, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; UCL.ADB, University College, Department of Anatomy and Developmental Biology, London, United Kingdom; ZOO/UCT, University of Cape Town, Department of Zoology, Cape Town, South Africa; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—ICL, inner (endosteal) circumferential layer; LAG, Line of arrested growth; OCL, outer circumferential layer; RBT, Relative bone wall thickness; t, average bone wall thickness; D, average cross-sectional diameter.

Materials and methods

The earliest mammals appeared in the Late Triassic, but fossils of these are fairly incomplete. *Adelobasileus* (Lucas and Luo 1993) and *Sinoconodon* (Crompton and Luo 1993; Zhang et al. 1998) are recognized today as the most basal mammals. However, the first well-represented early mammals in the fossil record, are the Morganucodonta (Kielan-Jaworowska et al. 2004, but see McKenna and Bell 1997 for an alternative interpretation), which are known from Late Triassic to Early Jurassic sites worldwide. The Morganucodonta were relatively small, shrew-like animals, having adult skull lengths measuring about 20–30 mm and total adult body lengths of about 150 mm (Kermack et al. 1973, 1981; Jenkins and Parrington 1976; Crompton and Luo 1993). Their rela-

tively small body size and the presence of sharp, tricuspid teeth are suggestive of an insectivorous diet. Various unnumbered skeletal elements from UCL.ADB of *Morganucodon watsoni* Kühne, 1949 (sometimes also referred to as *Eozoostrodon*; see Clemens 1979) from the Early Jurassic fissure fillings of the Pant Quarry, Wales, were sectioned in this study.

The multituberculates, which are rodent-like in external appearance, are the largest group of Mesozoic mammals, and begin to appear in the fossil record from about the Middle Jurassic (Kielan-Jaworowska and Hurum 2001). They are, however, best known from the Late Cretaceous and Early Tertiary of North America and Central Asia, though recent discoveries have extended their range to Africa and possibly South America (see Kielan-Jaworowska et al. 2004 for review). In this study, two femora of Late Cretaceous multituberculates, *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970 (ZPAL MgM-I/18) and *Nemegtbaatar gobiensis* Kielan-Jaworowska, 1974 (ZPAL MgM-I/81), from the Gobi Desert, Mongolia, were taken from diagnostic articulated specimens. The remains of *Kryptobaatar* were recovered from the Djadokhta Formation (?lower Campanian), while that of *Nemegtbaatar* are from the Baruungoyot Formation (?upper Campanian) (Kielan-Jaworowska et al. 2003).

In addition to these Gobi multituberculates, two eutherian species *Barunlestes butleri* Kielan-Jaworowska, 1975 (ZPAL MgM-I/77) from the Baruungoyot Formation and *Zalambdalestes lechei* Gregory and Simpson, 1926 (ZPALMgM-I/43) from the Djadokhta Formation were also studied. Both are placed in the family Zalambdalestidae. Mongolia is distinctly recognized for some uniquely complete eutherian specimens, such as *Zalambdalestes*, which has been reconstructed as a specialized jumping, hedgehog sized animal, with a long snout. *Barunlestes* is of approximately the same size but is more heavily built, with a more robust skull. A femur of *Zalambdalestes*, and a rib and femur of *Barunlestes* from diagnostic postcranial skeletons were thin sectioned in this analysis. Given that Mesozoic mammals are so rare, this small sample of *Barunlestes* also provided a rare opportunity to assess histological variation of two skeletal elements in a single individual.

Although detailed comparisons are made with the published literature on the bone microstructure of nonmammalian therapsids (e.g., Ricqlès 1969; Botha and Chinsamy 2000; Ray et al. 2004; Botha and Chinsamy 2004) to facilitate direct comparisons, we included in the current study a humerus (BPI/5671) and radius (BPI/5167) of the small non-mammalian cynodont, *Tritylodon* from the Early Jurassic *Massospondylus* range zone of the Elliot Formation, South Africa.

Several bones of the extinct pleurodont lepidosaur *Gephyrosaurus* sp. (UCL.ADB no number) (which probably looked like the small, heavily-built extant tuatara, *Sphenodon*), were also included in the current study. *Gephyrosaurus* sp. was specifically selected because it was contemporaneous with *Morganucodon*, and the studied bones were also re-

Table 1. List of investigated taxa.

Species name	Museum cat. number	Part of skeleton	Region and locality	Age and formation	Figure references
Barunlestes butleri	ZPAL MgM-I/77	femur, rib	Mongolia, Gobi Desert, Chulsan	?Late Campanian, Baruungoyot Fm.	Fig. 9
Gephyrosaurus sp.	UCL.ADB no number	femur	England, Wales, Pant Quarry	Early Jurassic	Fig. 3C
Heterocephalus glaber	ZOO/UCT no number	femur	Colony kept at Zoology Dept., UCT	Recent	Fig. 10
Kryptobaatar dashzevegi	ZPALMgM-I/18	femur	Mongolia, Gobi Desert, Bayan Zag	?Early Campanian, Djadokhta Fm.	Fig. 5
Morganucodon watsoni	UCL.ADB no number	ulna	Wales, Pant Quarry	Early Jurassic, fissure fillings	Fig. 3B$_1$
Morganucodon watsoni	UCL.ADB no number	femur	Wales, Pant Quarry	Early Jurassic, fissure fillings	Fig. 3B$_2$
Nemegtbaatar gobiensis	ZPAL MgM-I/81	femur	Mongolia, Gobi Desert, Hermiin Tsav	?Late Campanian, Baruungoyot Fm.[1]	Figs. 6, 7
Ornithorhynchus anatinus	ZOO/UCT no number	femur	Australia (vertebrate comparative collection, Zoology, UCT)	Recent	Fig. 4
Tritylodon sp.	BPI 5671, section Ty4B2	humerus	Clarens, South Africa	Early Jurassic, Elliot Formation	Fig. 2A
Tritylodon sp.	BPI 5167, section Ty1BII3	radius	Bethelehem, South Africa	Early Jurassic, Elliot Formation	Fig. 2B
Zalambdalestes lechei	ZPAL MgM-I/43	femur	Mongolia, Gobi Desert, Bayan Zag	?Early Campanian, Djadokhta Fm.	Fig. 8

[1] The red beds cropping out at the locality Hermiin Tsav, are regarded on the basis of the fauna as equivalent of the Baruungoyot Formation. Here we refer to them as Baruungoyot Formation for the sake of brevity.

covered from the Early Jurassic fissure fillings of the Pant Quarry in Wales. Indeed, since the animals are also similar-sized, several of the bones received were not positively assigned to either *Morganucodon* or *Gephyrosaurus* and were therefore labeled ambiguously.

The bone microstructure of the extinct mammals was compared with published histological descriptions of mammalian taxa. In particular, comparisons were made with that of the medium size, arboreal, Paleocene multituberculate, *Ptilodus* (Enlow and Brown 1958), as well as with a range of similar, small-sized extinct and extant mammalian taxa (Enlow and Brown 1958; Klevelzal and Kleinenberg 1969). Again, to enable direct comparisons we included in our analyses, femora of an extant monotreme, the duck-billed platypus, *Ornithorhynchus anatinus* Shaw, 1799 (ZOO/UCT no number), and the small eutherian, the naked mole-rat, *Heterocephalus glaber* Rüppell, 1842 (ZOO/UCT no number) (Rodentia, Bathyergidae). A rib and femur of *Ornithorhynchus* have previously been described by Enlow and Brown (1958), but the bone microstructure of *Heterocephalus glaber* has not been described previously. This rather atypical modern eutherian taxon was selected specifically because of its unusual life style and small size. As far as possible, long bones, particularly femora and humeri, were selected for histological study since

these generally preserve the best ontogenetic record of osteogenesis, particularly when sectioned in the midshaft region of the bone (Chinsamy and Dodson 1995; Chinsamy 2005). Furthermore, assessment of variation in the bone microstructure of various skeletal elements of nonmammalian synapsids (e.g., Ray and Chinsamy 2004; Ray et al. 2004) agrees with experimental findings that long bones, such as humeri and femora, have the fastest bone depositional rates in a skeleton (e.g., Starck and Chinsamy 2002). The histology of these elements in extinct animals therefore provides a reliable indication of growth during life. In the current study, other skeletal elements were also included when available (see Table 1).

Thin sections were prepared according to the methodology outlined in Chinsamy and Raath (1992). Because of the small size of the early mammal bone samples, and the rarity of the material, the histological sections were manually ground down on frosted sheets of glass with progressively finer grit of carborundum powder. Final polishing was done using a velvet polishing cloth and a diamond polishing suspension (Struers OP-U).

The relative bone wall thickness (RBT) of each of the thin sections is the ratio of average bone wall thickness, t, to the average cross-sectional diameter of the bone, D, expressed as a percentage, i.e. % RBT = $t/D \times 100$ (Bühler 1986).
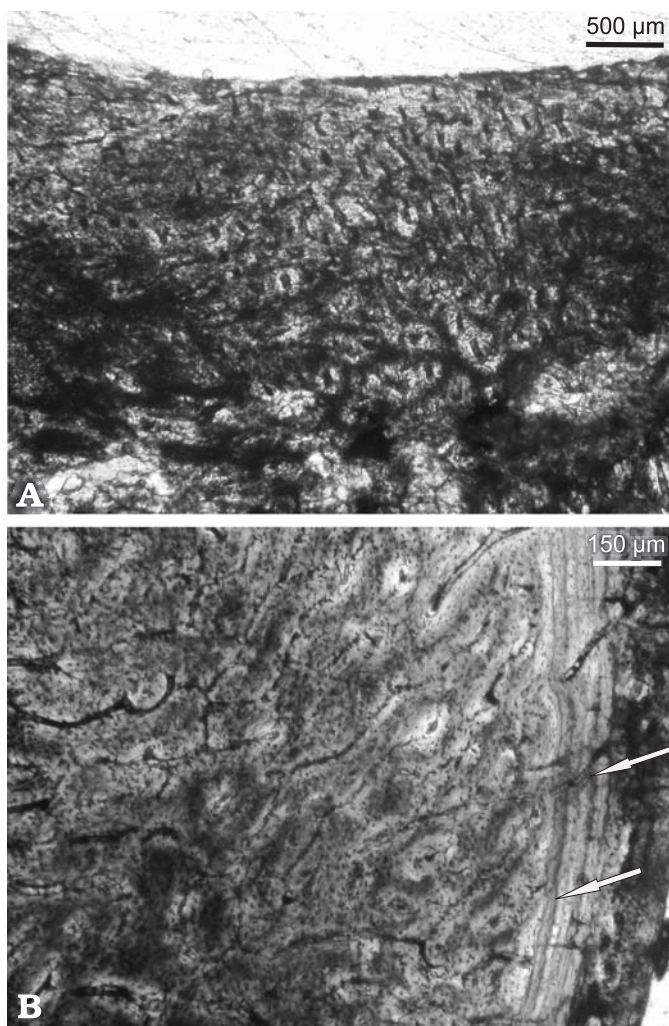
Fig. 2. *Tritylodon* sp. Early Jurassic, *Massospondylus* Range Zone, Elliot Formation, South Africa. **A**. Humerus, BPI/5671 section Ty4B2, showing the fibro-lamellar nature of the compacta. **B**. Radius, BPI/5167, section Ty1BII3, showing the peripheral development of parallel fibred bone with rest lines (arrows).

Results

Tritylodontian

***Tritylodon* sp**.—The *Tritylodon* humeral section depicted in Fig. 2 shows a thick cortical bone wall consisting of fibro-lamellar bone with abundant primary and secondary osteons distributed in the cortex. A cross section of a radius shows a similar bone tissue (Fig. 2B), but here a change in bone depositional rate is observed in the peripheral region, where lamellar bone with several closely spaced rest lines occurs.

Lepidosaurian

***Gephyrosaurus* sp.** (Fig. 3A).—Like the *Morganucodon* samples, several sections of *Gephyrosaurus* bones showed diagenetic alteration. However, there were some sections in

which the histology could be clearly assessed. Thin sections of the femur revealed a more or less elliptical cross section with an average bone wall thickness of about 79 microns (RBT of 20%). The compacta consists of essentially parallel-fibred bone tissue interrupted by several lines of arrested growth (LAGs). Several other sections also showed distinct LAGs. A maximum of nine LAGs were recorded in a transverse section of a femur (ZOO/UCT/196). The first LAG visible from the medullary cavity appears to be a hatchling line (e.g., Castanet and Baez 1991) since the bone formed earlier seems to be "embryonic bone" with its more haphazardly oriented, globular shaped, osteocyte lacunae. Following the hatchling line is a wide region of parallel fibred bone tissue, and then a series of fairly closely spaced LAGs. The next five LAGs are quite closely spaced, while the subsequent three are more widely spaced i.e., wider zonal regions are present.

Morganucodontan

Morganucodon watsoni (Fig. 3B, C).—The majority of the *Morganucodon* bone sections examined showed extensive diagenetic alteration. Only a few sections preserved microstructural details. Of these, an ulna of *Morganucodon* showed distinct woven bone tissue with large, irregularly oriented osteocyte lacunae and several primary osteons (Fig. 3B$_1$). No secondary osteons were visible, though several enlarged erosion cavities are evident in the compacta (Fig. 3B$_2$). In the same section, it appears that substantial endosteal resorption had occurred (Fig. 3B$_1$), and parallel-fibred bone tissue is evident only in a localized area peripherally. This area includes several rest lines, which indicate pauses in the rate of bone formation, and hence, pauses in growth. In a humeral section (not figured) a distinct region of parallel fibred bone tissue is also preserved, though no assessment of earlier bone tissue can be made. Bone wall thickness can be measured in a number of the skeletal elements, and for comparison with other specimens sectioned, the RBT of the femur measured 26%. In the femur, although microstructural details of the mid-cortical area are not discernible because of diagenesis, a fairly thick layer of endosteal bone is visible around the medullary cavity (Fig. 3C).

Monotreme

Onithorhynchus anatinus (Fig. 4).—Transverse thin sections of a femur of the extant monotreme *Ornithorhynchus* reveal a fairly thick, richly vascularized, compact bone wall. The bone wall measures about 2.3 mm in some areas, and consists of a mixture of bone tissue types. The overall texture of the bone appears to be a woven bone matrix, although in some areas this is interrupted by lamellar deposits of bone with osteocyte lacunae oriented in parallel (Fig. 4). The type of vascularization and the orientation of the vascular channels varies from simple blood vessels with longitudinal, circumferentially and radial orientations, to primary osteons with longitudinal and reticular arrangements. Some isolated secondary osteons are
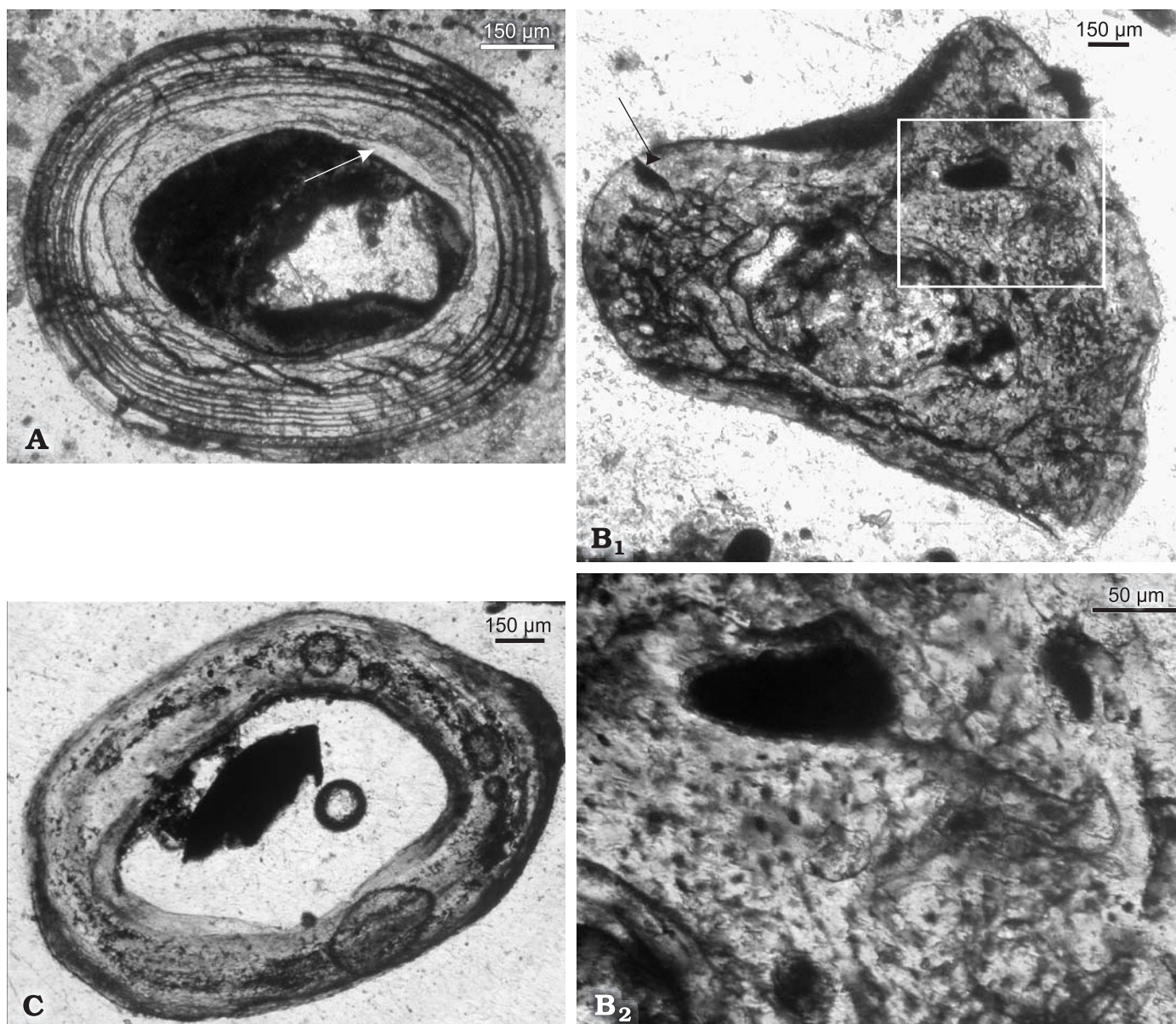
Fig. 3. Sections through bones of a lepidosaurian *Gephyrosaurus* sp. (**A**) and morganucodontan *Morganucodon watsoni* Kühne, 1949 (**B, C**), both from Early Jurassic, Pant Quarry, Wales. **A**. *Gephyrosaurus* sp. section of a femur (UCL.ADB no number; section catalogue number ZOO/UCT/193), showing the parallel-fibred nature of the compacta, and several lines of arrested growth (LAGs). Arrow indicates the embryonic bone. **B, C**. *Morganucodon watsoni*. **B**. Ulna, UCL.ADB no number; section catalogue number ZOO/UCT/132. B$_1$. Transverse section showing the predominantly woven nature of the compacta, and the general organization of the compacta. Arrow indicates the parallel-fibred bone in the localized area. B$_2$. A higher magnification of the framed area in B$_1$, showing the large erosion cavities, and the irregular orientation of the globular osteocyte lacunae. **C**. Femur (UCL.ADB no number; section catalogue number ZOO/UCT/164); transverse section showing the altered nature of most of the bone.

also present. Large parts of the compacta consists of compacted coarse cancellous bone, and in some instances, the entire bone wall is made up of this tissue. In parts of the midshaft section of the femur (ZOO/UCT/193), a narrow outer circumferential layer occurs, which consists of poorly vascularized lamellar bone. The inner medullary margin of the bone is highly resorptive, and consequently large trabecular spaces open into the medullary cavity, although the central part of the cavity is vacant. No inner circumferential layer of bone was evident.

Multituberculates

Kryptobaatar dashzevegi (Fig. 5).—Thin sections in the midshaft region of the *Kryptobaatar* femur revealed a fairly thin-walled compact bone region with a large medullary cavity (Fig. 5A). The average relative bone wall thickness is about 10% of the cross sectional diameter of the bone. The bone appears to be a mixture of parallel-fibred and woven textured type of bone tissue. Several channels occur within the bone, which appear to be at an early stage of primary
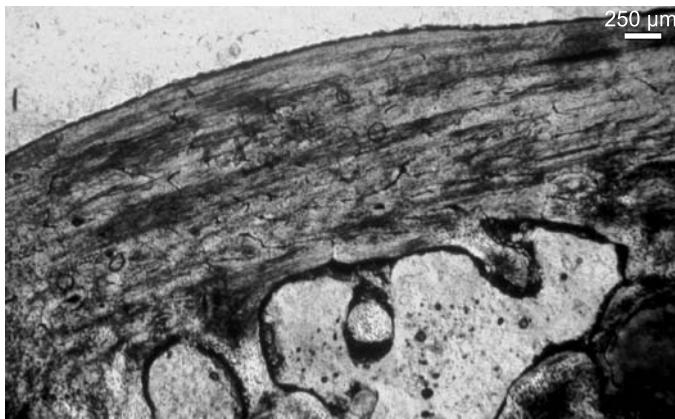
Fig. 4. *Ornithorhynchus anatinus* (Shaw, 1799); Recent, ZOO/UCT no number, femur, section catalogue number, ZOO/UCT/194. Transverse section showing the extensive fibro-lamellar bone and the episodically formed lamellar deposits of bone.

osteon formation. The peripheral and medullary margins of the bone are uneven, and are distinctly resorptive in nature (Fig. 5B).

Nemegtbaatar gobiensis (Figs. 6, 7).—The serially sectioned femur of *Nemegtbaatar* provided a good assessment of the microstructural changes associated with the growth in length and girth of the proximal part of the femur. Unfortunately, none of the sections were in the midshaft region, i.e., the area least affected by remodeling. The regions B_1, B_2, B_3, and B_4 in Fig. 6A show exactly where the cross sections were taken from along the femoral shaft.

All cross sections of the bone show distinct changes in the histological composition of the compacta in response to medullary cavity expansion, metaphyseal remodeling, and drift. Distinct changes in the cross sectional shape of the bone is also observed. Section B_4 shows a complex, stratified cortex, with variable microstructure across the section (Figs. $6B_4$, 7A). The compacta is largely made up of compacted, fine cancellous bone (Enlow 1962). Superficially this tissue looks like woven fibro-lamellar bone, however, upon closer inspection it is evident that this bone lies below a distinct tide line (= erosion line), which indicates its endosteal nature (Fig. 7A). In places, the lamellae have a more convoluted appearance. The endosteal bone varies from the compacted fine cancellous bone tissue described above, to a type with more convoluted lamellae, and also to a more lamellated type of bone tissue. The periosteal bone deposits mainly consist of parallel fibred bone with a distinct line of arrested growth interrupting the bone deposition (Fig. 7A). No cancellous bone is observed in the medullary cavity. The RBT is about 15%.

In general, the cortices of the other three sections have a similar, complex organization of bone. In Fig. 6, drifting in the medial direction is clearly evident. In section B_3, resorption occurs on the medullary side of the region that is drifting. This trend is observed in section B_2 as well, and here

there are increased deposits on the lateral margin of the bone, as well as peripherally. A small trabecular extension is observed in both section B_2 and B_3. The drifting is most pronounced in section B_1, and the compacta in this section, and in section B_2, largely comprises of a periosteal deposits of lamellar bone with some radially and longitudinally oriented channels. A small patch of bone appears to be true periosteally deposited woven bone, below which a tide line is present (Fig. 7B). Under the tide line deposition of endosteally formed lamellated bone occurs. The opposite side of the section shows resorption, and the more globular, haphazardly oriented, osteocyte lacunae are visible (Fig. $6B_2$). At the level B_1 of the femur, in the region of drifting (Fig. $6B_1$), there also appears to be resorption along the peripheral margins of the bone. Sharpey's fibres are abundant in this region, and canaliculi appear to be highly branched.
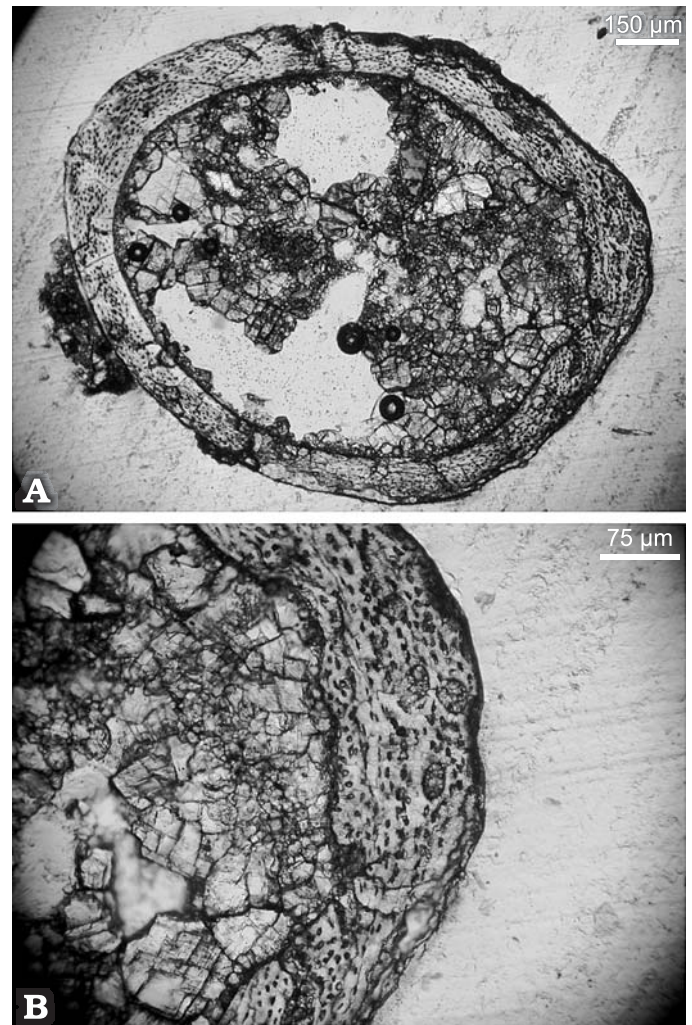

Fig. 5. *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1971 ?early Campanian, Djadokhta Formation, Bayan Zak, Gobi Desert, Mongolia, femur (ZPAL MgM-I/18; Section catalogue number, ZOO/UCT/184). **A**. Low magnification of the femur showing the overall structure of the cross section. Note the woven bone nature of the thin bone wall. **B**. A higher magnification of the same section, illustrating the channels in the bone, and the irregular peripheral and medullary margins of the bone wall.
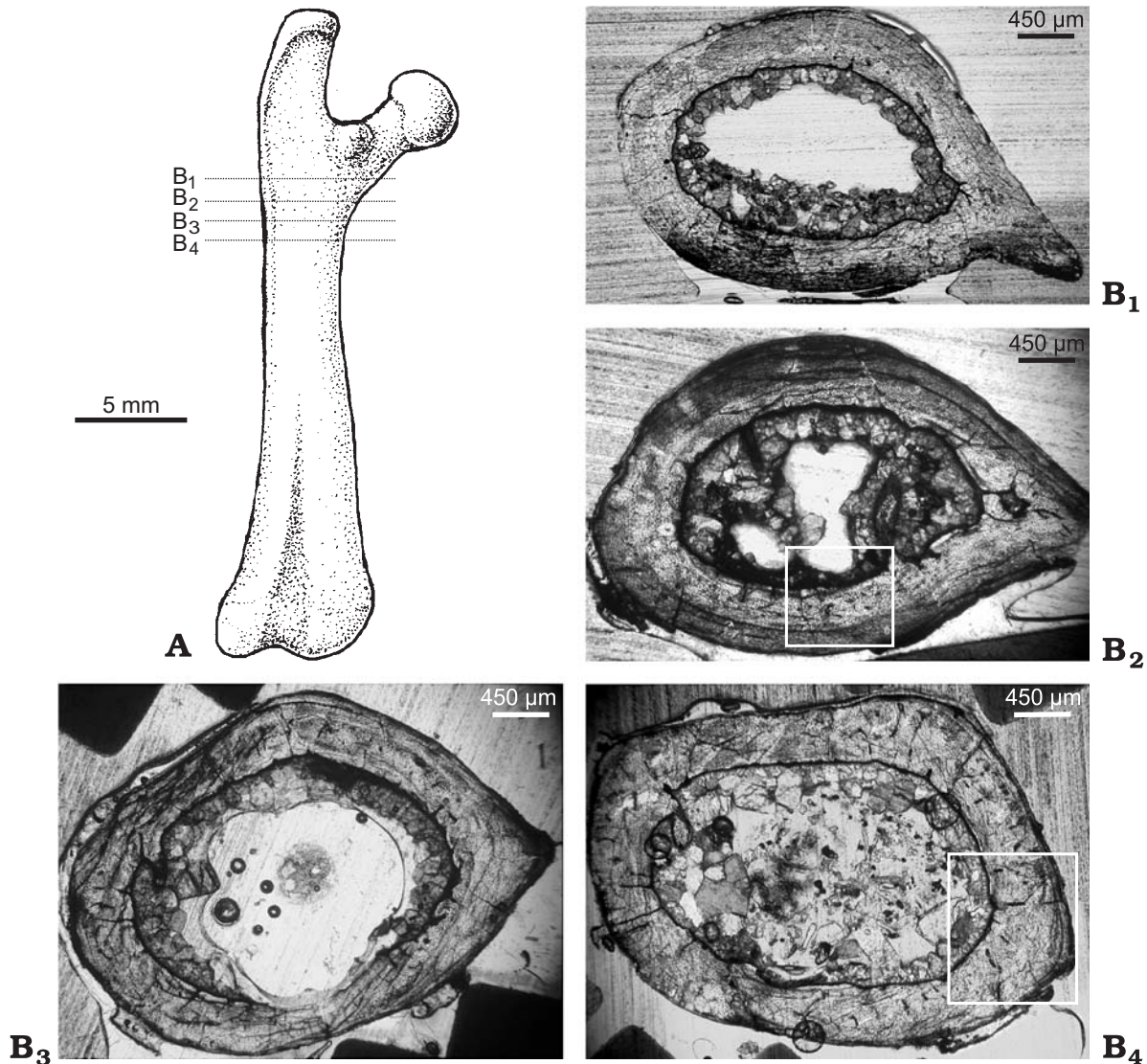
Fig. 6. *Nemegtbaatar gobiensis* Kielan-Jaworowska, 1974; ?late Campanian, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia. **A**. Reconstruction of the femur in anterior view. showing the region (notations B_1, B_2, B_3, B_4) from which the sections shown in B have been taken. **B**. Successive sections of the femur from the upper part of the shaft of the specimen ZPAL MgM-I/81. B_1 section catalogue number, ZOO/UCT/ 180; B_2 section catalogue number, ZOO/UCT/ 181; B_3 section catalogue number, ZOO/UCT/182; and B_4 section catalogue number, ZOO/UCT/183. Note the distinct changes in the nature of the compacta and shape of the medullary cavity and overall shape of the cross section from B_1 to B_4. Detail of framed regions in B_2 and B_4 are provided in Fig. 7.

Eutherians

Zalambdalestes lechei (Fig. 8).—The RBT of the femoral cross section is about 17%. The compacta in *Zalambdalestes* consists of parallel-fibred bone tissue (Fig. 8). The compacta is rather poorly vascularized, except in a localized region where several simple blood vessels are located. A few poorly defined primary osteons as well as isolated secondary osteons are observed. In the peripheral region, the osteocytes appear to be more flattened and less abundant (Fig. 8B). A single LAG is visible near the peripheral margin of the bone wall. The medullary margin is irregular, and it appears that endosteal resorption was underway at the time of death.

Barunlestes butleri (Fig. 9)

Rib.—A complete transverse section of a rib was available. The bone wall is fairly thick, with a RBT of about 31%. It largely comprises of parallel-fibred bone tissue, in which several rest lines are recognizable. The bone is generally poorly vascularized, except for a localized area in the region of drift, the osteocytes tend to be haphazardly oriented, and a few channels for blood vessels are visible in the compacta (Fig. 9A).

Femur.—The *Barunlestes* femoral sample examined comprised only a small fragment. The section shows an outer parallel-fibred bone tissue with several LAGs (Fig. $9B_1$, B_2). In a localized part of the section, there appears to be a bone tissue with more globular haphazardly oriented osteocyte lacunae
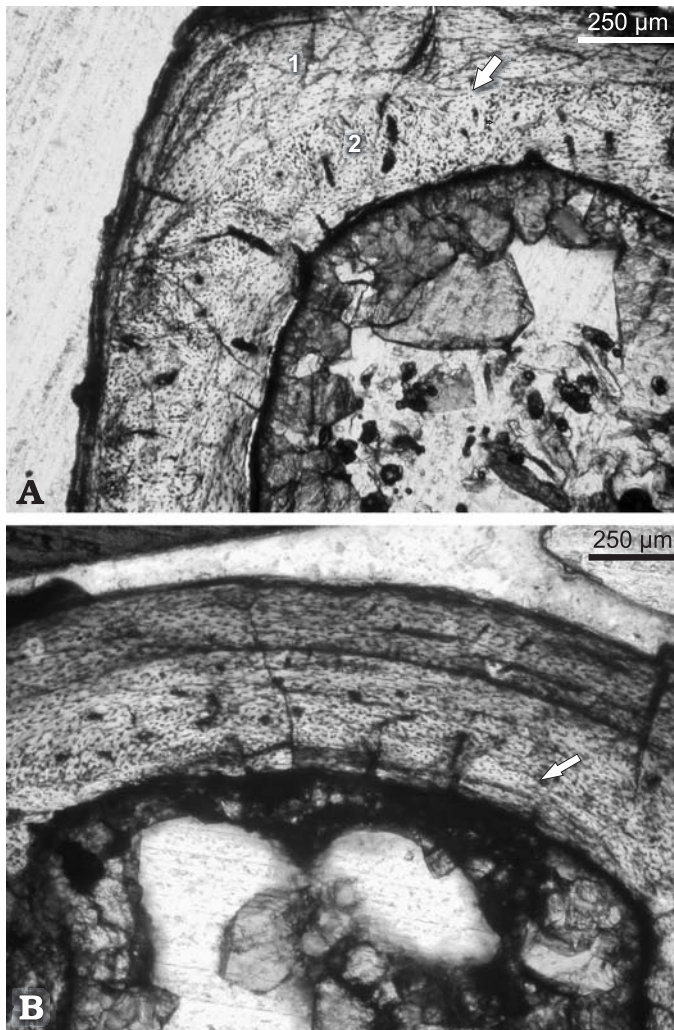
Fig. 7. *Nemegtbaatar gobiensis* Kielan-Jaworowska, 1974, ?late Campanian, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia. ZPAL MgM-I/81, section catalogue number, ZOO/UCT/183. **A**. Higher magnification of framed region in Fig. 6B$_4$ showing the complex nature of the compacta. Region 1 is a periosteal deposition of parallel-fibred bone, region 2 is a compaction of fine cancellous bone. Arrow indicates the tide line. **B**. Higher magnification of framed region in Fig. 6B$_2$ (section catalogue number, ZOO/UCT/181), illustrating the true woven bone. Arrow indicates the tide line.

(Fig. 9B$_2$), which may be correlated with a faster rate of bone deposition.

Extant eutherian

Heterocephalus glaber (Fig. 10).—Cross sections of the femur display a rather thick bone wall, with an average thickness of about 0.8 mm and a RBT of about 30%. Two distinct regions are clearly visible in the bone wall: a poorly vascularized outer circumferential layer (OCL) that consists of a parallel-fibred bone tissue, and an inner, richly vascularized region consisting of a more woven type of bone tissue. The perimedullary region of the bone is uneven and highly resorptive. Several radially oriented vascular channels ex-

tend from the medullary cavity to the mid cortical part of the bone wall. The vascular channels lack osteonal development around them. Although some enlarged erosion cavities are visible in the compacta, no secondary osteons were observed (Fig. 10).

Discussion

As early as 1947, Amprino recognized that the type of bone tissue formed is directly related to the rate at which it was deposited. In recent years, several experimental studies on extant vertebrates have quantified the rates at which different bone tissues form (e.g., Margerie de et al. 2002, 2004; Starck and Chinsamy 2002), and although there is considerable overlap in the types of bone tissues that result at particular rates (Starck and Chinsamy 2002), qualitatively "Amprino's rule" still holds. Thus, when analyzing the bone microstructure of extinct animals, the type of bone tissue present provides a qualitative assessment of the rate at which the bone formed i.e., depending on the type of bone tissue, one can reasonably deduce whether it formed at a "fast" or "slow" rate. For example, fibro-lamellar bone with its characteristic woven bone matrix and haphazardly-oriented osteocyte lacunae is typically deposited at a faster rate than lamellar bone tissue with its more organized matrix and osteocyte lacunae. However it must be emphasized that deducing an actual (i.e. quantitative) rate at which the bone formed is imprecise and speculative. Histological characteristics of the bone, such as the presence of annuli or LAGs, provide further information regarding the continuity or discontinuity of growth, while other microstructural details (e.g., the particular type of bone tissue) provide a reasonable assessments of various other aspects of the life history of the animal (e.g., Chinsamy 1997, 2005).

The analysis of the bone microstructure of the Late Jurassic *Morganucodon* and the Late Cretaceous multituberculates and eutherians reveals evidence pertaining to their growth strategies, especially when compared to their ancestors, the non-mammalian cynodonts, and to modern mammals (eutherians and monotremes).

Implications of the observed bone histology in the studied taxa

Nonmammalian therapsid *Tritylodon*.—The predominance of uninterrupted fibro-lamellar bone in the *Tritylodon* sections studied, suggests that these tissues were formed at a sustained, relatively rapid rate. A change to a slower rate of bone formation during later ontogeny is indicated by the presence of lamellar bone in the peripheral part of the cross section of the radius (Fig. 2B). This suggests that overall body growth was slowing down, and that *Tritylodon* had a determinate growth strategy. Closely spaced rest lines that
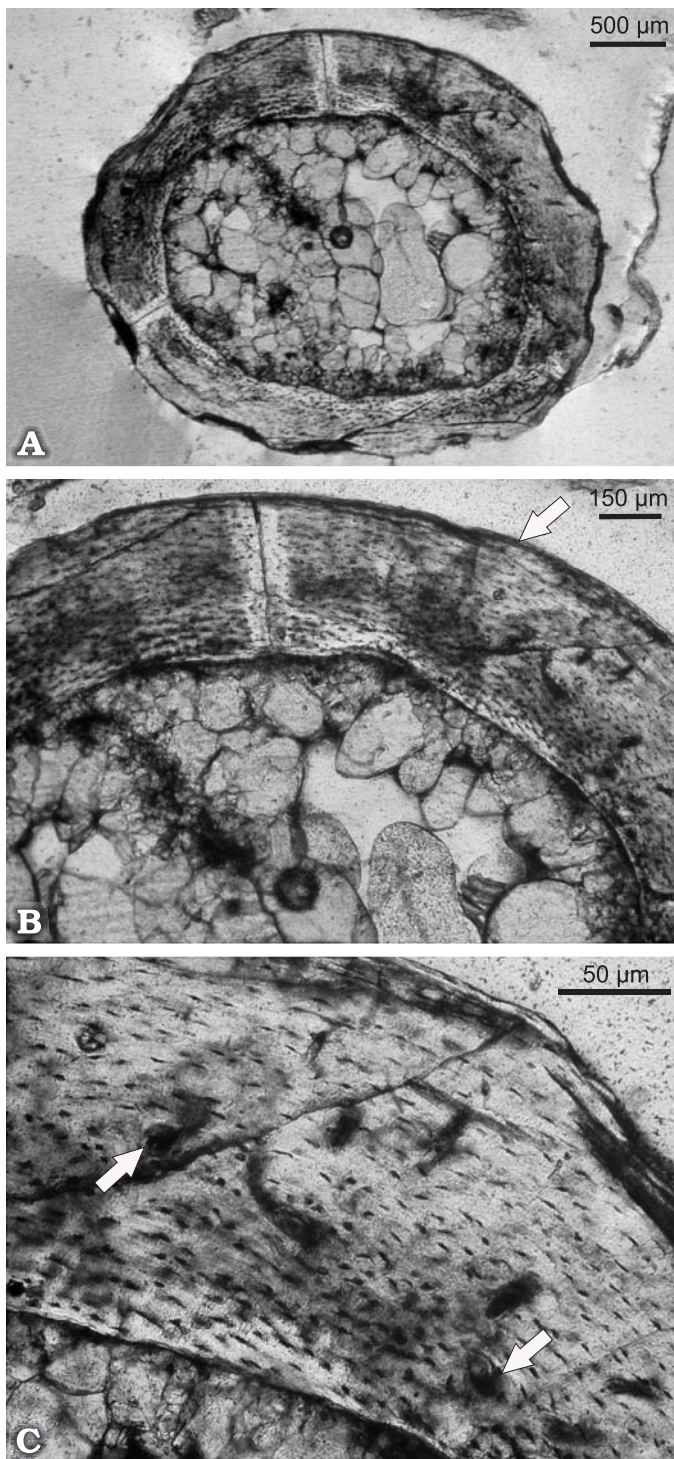
Fig. 8. *Zalambdalestes lechei* Gregory and Simpson, 1926; ?early Campanian, Djadokhta Formation, Bayan Zak, Gobi Desert, Mongolia, ZPAL MgM-I/43, transverse section of a femur (section catalogue number, ZOO/UCT/186). **A**. Low magnification showing the relatively thin bone wall and the relatively poorly vascularized parallel-fibred compacta. **B**. Higher magnification of the same, showing the parallel organization of the osteocyte lacunae and the vascularization of the bone. Arrow indicates a single LAG located near the peripheral margin of the bone wall. **C**. Still higher magnification of the same section, showing some simple vascular channels and primary osteons (arrows).

interrupt the peripheral lamellar layer of bone indicate that during late ontogeny, a slow rate of bone deposition occurred periodically.

Fibro-lamellar bone predominates in the cortical bone tissues of several nonmammalian therapsids, e.g., *Bienotherium,* and *Oligokyphus* (Ricqlès 1969), *Diademodon* and *Cynognathus* (Botha and Chinsamy 2000), *Trirachodon* (Botha and Chinsamy 2004), as well as in a range of traversodontids (Ricqlès 1969). However, in some non-mammalian cynodonts, such as *Diademodon* (Botha and Chinsamy 2000), *Trirachodon* (Botha and Chinsamy 2004), and *Procynosuchus* (Ray et al. 2004), periodic pauses in growth (represented by annuli and/or LAGs) interrupt the deposition of fibro-lamellar bone. Thus, among the nonmammalian cynodonts, both sustained and episodic (interrupted/periodic) growth strategies occur (e.g., Botha and Chinsamy 2000; Ray et al. 2004).

The growth pattern of rapid, sustained early growth, and later slower, episodic growth observed in *Tritylodon* has also been observed in the gorgonopsid, *Aelurognathus* (Ray et al. 2004), the dicynodont, *Diictodon* (Ray and Chinsamy 2004) and the therocephalian, *Pristerognathus* (Ray et al. 2004).

Early Jurassic *Morganucodon* and *Gephyrosaurus*.—Although a large number of *Morganucodon* and *Gephyrosaurus* bones were diagenetically altered, some sections preserved unaltered bone tissue, and therefore permitted an assessment of the bone microstructure of these taxa.

Morganucodon formed fibro-lamellar bone during early ontogeny, but later in life formed a more parallel-fibred bone tissue that was periodically interrupted by growth lines. Although a clearly defined outer circumferential lamellae (OCL) is lacking, the presence of parallel-fibred bone with LAGs suggests that later growth was slowed and intermittent (Fig. 3B$_1$).

The bone histology of *Gephyrosaurus* is similar to that of extant squamates (e.g., Castanet and Baez 1991; Chinsamy et al. 1995) (Fig. 3A). The distinctive LAGs present in the bone suggest that overall growth of the animal was affected episodically, possibly by seasonally fluctuating ambient conditions. Remnants of "embryonic bone" preserved around the perimedullary region suggest that medullary remodeling was not extensive, and that diametric bone growth generally occurred in a slow, appositional manner. This type of growth has been observed in the lizard *Gallotia stehlini* where 90% of all specimens studied preserved embryonic bone below the first LAG (Castanet and Baez 1991). In such cases, skeletochronology is simplified as there is no need to account for resorption of earlier growth marks. In the compacta of a femoral thin section of *Gephyrosaurus*, 9 LAGs (including the hatching line) can be counted, which (assuming 1 LAG is formed per year) suggests a minimum age of nine years for the individual. The first zonal region after the hatching line is distinctly wider than the subsequent ones, which could be interpreted as signaling the attainment of sexual maturity in the first year post hatching (this would need to be verified by studying a larger sample of *Gephyrosaurus*). It is possible
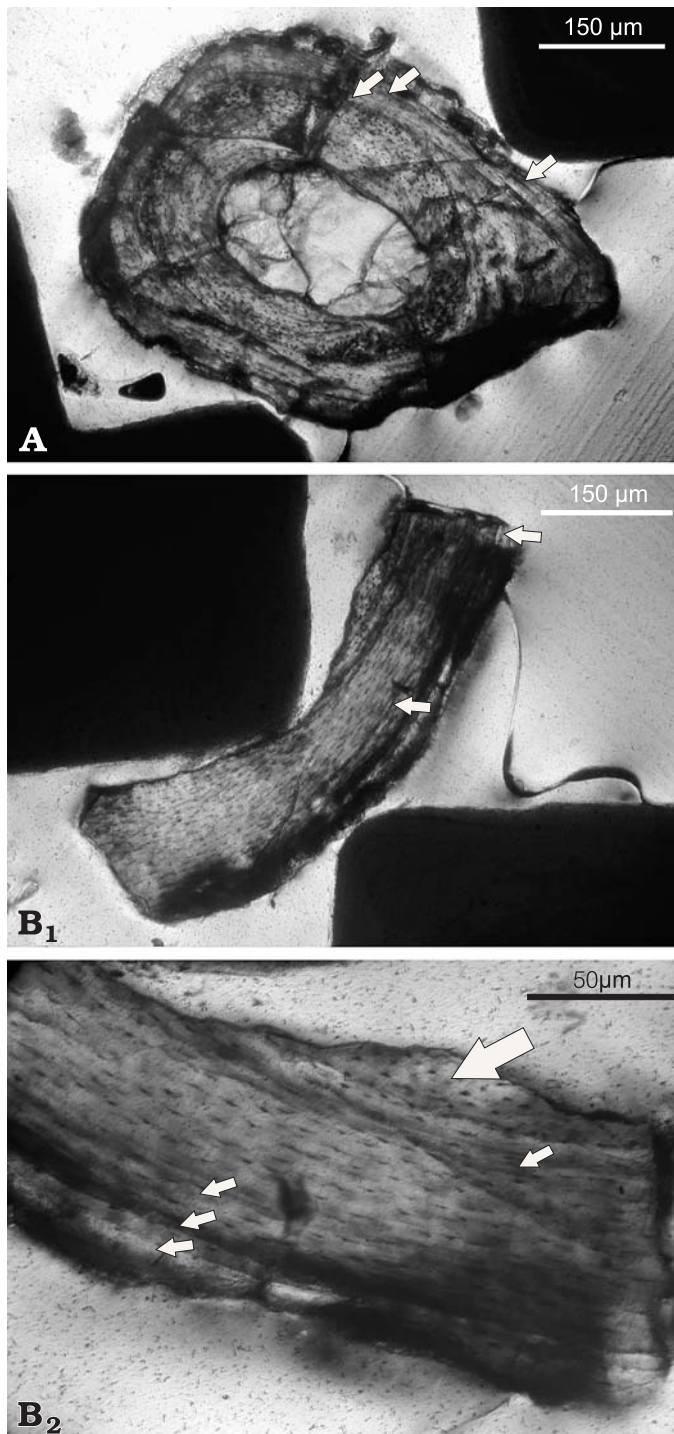
Fig. 9. *Barunlestes butleri* Kielan-Jaworowska, 1975, ?late Campanian, Baruungoyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia. ZPAL MgM-I/77, section catalogue number, ZOO/UCT/189. **A**. Transverse section of a rib, showing the poorly vascularized compacta and the parallel fibred nature of the compacta, as well as several lines of arrested growth (arrows). **B**. The femur from the same ZPAL specimen, section catalogue number ZOO/UCT/189 (on same slide as rib). B$_1$. Partial transverse section of the femur on the same slide showing the similarly poorly vascularized compacta of parallel fibred bone in the bone wall. B$_2$. Higher magnification of the femur in B$_1$. Small arrows in B$_2$ indicate lines of arrested growth; large arrow indicates the more globular haphazardly oriented osteocyte lacunae.

that the wider spacing of the outer 3 zonal regions (as compared to the preceding 5) is a reflection of favorable environmental conditions during those particular seasons (Fig. 3A).

The distinctive characteristics of the bone microstructure of *Morganucodon* and *Gephyrosaurus* permitted a clear distinction of bones of each taxon. This was especially useful in the instances where isolated postcranial bones of *Morganucodon* and *Gephyrosaurus* could not be taxonomically distinguished previously (see methods).

An extant monotreme *Ornithorhynchus*.—Femoral thin sections of *Ornithorhynchus* revealed a fairly thick bone wall comprising a mixture of bone tissues types that formed as a result of various episodes of growth and remodeling. Secondary osteons are fairly abundant in the compacta, and large trabecular spaces were present in the medullary cavity. This contrasts with the findings of Enlow and Brown (1958), who noted the absence of Haversian (secondary) reconstruction, and the presence of a non-cancellous central medullary cavity in the femur and rib of *Ornithorhynchus*. The differences between the present *Ornithorhynchus* samples and those of Enlow and Brown's (1958) study could represent intra-bone differences in bone morphology. A further point worth noting is that Enlow and Brown (1958) also described *Ornithorhynchus* bones as having unusual primary osteons with small lumina that were surrounded by a ring of acellular, perivascular, non-lamellar tissue. However, although we recognized a mixture of different types of vascularization i.e., from simple vascular canals to primary and secondary osteons, we did not notice anything unusual about the osteonal structure of the primary osteons in our sample.

The overall structure of the bone suggests that it was formed rapidly. However, evidence of a slowing down in the rate of bone deposition is suggested in the peripheral parts of the bone by the presence of poorly vascularized lamellar bone tissue with osteocyte lacunae organized in parallel. Although not visible in the micrograph figured by Enlow and Brown (1958: plate XXVIII: 3), they describe the presence of "unorganized, non-lamellar osteoid tissue" between regions of lamellar bone. It is possible that the lamellar bone deposits (described by Enlow and Brown 1958, and also observed in the current study) represent annuli, but in the absence of life history data, it is uncertain whether they are true annuli (Fig. 4) or simply a reflection of localized slow rates of bone deposition.

Multituberculates.—*Nemegtbaatar* sections (Figs. 6, 7) all show complex cortical stratifications associated with structural remodeling of the growing femur. The presence of compacted, fine-cancellous bone in the cortex indicates that this region was once close to the epiphyseal growth plate (Enlow 1962). As the femur grew in length this region was relocated from its original medullary location into the cortical region of the growing bone. Such mixed bone tissues have been noted in the bones of young rapidly growing individuals, and occurs in the bones of white rats at various stages of ontogeny (Enlow 1962).
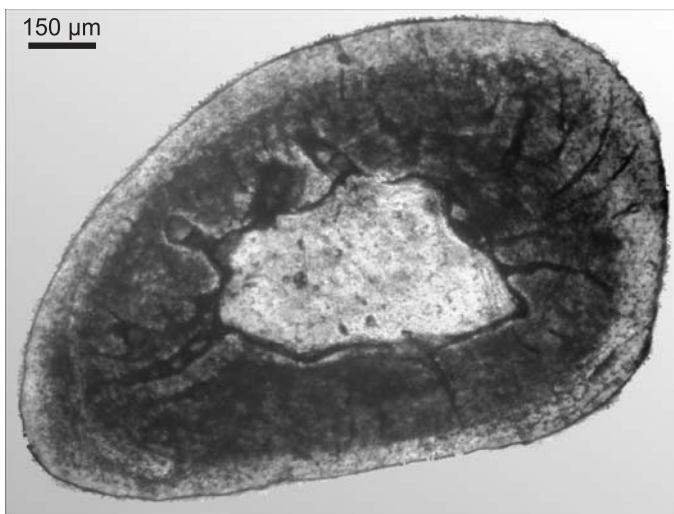
Fig. 10. *Heterocephalus glaber* Rüppell, 1842. Recent, ZOO/UCT no number; femur, section catalogue number, ZOO/UCT/192, showing the well-vascularized compacta and the narrow outer region of parallel fibred bone (OCL).

The small patch of periosteally formed woven bone tissue in *Nemegtbaatar* (Fig. 7B) suggests that during early ontogeny, the initial periosteal cortical bone tissue formed rapidly. However, in the sections we studied, most of this early formed bone tissue was already resorbed, and mainly the later, periosteal lamellar bone with longitudinally and radially oriented channels is evident. Thus, given the overall structure of the bone (the occurrence of compacted fine cancellous bone in the cortical bone tissues, the presence of a small localized region of woven bone, as well as vascularized lamellar bone), it appears that *Nemegtbaatar* had a fast rate of growth early on, which slowed down during later ontogeny.

The multituberculate *Kryptobaatar* is distinctive in having the entire cortical bone consisting of a woven bone tissue with primary osteons, which suggests a rapid rate of bone formation. The uneven peripheral and perimedullary bone margins, and early stages of osteonal development suggest that the bone is from a young, immature individual. Consequently, it is not known whether bone formation slowed down in later stages.

The well-vascularized compacta of the Mesozoic multituberculates compares well with that of the mandible of the Paleocene mutituberculate, *Ptilodus,* described by Enlow and Brown (1958). These authors specifically noted that *Ptilodus* has a distinct, triple-layer structure of bone with an OCL and an ICL that enclosed a well-vascularized intermediate region of woven bone. Since our *Kryptobaatar* sections appear to be from a young individual, only the woven bone region appears to be preserved, while in *Nemegtbaatar* traces of all three regions described for *Ptilodus* are present.

Mesozoic eutherians *Zalambdalestes* and *Barunlestes*.—Unlike the previous taxa, which all showed an initial high rate of bone formation followed by a slower rate during later stages, the Mesozoic eutherians *Zalambdalestes* (Fig. 8) and *Barunlestes* (Fig. 9) both show a relatively slow rate of growth with periodic pauses indicated by the presence of rest lines. The *Zalambdalestes* specimen appears to have been a young individual with parallel fibred bone tissue and mainly simple blood vessels evident in its compacta. Although the *Barunlestes* rib preserves a fairly thick cortical region, only parallel fibred bone tissue with rest lines is present. However, in the femoral fragment studied it looks as though an earlier tissue with more haphazardly organized osteocytes (suggesting a faster depositional rate) formed during early ontogeny. This suggests that a slower rate of growth soon replaced an earlier faster rate of growth.

The overall nature of the Mesozoic eutherian bone tissue suggests a slow rate of bone deposition, with *Barunlestes* having an even slower growth rate than *Zalambdalestes*.

Small extant eutherian *Heterocephalus glaber*.—The woven texture of the inner layer of the compacta of *Heterocephalus glaber* suggests that it was deposited at a faster rate than the outer circumferential layer (OCL), which consists of lamellar bone. Klevezal (1996) noted that although diametric (appositional) growth decreases in extant mammals once adult body size is attained, it generally does not stop, and often accretionary deposits of bone occur in the peripheral part of the compacta. Thus, the avascular, lamellar bone of the OCL in *Heterocephalus* indicates that although the animal had reached adult size, appositional growth still continued at a slow rate. In several extant mammals, particularly those from temperate areas with strong seasonality, the OCL is often interrupted by LAGs (Klevezal 1996). No LAGs are recorded in the OCL of the *Heterocephalus* specimens in this study; this could be because the animal was from a captive colony (housed indoors), and would not have had to endure seasonal fluctuations. (This may also occur naturally, as *Heterocephalus* in the wild live in burrows, therefore experiencing minimal ambient fluctuations.) It is worth noting that the simple blood vessels in the compacta are radially oriented and are embedded in a woven bone matrix, which suggests that the bone was formed at a relatively faster rate than the bone in the OCL (Margerie de et al. 2004). The lack of intensive secondary reconstruction is consistent with observations made in several small mammals (e.g., bats, moles, squirrels) (Enlow and Brown 1958; Klevezal 1996).The relatively thick bone wall of *Heterocephalus glaber* appears to be an adaptation for its fossorial lifestyle (Botha and Chinsamy 2004).

General implications of the observed bone microstructure

It is evident that the mammals and the non-mammalian cynodont studied have a bone microstructure distinct from that of the pleurodont lepidosaur *Gephyrosaurus*. Given that the growth rate of bone roughly corresponds with the overall

growth of the whole animal (Klevezal 1996), it is reasonable to deduce that the pleurodont lepidosaur and mammalian taxa experienced different growth trajectories. As indicated by the interrupted parallel-fibred nature of the compacta, the pleurodont lepidosaur growth was seasonally affected: it grew relatively fast during the favorable season, and growth ceased during the unfavorable season.

Except for the *Kryptobaatar* and *Zalambdalestes* bones, which seem to be from individuals that have not yet attained adult body size, all other mammalian bone studied, irrespective of whether they are extant or extinct, show a change to a slower rate of bone deposition later in ontogeny. This indicates that although growth had slowed down appreciably, small amounts of slowly formed bone continued to be deposited peripherally (e.g., Klevezal 1996; Chinsamy and Dodson 1995). The fact that the Early Jurassic mammal *Morganucodon*, the cyndodont *Tritylodon*, as well as other, more basal nonmammalian therapsids, e.g., *Aelurognathus*, *Pristerognathus* (Ray et al. 2004), and *Diictodon* (Ray and Chinsamy 2004), all show a tendency for this type of growth pattern, suggests that a determinate growth strategy evolved early in the ancestry of mammals.

Perhaps in response to selection for fast growth most extant mammals generally grow with sustained rapid rates (as reflected by uninterrupted bone tissue) i.e., most have relatively reduced developmental plasticity (Smith-Gill 1983). However, it appears that in response to unfavorable environmental conditions, some mammals e.g., small forms living in temperate conditions, can form periodically interrupted bone (Klevezal and Kleinenberg 1969; Chinsamy and Dodson 1995; Chinsamy 1998). Extensive work by Klevezal (1996) suggests that strong seasonality usually invokes growth marks in the OCL of mammalian bone. However, Klevezal (1996) cautions that the LAGs in the OCL are not reliable indicators of age since in mammals these lines often do not form in the early years of an individual's life.

It is interesting to note that although *Heterocephalus glaber* is generally considered to have a low basal metabolic rate and with body growth rates lower than most mammals of similar size (see Jarvis and Bennett 1991), its compacta nevertheless appears to have formed at a more rapid rate than that of the two Mesozoic eutherian genera, and indeed, more rapidly than those of many other extant small eutherians (e.g., moles, bats, marmots, squirrels), which tend to have rather poorly vascularized compacta (Enlow and Brown 1958). Thus, size alone cannot explain the differences observed among the extant mammalian taxa. It is also worth noting that, although not conclusive, the periodically interrupted nature of *Ornithorhynchus* bone suggests a flexible growth strategy similar to that observed in the bone formed in the nonmammalian therapsids, *Diademodon* (Botha and Chinsamy 2000) and *Trirachodon* (Botha and Chinsamy 2004).

The overall nature of the bone tissue of the two Mesozoic eutherians suggests a much slower rate of bone deposition than that of the extant eutherians, as well as the multituberculates, *Morganucodon*, and the nonmammalian therapsids.

Indeed *Barunlestes* appears to have an even slower growth rate than *Zalambdalestes*. *Zalambdalestes* and *Kryptobaatar* are from the Djadokhta Formation, while *Barunlestes* and *Nemegtbaatar* are from the Baruungoyot Formation, but these formations are considered to represent similar, semi-desert-like environmental conditions (Jerzykiewicz 2000). Other than the fact that eutherians are generally considered to be insectivores, whereas the multituberculates are considered omnivores/ herbivores, these four taxa are relatively similar in size, and occupied similar habitats. Therefore, from a paleoecological perspective, it may be significant that the multituberculates apparently had faster growth rates than the eutherians.

The flexible growth strategy indicated by the cyclical pattern of bone deposition (Starck and Chinsamy 2002) in several nonmammalian therapsids suggests that a flexible growth strategy, even after reaching "adult" size, is plesiomorphic for the mammalian lineage (Ray et al. 2004). Furthermore, it seems that the multituberculates grew at a faster rate than the contemporary eutherians which retained the plesiomorphic condition of flexible growth rates.

Such differences in growth strategy may account for some of the observations in the fossil record. During the Late Cretaceous, multituberculates dominated both central Asian and North American mammal faunas, comprising on average 70% of recovered specimens in central Asia and 50% or more in North America. Western Asia represents an exception since here ungulatomorph eutherians dominated while multituberculates comprise only 1% of collected mammal specimens (Kielan-Jaworowska and Nessov 1992; Nessov et al. 1998). Perhaps the fast growth rate of multituberculates, as suggested by their bone microstructure, provided an adaptive advantage, and may account for their abundance in the Late Cretaceous of the Gobi region. Being of similar size to the Eutheria described, but with a faster growth rate, they may have reached sexual maturity earlier than the eutherians and therefore reproduced at a faster rate.

Many authors (Van Valen and Sloan 1966; Hopson 1967; Kielan-Jaworowska and Gambaryan 1994) mention the apparent competitive inferiority of multituberculates relative to eutherians during the Tertiary, which may have led to multituberculate extinction at the end of the Eocene. It is possible that the flexible growth strategies of the eutherians may have given them an adaptive advantage after the Cretaceous–Tertiary extinction event, by enabling them to invoke faster (energetically costly) or slower (energetically less costly) developmental regimes in response to increased environmental variability and seasonality, thus enabling them to radiate and become the dominant mammals.

Acknowledgments

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