Bone histology and growth of the prosauropod dinosaur
***Plateosaurus engelhardti* MEYER, 1837**
from the Norian bonebeds of Trossingen (Germany) and Frick
(Switzerland)

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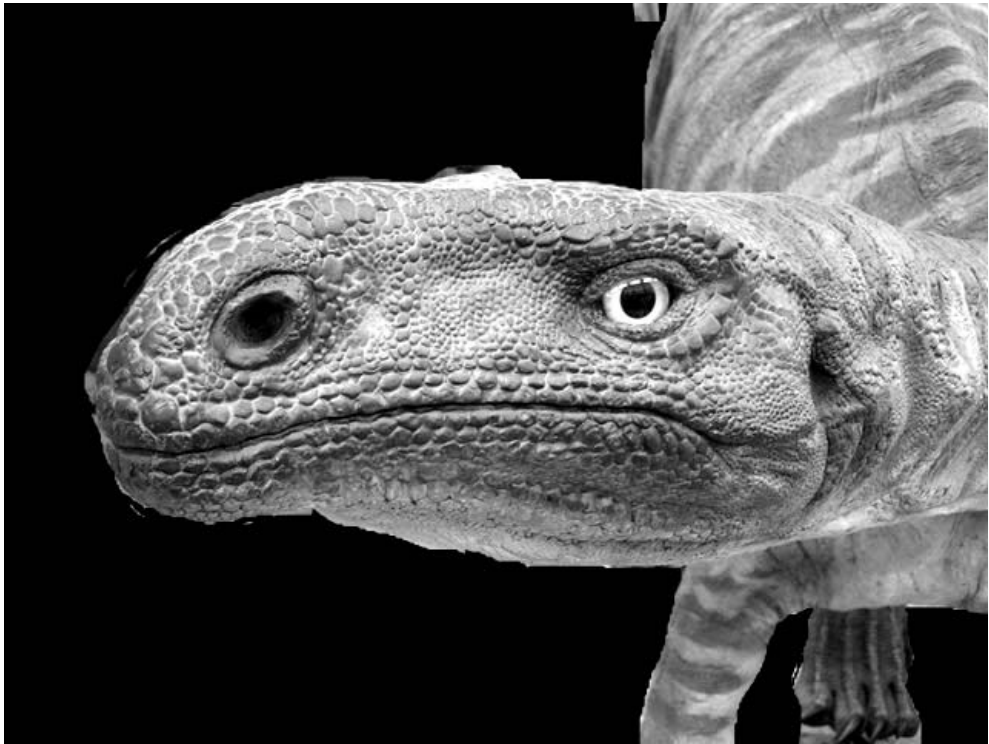Rheinischen Friedrich-Wilhelms-Universität Bonn

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Abstract

Predominately long- and flat bones of the prosauropod *Plateosaurus engelhardti* from the Norian localities of Trossingen and Frick were sampled for paleohistological study. Both localities yield rich material of adult individuals with a body size of 4.70 m to 10 m.

Altogether 50 bones from approximately 27 individuals were sampled by different methods (coring, cross sectioning, analysis of existing fracture surfaces). Most bones consist of the laminar fibro-lamellar complex, always cyclically interrupted by lines of arrested growth (LAGs). In some bones, the laminar fibro-lamellar complex changed in the exterior cortex to lamellar-zonal bone, later grading into avascular lamellar bone. Thus, growth was clearly determinated in *P. engelhardti*.

Like most other dinosaurs *Plateosaurus engelhardti* shows high growth rates, indicating an advanced ("dinosaurian") physiology. On the other hand, *Plateosaurus engelhardti* shows a strong dependency on environmental conditions. Additionally, its final size is represented by a very broad range (between 6.5 m to 10 m). Both reflect a more reptilian growth pattern as is known from other dinosaurs. It marks the basal status of *Plateosaurus engelhardti*. Thus, in *Plateosaurus* the foundation is seen for the evolution of gigantism in sauropods.

1. Introduction

1.1 General aspects

Dinosaurs are one of the most fascinating groups of vertebrates that everlived. Despite various studies of their extensive fossil record concerning e.g. anatomy, morphology, and phylogeny, and due to their extinction (except birds), and lack of any good modern analogues, there still a lot of open questions, mainly concerning biological features and life history aspects about dinosaurs.

Until now, the only direct way to obtain information about past events in an individual's life is the use of the record preserved in hard tissues (CASTANET et al. 1993, CASTANET 1994, CURRY 1999, SANDER 1999, 2000). Particularly bone histology

(skeletochronology) provides information about aspects of paleobiology like individual age, age at sexual maturity, growth rates and growth patterns, sexual dimorphism, and cycles of activity and reproduction. From these data, information can be deduced about physiology and metabolic rate, ontogeny, evolution, and phylogeny (CASTANET et al. 1993, CHINSAMY 1993a, b, 1994, ERICKSON & TUMANOVA 2000, HORNER et al. 2000, SANDER et al. in press).

Skeletochronology today is a standard method of aging extant fishes and ectothermic vertebrates (RICQLÉS et al. 1991, CASTANET et al. 1993, CHINSAMY 1994) and nearly the only way for doing so in extinct vertebrates (CASTANET 1994). The method is based on the count of cyclically deposited growth marks preserved in the microstructure of bones.

Examination of bone microstructure in dinosaurs began with the first fossil finds of dinosaurs as summarized in ERICKSON & TUMANOVA (2000), and HORNER et al. (2000). But all the early works have only a descriptive character, and further analyses of the histological data and resulting implications were not done. Primarily RICQLÈS (1968, 1980, 1983) started comparative histological studies in the middle 1960's, mainly of dinosaur bones, and he extracted paleobiological information from these data. Others followed, and since the 1990's more and more authors (REID 1990, CHINSAMY 1993, VARRICCHO 1993, FARLOW et al. 1995, CURRY 1999, SANDER 1999, 2000) have become interested in bone histology research and its possibilities for collecting e.g. paleobiological data. Thus, today a lot of bone histological research is done and published, dealing with various fossil vertebrate groups.

A summary about the current state of bone histological research in extinct tetrapods, predominately in dinosaurs, are given by FARLOW & BRETT-SURMAN (1997). Important studies about bone histology and using growth marks for aging of recent tetrapods (skeletochronology) are ZUG et. al. (1986), CASTANET & SMIRINA (1990), CASTANET et. al. (1993), CASTANET (1994), and KLEVEZAL (1996).

1.2 Introduction to the terminology of bone histology

Paleohistology is a large field which deals with numerous structures, like bones, teeth, scales, scutes, shells, and other "hard" material of vertebrates and invertebrates preserved during fossilization (PADIAN 1997). The current study deals only with fossil tetrapod bone histology. Therefore, only a short introduction to bone histology and the terminology used is given here. For a more detailed discussion of bone histology see FRANCILLON-VIEILLOT et al. (1990), RICQLÈS (1991), CHINSAMY (1994), and REID (1997).

Tetrapod bones can be divided into different categories based on their general shape and ontogenetic origin. In the current study, mainly long bones such as the femur, tibia,

fibula, and humerus, and two flat bones, scapula and pubis, were sampled. Additionally, a few short bones were sampled rather randomly. Long bones can be divided into the diaphysis or shaft region, the epiphyses, which are the two extremities, and the transitional region between epiphyses and diaphysis, called metaphyses. The diaphysis of long bones consist of the cortical compacta (cortex), the inner cancellous bone area, and the medullary cavity, located approximately in the center of the bone. Epiphyses and metaphyses consist mainly only of cancellous bone.

A three-layered or diploe structure characterizes flat bones. They lack a free medullary cavity but have a central zone of cancellous bone sandwiched between two thin layers of cortical compacta (FRANCILLON-VIEILLOT 1990). Flat bones lack typical epiphyses; instead they are termed the proximal and distal bone end. The term "shaft" is used in connection with flat bones for the elongated middle area of bone.

The cortex generally consists of primary bone tissue, which can be built up of various bone types. Under the microscope, primary bone always contains clearly visible osteocyte lacunae connected by a dense network of canaliculi. Visible with the naked eye are the spaces for the blood vessels, called vascular canals. Their number depends on bone tissue as well as on species, and they can appear in various orientations. Thus, a specific bone type is not only characterized by its bone tissue, the vascular system is also very important for classification and interpretation. When a vascular canal is enclosed by primary bony tissue, it is called a primary osteon. Nevertheless, bone tissue can also be avascular.

Secondary bone tissue is the result of substitution of primary bone tissue by secondary bone in a process called remodeling. Initially, remodeling starts with erosion of bone by osteoclasts along vascular canals (resorption). Later, after resorption has decreased, the whole cavity, even the original vascular canal, is refilled by centripetally deposited bone and is now called a secondary osteons or a haversian canal. Usually the wider the cavity, the younger the secondary osteon is. Secondary osteons can clearly be distinguished from primary osteons by a resorption line or cementing line surrounding them. Haversian bone appears when several generations of secondary osteons are deposited and the bone between the latest generation of secondary osteons is also secondary (CHINSAMY 1994). The functional meaning of reconstruction and remodeling is not really clear yet. It seems to be linked with the mechanical and physiological stresses which a bone or a part of bone has to endure during its life. It also seems to be a gradual process related to the age of the tissue at a specific site. Remodeling is not a species- or bone-specific feature as very young individuals can also show remodeling.

For skeletochronology the primary bone tissue is the most interesting part of bone microstructure because it contains the main information about growth rates, which means the rate of bone deposition and degree of vascularization, as well as growth marks.

Primary bone tissues are classified according to the thickness and arrangement of the collagen fiber bundles that build the bone tissue. FRANCILLON-VIEILLOT et al. (1990) distinguish three main types of bone tissue in vertebrate bones, but additionally there occur many intermediate bone tissues (FRANCILLON-VIEILLOT et al. 1990, REID 1997b).

Lamellar bone corresponds with a high level of spatial organization. The crystals are oriented only in one direction. Lamellar bone stands for slow growth, due to the rule that the higher the level of organization is, the slower is growth. Lamellar bone consists of successive thin layers called lamellae and has a plywood-like structure. The collagen fibrils in one lamellae are virtually parallel but their direction changes from one lamella to the next. Thus, lamellar bone will appear alternately dark and bright in polarized light.

In parallel-fibered bone, the closely packed collagen fibril all have the same general orientation. Parallel-fibered bone appears homogeneously dark or light under polarized light, depending on the orientation of the collagen fibrils (FRANCILLON-VIEILLOT et al. 1990). This bone tissue appears to be intermediate between woven bone, to be discussed next, and lamellar bone.

Woven-fibered bone consists of coarse and loosely packed collagen fibers of varying sizes. There is no spatial order, and this bone tissue corresponds therefore to fast growth and a high vascular density. Under polarized light, the woven bone shows no extinction.
If a bone tissue largely consists of one of these three bone types, it is called woven-fibered bone tissue, parallel-fibered bone tissue, or lamellar bone tissue.

In many tetrapod bones, woven bone is associated with lamellar bone. The resulting structure is called fibro-lamellar bone tissue or fibro-lamellar complex. This bone tissue grows by first laying down a three dimensional network of vascular canals. Between the vascular canals, the bone tissue is deposited, mostly in form of primary osteons. A primary osteon built in the fibro-lamellar bone tissue contains the lamellar bone in the central part of the primary osteon and is surrounded by the woven or fibrous bone. Fibro-lamellar bone tissue is always densely vascularized with various arrangements of vascular canals. It is a very common bone tissue in dinosaurs, birds, and mammals, and is indicative for rapid growth (RICQLÉS 1980, REID 1987, FRANCILLON-VIEILLOT 1990, RICQLÉS et al. 1991, CHINSAMY 1993b, 1994). According to RICQLÉS et al. (1991), the fibro-lamellar bone (FBL) is a prerequisite for large tetrapods to reach adulthood within reasonable longevities.

Three main types of vascularization can be found in the fibro-lamellar bone tissue. Vascularization can be distinguished by the orientation, by the shape of single vascular canals, and by the network of the vascular canals. Laminar bone tissue describes a kind of vascular system with mainly longitudinal and circular primary osteons which are oriented in more than one direction. In plexiform bone tissue, vascularization is one step higher in the vascular density and beside the laminar vascularization plexiform bone tissue contains radial vascular canals, even in more than one direction. The highest vascular density is represented by reticular bone tissue. Here, vascular canals have an oblique orientation in more than one direction and are rather irregular.

A second common bone type is the lamellar-zonal bone that is characterized by an alternate deposition of lamellar and parallel-fibered bone with mostly longitudinal vascular canals and significant growth marks (FRANCILLON-VIEILLOT et al. 1990). Lamellar-zonal bone is associated with slow and cyclically interrupted growth, such as is known from many extant ectothermic tetrapods.

Growth rates are not only determined by bone tissue, but also the thickness of the single bone layers give information about the speed of deposition. Wide layers of bone grow more rapidly than fine layers of bone (RICQLÉS et al. 1991).

As a new study of STARCK & CHINSAMY (2002) had shown that rates of bone deposition and bone microstructure vary strongly in response to environmental conditions. Thus, quantitative comparison of bone tissue and growth rates from extinct and extant vertebrates remains difficult (STARCK & CHINSAMY 2002). Others, like ERICKSON & TUMANOVA (2000) had given attention to this point before and mentioned uncertainties regarding environmental influences on dinosaurian growth. ERICKSON et al. (2001) pointed out that the same bone tissue can be produced at different rates. The best example is that some reptiles under certain environmental conditions can attain maximal growth rates within the lower bounds of mammalian rates (ERICKSON & TUMANOVA 2000).

Growth in general is continuous or periodically interrupted. Periodic growth occurs independently of bone tissue or type, and primary bone tissues can be subdivided by growth lines or other growth marks (RICQLES 1983, REID 1990, CHINSAMY 1994, PADIAN 1997). Growth marks are successive layers that are characterized by differences in bone tissue, orientation of vascular canals, and vascular density (REID 1990). Such growth marks are heterogeneous in form and causation (PADIAN 1997), but all indicate a cyclical manner of growth. In many tetrapod long bones, growth cycles are built up of the fast-growing and highly vascularized zone and the slower growing and less vascularized annulus. Often growth

cycles end in a line of arrested growth (LAG). A LAG can be accompanied by a ring of avascular bone (PADIAN 1997). Lines of arrested growth indicate a temporary but complete growth stop during ontogeny (CHINSAMY 1994, PADIAN 1997). Beside major LAGs subordinated LAGs or second order LAGs can be distinguished (REID 1990). Because there is no other cycle known to produce such a pattern, a zone and an annulus/LAG form one annual growth cycle (CHINSAMY 1994). Zones, annuli, and LAGs do not inevitably occur or go together, but LAGs are most of the time present when growth is cyclical. Skeletochronology and aging of individuals in extant and extinct tetrapods usually is based on the count of annually deposited growth cycles (CASTANET & SMIRINA 1990; FRANCILLON-VIEILLOT et al. 1990). However, a bone tissue can also be azonal which indicates continuous growth.

In contrast to earlier views (RICQLES 1974, 1976, 1978, BAKKER 1986), today it is generally accepted and documented among various studies that growth marks and LAGs are very common in dinosaur bones (REID 1990).

1.3 Previous work: Results on and problems of tetrapod bone histology
1.3.1 General aspects

The most important premise of paleohistological studies is the actualistic principle (CHINSAMY & DODSON 1995, REID 1997). This means that types of bone tissues and growth rates were principally similar and comparable in extant and extinct organism (HORNER et al.1999). Thus, growth rates of extinct tetrapods, as deduced from bone tissues and in comparison with growth rates of living tetrapods, can give an indication of their physiology and other biological aspects.

The qualitative analyses of life history is based on Amprino's rule (RICQLÉS et al 1991), which states that a particular bone tissue is deposited always at the same general rate (AMPRINO 1947). This rule has been tested in many different recent taxa and seems to be generally valid, although the database is still limited (RICQLÈS et al. 1991, REID 1997). Based on these premises, histological studies on recent animals can provide a detailed and solid database for paleohistological studies.

General assumptions, deduced from recent tetrapod bone histology, are that a bone with increasing thickness of the cortex shows decreasing vascularization accompanied by an increasing organization of the tissue and an increasing number of growth rings. Simultaneously, growth cycle distance decreases. Thus, a general decrease of growth rate with increasing age (= thickness of cortex) is implied (CHINSAMY 1993b, 1994).

More specific results are that avascular tissue or nearly avascular tissue occurs only when growth had stopped or the growth rate is generally very low. In contrast, highly vascularized bone tissue generally goes together with rapid growth. The higher the vascular density, the faster growth is, regardless of which bone tissue is deposited (RICQLÉS et al. 1991).

1.3.2 Skeletochronology

Interpretation of growth marks involves various problems (REID 1997). Thus, a great point of discussion but also a basic premise in most works dealing with skeletochronology is the annual deposition of the lines of arrested growth or of any other cyclical growth marks. Following several authors (ZUG et al. 1986, CASTANET & SMIRINA 1990, FRANCILLON-VIEILLOT et al. 1990, REID 1990, RICQLÉS et al. 1991, CASTANET et al. 1993, CHINSAMY 1994, REID 1997, HORNER et al. 1999, ERICKSON & TUMANOVA 2000), growth marks and LAGs are interpreted as having been annual in the current study. This premise is supported by studies of recent reptiles of known age (REID 1990, CASTANET et al. 1993). HORNER et al. (2000) pointed out that LAGs in fibro-lamellar tissue may not entirely comparable to the LAGs known from living ectotherms, which are deposited in lamellar-zonal tissue. On the other hand, they illustrate annual LAGs in the elk (*Cervus*) and the polar bear, the bones of which consist of fibro-lamellar bone, and they use the annual nature of LAGs in their own studies (HORNER et al. 2000).

HORNER et al. (1999) suggested that some growth lines can indicate, for example, illness, starvation, or temporary stress, due to the fact that such diseases of an individual often go together with a growth cessation. Such "diseases-LAGs" appear also in bones of mammals and birds and were surely not deposited annually. CHINSAMY and DODSON (1995) mentioned that trauma can produce a temporary pause in growing mammals and birds.

Another problem in using bone histology for age estimates is that each skeleton undergoes substantial histological changes during ontogeny because of longitudinal growth, changes in shape, reproductive activity and fatigue repair (ERICKSON & TUMANOVA 2000). Additionally, every bone of a skeleton has its own ontogenetic history (RICQLÉS personal communication). Growth rate and bone tissue can vary within a single bone during ontogeny as well as in different bones of a single individual (RICQLÉS et al. 1991, CHINSAMY 1993b). Thus, growth stops at somewhat different stages in the varying bone types (CHINSAMY 1994) due to morphological growth allometries. Some bones, for example, grow asymmetrically, and growth cycles may be restricted to the parts where growth was slowest (REID 1997b).

This means that the same bone sampled at different regions as well as different kinds of bones of a single individual may present a different microstructure of bone and therefore a different growth history, mainly expressed by a varying number of LAGs (RICQLÈS 1983, CHINSAMY 1993a, HORNER et al 2000) or by the deposition of different bone types. On the one hand, this makes standardized sampling locations for each bone type necessary (RICQLÈS 1983, REID 1990, CHINSAMY 1993a, b). On the other hand, it is necessary to sample different kinds of bone from an individual to get the most complete growth record. If this is not possible, long bones like femora and tibiae should be preferred. In most taxa long bones have the greatest number of LAGs and are generally well suited for bone histological research as has been documented in several studies (e. g. CHINSAMY 1990, 1993a, b, HORNER et al. 2000, SANDER 1999, 2000, ERICKSON & TUMANOVA 2000). According to RICQLÈS (1983), some pelvic girdle bones are also well suited for recording growth cycles.

Due to resorption from the medullary cavity outward and reconstruction of bone, only the last part of growth is completely recorded in the cortex of adult individuals. Resorption and remodeling starts early in ontogeny, and both vary in extent from bone to bone and group to group. Thus, the growth record in most bones of sub-adult and adult individuals is quite incomplete and makes estimates of the number of resorbed cycles by extrapolation necessary (CHINSAMY 1993a, REID 1997).

Additionally, many tetrapods grow in the different ontogenetic stages (embryonic to adult) with different growth rates (VARRICCHO 1993, CHINSAMY 1994, CURRY 1999, HORNER et al. 2000, SANDER 2000, ERICKSON & TUMANOVA 2000). It thus is necessary to sample different ontogenetic stages of one taxon to get the most complete growth record with a minimum of error. Unfortunately, this is seldom possible due to the rareness of the available fossil material.

1.3.3 Bone histology and growth in recent tetrapods

Highly vascularized azonal fibro-lamellar bone tissue is typical for birds and mammals (CHINSAMY 1994). Both groups grow continuously fast from the juvenile to the adult individual (FRANCILLON-VIEILLOT et. al. 1990, CHINSAMY 1994). Growth lines are generally rare in birds and mammals and occur largely only in the outermost cortex in mature and adult individuals in form of closely deposited LAGs, usually within low to avascular lamellar-zonal bone (CHINSAMY 1994, CHINSAMY & DODSON 1995, REID 1997, HORNER et al. 2001, ANDRASSY 2004). This indicates determinate growth in these groups. Adult size is reached in birds and mammals approximately at the same time or only a short time after sexual maturity

is reached. The onset of sexual maturity corresponds generally with a drop in growth rate (CHINSAMY & DODSON 1995).

Low to intermediate vascularized lamellar-zonal bone is characteristic for recent ectothermic tetrapods. Throughout their whole ontogeny, the usually slow growth is seasonally/cyclically interrupted by LAGs. This indicates clearly that their growth depends strongly on exogeneous factors (winter/summer period; rainy/dry season in more tropical areas). Reptiles grow in their first few years with relative high growth rates, but nevertheless with cyclical interruptions. After reaching sexual maturity, in contrast to mammals and birds they continue growth for sometimes several years, but with clearly lower growth rates than in their first years of life. Thus, sexual maturity is often reached long before maximum size. Recent studies show that reptiles generally grow faster in the favorable season than in the unfavorable season (CASTANET & CHEYLAN 1979; CHINSAMY 1994). Thus, the favorable season is represented by the broad zones, whereas the unfavorable season is represented by the more narrow annuli (CHINSAMY & DODSON 1995). In temperate environments, the favorable season corresponds usually with spring and summer whereas the unfavorable season corresponds with autumn and winter. It is of quite some interest that reptiles living in a-seasonal environments as well as reptiles that were housed under permanent optimal conditions in captivity also show annual growth rings (RICQLÈS 1976, CHINSAMY 1994). As a laboratory experiment has shown, endogeneous determination of seasonal rests, independent of weather conditions, is documented for alligators (NEILL 1971), among others. NEILL (1971) found that the loss of appetite and the lowering of glycogen levels, which generally accompany the inactive season in winter, occur in captive alligators independently of illumination and temperature. The same endogeneous determination can be assumed for cyclical growth in alligators. Thus, cyclical growth depends not only on exogeneous factors, but the production of these lines may merely be a function of endogeneous rhythms. A further important observation in recent reptiles is that at least the juveniles of crocodiles and some turtle species are able to grow under optimal exogeneous conditions (climate, food availability/quality) fast enough to form fibro-lamellar bone (RICQLÈS 1983, REID 1997) and can attain growth rates similar to mammalian rates (ERICKSON & TUMANOVA 2000).

On the other hand, bad environmental conditions over long periods can also affect the growth history of an individual. An extreme case was recently described for the marine iguana *Amblyrhynchus christatus* of the Galapagos that can shrink up to 20% of its original body length in only two years as a result of low availability of food, resulting from "El Nino"

events. After environmental conditions have stabilized (subsequent "La Nina"), body length increases again (WIKELSKI & THOM 2000).

Oviparity is also documented in the skeleton for nesting *Iguana iguana* in the development of lines of arrested growth (ZUG & RAND 1987). CHINSAMY (1990) found in the robust morph of *Syntarsus rhodensiensis* extensive osteoporotic resorption cavities which probably were formed during egg laying. Among others, CHINSAMY (1997) describes for recent female birds the deposition of endochondral bone in the medullary cavity which acts as mineral store during ovulation. Histological changes during the reproduction period are also documented for alligators (WINK et al. 1987).

1.3.4 Growth in dinosaurs

Comparison of histological data shows that the very diverse group of the dinosaurs shows a relatively uniform bone microstructure, presumably inherited from a common ancestor.

Some dinosaurs grew continuously and rapidly with high vascularized fibro-lamellar bone, and their growth rates are comparable to that of large fast growing mammals (REID 1997, ERICKSON et al. 2001) and precocial birds (ERICKSON et al. 2001). Others show lower vascularized fibro-lamellar bone or a bone type indicating slower growth within a periodic growth pattern as seen in modern reptiles. Some other dinosaurs show both growth patterns in different parts of their skeletons (REID 1997, ERICKSON et al. 2001). Deposition of dense lamellar bone with closely spaced LAGs is rare in dinosaurs but is documented for some. Its assumed that such closely spaced LAGs indicate a determinate growth in dinosaurs, too. Further, it is documented that these dinosaurs had lived for several years after active growth ceased (REID 1997, SANDER 2000). A similar tissue in the outermost cortex of some tetrapods is described as external fundamental system (HORNER et al. 2000).

CHINSAMY & DODSON (1995) raised the question why dinosaurs were able to form fibro-lamellar bone: Was it because they have had an innately high metabolic rate or was the deposition of fibro-lamellar bone driven by favorable environmental conditions, like it is possible in some captive reptiles? Compared with bone tissues known from recent groups dinosaur bone tissue seems to be "intermediate" between the tissue of ectotherms and endotherms (equally if LAGs were present or absent). This had lead to much debate and controversy discussion about the physiological status of dinosaurs. According to REID (1990) dinosaurian physiology should not be pictured as reptilian or avian/mammalian, but simply dinosaurian, and as having no true modern counterpart. However, bone histology is not

directly correlated with thermoregulation, but it gives insights into bone depositional rate, growth rate, and growth strategy (REID 1990, CHINSAMY 1994). ERICKSON & TUMANOVA (2000) mentioned that growth rates are a strong indicator of metabolic and physiological status in vertebrates, but environmental influences on dinosaurian growth were not be considered.

Some authors had assumed that the presence of growth cycles, like LAGs, represents a clear indication that dinosaurs grew more in the reptilian way, while others argued that the fibro-lamellar bone tissue and the appearance of Haversian bone in dinosaurs were a criterion for a mammal-like endothermic physiology, as reviewed in CHINSAMY (1993b, 1994). But REID (1997b) mentioned that fibro-lamellar bone and Haversian bone are not documented in many small birds and mammals, although they have the highest metabolic rates. Today it is generally recognized that fibro-lamellar bone tissue is not restricted to endotherms (CHINSAMY 1993), as it was assumed sometimes by earlier workers (BAKKER 1986). ENLOW (1969), RICQLÈS (1974, 1983), and REID (1987, 1990) had described the appearance of fibro-lamellar bone tissue among a wide range of ectotherms and therapsids. Even some crocodiles and turtles show it (REID 1997), too. On the other hand, zonal growth is not inevitably restricted to ectothermic tetrapods (CHINSAMY & DODSON 1995). HORNER et al. (1999) pointed out that LAGs, and therefore cyclical growth, is a plesiomorphic feature for vertebrates and suggested that LAGs had no particular physiological meaning because they appear in several orders of mammals. This was also documented by KLEVEZAL (1996) and ANDRASSY (2004). HORNER et al. (2000) suggested that the occurrence or absence of LAGs has nothing to do with the ontogenetic stage, the metabolic rate or environmental tolerance.

As result of the various histological studies about dinosaur bone histology, today it seems to be clear that most dinosaurs grew with bone tissues and growth rates which in this combination are not present in any extant tetrapods and which is therefore not really easily compared. Most dinosaurs grew with higher rates than extant reptiles, but not all grew as fast as mammals and birds do. Thus, the bone microstructure in dinosaurs shows that they differed physiological from modern tetrapods (REID 1990, 1997). Nevertheless, dinosaurs must have had a stable and efficient circulatory system, comparable and maybe similar but not necessarily equal to that of large recent mammals. CHINSAMY (1994) argues that the cyclical growth in some dinosaurs shows that at least these dinosaurs were not able to maintain a high growth rate throughout each year or their whole life.

That fibro-lamellar bone in dinosaurs is not only a product of mass effects, as HOTTON (1980) had suggested, is shown by its occurrence in hatchlings and in smaller dinosaurs (REID

1997). ERICKSON et al. (2001) show that dinosaurs had growth curves, similar to those of other tetrapods, but with unique growth rates in respect to their body mass. They concluded that growth rates in vertebrates generally increase with respect to body mass (ERICKSON et al. 2001).

1.4 Aims of research

The prosauropod *Plateosaurus engelhardti* from the Norian Knollenmergel beds (Keuper) of Central Europe is of great interest for bone histological research. One reason is its relatively early (Triassic) occurrence. Only a few studies deal with Triassic dinosaurs, like *Syntarsus rhodensiensis* (CHINSAMY 1990) and *Massospondylus carinatus* (CHINSAMY 1993). Up to now, most bone histological studies had concentrated on Jurassic and Cretaceous dinosaurs like sauropods (CURRY 1999, SANDER 1999, 2000, SANDER & TÜCKMANTEL 2003, SANDER ET AL. in press), hadrosaurs (HORNER et al. 1999, HORNER et al. 2000), and ceratopsians (ERICKSON & TUMANOVA 2000). These "late" dinosaurs all show very high growth rates, which indicate rapid growth, similar to that of recent mammals. Thus, the physiology of those dinosaurs must be quite highly developed to make such fast growth possible. A basic question thus is when this high growth rates evolved or if the dinosaurs had it quite from their origin.

Another reason which makes the prosauropod *Plateosaurus engelhardti* attractive for histological study is that the prosauropods are related to the sauropods, and possibly the bone histology of *Plateosaurus engelhardti* can answer the question of or at least give hints on how the sauropods beginning in the Late Triassic were able to grow to such gigantic body sizes.

Additionally, *Plateosaurus engelhardti* is well suited for bone histological study because there are several dozens of complete and incomplete individuals of the same or closely related species from at least three *Plateosaurus* bonebeds. Thus, a selection of useful and well-preserved sample material, mainly long bones, is available and provides a very good database for bone histology.

Thus, a bone histological study of an ontogenetic series of *Plateosaurus engelhardti* from hatchling to juvenile to sub-adult and adult is not possible, due to the lack in the fossil record of individuals smaller than 4.80 m total body length.

The specific aims of the present work are to describe and document the bone histology of *Plateosaurus engelhardti*. The main focus is on the bone tissues and the kinds of vascularization of different bones and at different sampling locations in single bones. Histological differences within samples of single individuals and between the different bones

as well as histological differences between samples from the different localities (Frick and Trossingen) are to be documented and discussed. Growth rates, counts of growth marks, and extrapolation methods are used for aging the adult individuals.

On the basis of these data, life history aspects such as longevity (age at death time), possible age at sexual maturity, growth determination, age at growth cessation, and sexual dimorphism are deduced for *Plateosaurus engelhardti.* Bone histology can also answer the question if there is a correlation between age and body size. Additionally, the growth strategy and life history data of *Plateosaurus engelhardti* will be compared briefly with that of other prosauropods, sauropods, and some recent tetrapods.

1.5 Museum abbrevations

AMNH   American Museum of Natural History, New York, USA

HMT   Heimatmuseum Trossingen, Trossingen, Germany

IFG   Institut für Geowissenschaften, Universität Tübingen, Germany (früher: GPIT, Institut für Paläontologie und Geologie der Universität Tübingen)

IPB   Institut für Paläontologie, Universität Bonn, Germany

MSF   Sauriermuseum Frick, Frick, Kanton Aargau, Switzerland

NAA   Naturama, Aarau, Kanton Aargau, Switzerland

PIMUZ   Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland

SMA   Sauriermuseum Aathal, Aathal, Kanton Zürich, Switzerland

SMNS   Staatliches Museum für Naturkunde, Stuttgart, Germany

2. Previous work on prosauropod bone histology

Several of the early works on bone histology make mention of prosauropods, especially *Plateosaurus.* But most of them have only a descriptive character (SEITZ 1907, GROSS 1934). CURREY (1962) already used bone histology to imply that prosauropods had a physiology similar to that of large advanced herbivorous mammalians and not similar to that of primitive reptiles, and also not similar to that of small and carnivorous mammals. Counting growth cycles and computing growth rates to obtain information about life history was only done by RICQLÈS (1968) and later by CHINSAMY (1993). In fact, RICQLÈS (1968) was the first to recognize the importance of prosauropods for sauropod evolution. Nevertheless, all previous authors agree that the main primary bone tissue in prosauropod long bones consist of laminar fibro-lamellar bone.

One of the first to comparatively study on bone histology in fossil tetrapods was SEITZ (1907). Among other taxa, he described the histology of a tibia of *Plateosaurus*. SEITZ (1907) observed laminar bone tissue with predominating longitudinally and only partially radial vascular canals although he did not use this terminology. Predominately in the inner compacta along the longitudinal canals, the tibia shows erosion and Haversian reconstruction in form of secondary osteons. A longitudinal section of the same bone shows a longitudinal orientation of the primary vascular canals. In addition, a number of circular canals are scattered throughout the section.

In his study about the microstructure of bones in different fossil "stegocephalians" and reptiles, GROSS (1934) described a cross section and a radial section through a tibia of *Plateosaurus* from the locality of Halberstadt. The cross section shows laminar bone with dominating circular and fewer radial vascular canals. GROSS (1934) first mentioned numerous secondary osteons in this sample but only gave a short description of the histology of the sample without any biological interpretation. Beside this, GROSS (1934) illustrated growth rings but at that time he did not recognize their meaning (CHINSAMY & DODSON 1995).

ENLOW & BROWN (1957) mentioned the histology of *Plateosaurus* only in a short paragraph in connection with that of *Brachiosaurus*. They described the bone structure of "certain compact areas" (ENLOW & BROWN 1957) of both taxa as typical plexiform tissue in which Haversian bone dominated locally. ENLOW & BROWN (1957) only referred to the figure of *Plateosaurus* in GROSS (1934: 754, figure 13) but did not study *Plateosaurus* first-hand. They recognized the convergent evolution of this bone tissue with that of several mammalian groups, predominately the artiodactyls.

CURREY (1962) gave a detailed description of the cortical compact bone of a vertebral center of a prosauropod dinosaur from the middle Upper Triassic of Zimbabwe and of an unidentified long bone from another prosauropod species. Right in the beginning, he drew attention to the fact that different bones show a different histology, even in the same individual. CURREY (1962) described for both specimens a laminar vascular system with alternating lamellar and woven bone tissue. Indeed, he recognized that the amount of woven bone in the long bone sample is significantly higher than in the vertebral bone sample. There also were differences in laminae thickness, and the long bone shows Haversian systems scattered throughout the cortex. He described that the laminae in the prosauropod sample were spaced more closely than the laminae in mammal bone samples he studied for comparison. As did ENLOW & BROWN (1957), CURREY (1962) pointed out that this kind of

laminar vascularization is very untypical for modern reptiles but common in recent artiodactyls. After the comparison with the bone histology of recent tetrapods CURREY (1962) concluded that laminar bone is associated with a herbivorous way of life. He pointed out that the dinosaurs seem to agree more with some herbivorous mammals in physiological specialization than with living reptiles.

RICQLÈS (1968) summarized the work on *Plateosaurus* bone histology published up to that time, and on the basis of the published illustrations added the conclusion that the primary bone tissue in *Plateosaurus* consists of normal laminar tissue with predominately longitudinal vascular canals. Circular vascular canals are less frequent but well developed, whereas radial vascular canals are very rare in the *Plateosaurus* bone tissue. Secondary osteons were described as very common in the samples. RICQLÈS (1968) identified this bone tissue in the *Plateosaurus* long bones as plexiform. Afterwards he added his own histological observations from a quadrupedal prosauropod, the melanosaurid *Euskelosaurus browni* of the Upper Triassic Maphutseng Formation of Lesotho. He found the primary bone tissue of *Euskelosaurus browni* to be very similar to that of *Plateosaurus.* It shows scattered bundles of longitudinal vascular canals with regular layers of circular vascular canals and only a few radial vascular canals. RICQLÈS (1968) compared the bone tissue of the prosauropods with that of the sauropod "*Bothriospondylus*" (now assigned to *Lapparentosaurus*). He came to the conclusion that both groups show a plexiform bone type but differ in some details. He believed it possible that the sauropod tissue evolved from the prosauropod tissue.

On the basis of a shaft segment of a femur and three rib fragments, REID (1990) described the bone histology of the prosauropod *Massospondylus.* The compact bone of the femur is non-zonal with a laminar vascular system. The cortex of the rib fragments show finely lamellated zonal tissue in which zones are separated by rest lines or annuli between paired rest lines. The vascular canals run longitudinally, and the vascular density is generally sparse to moderate, locally even avascular. Secondary osteons in the deeper parts of the cortex are present. There is a core of secondary cancellous and compact bone. Seven zones could be counted between the secondary bone area and the external surface of the rib (REID 1990).

REID (1990) studied a second genus of prosauropods (*Euskelosaurus*), sampling a segment from the middle part of a rib. This rib also shows clearly zonal bone in the outer parts of the sample. Resting lines, to which annuli are locally added, separate the zones here as well. Altogether, 12 zones could be counted in this rib. Vascular density is high in most parts of the bone. The rib shows longitudinal vascular canals at the center of small cylindrical primary osteons, which are set within a "non-lamellated matrix" (REID 1990: 26). Secondary

osteons are scattered irregularly throughout the cortex. REID (1990) agrees with RICQLÉS (1968) that *Euskelosaurus* generally forms zonal and non-zonal bone, and that limb bones consist of laminar fibro-lamellar bone.

CHINSAMY (1993) did the first comprehensive work on prosauropod bone histology, studying transverse sections in a growth series of femora of the South African prosauropod *Massospondylus carinatus*. The sections were all taken from below the fourth trochanter. CHINSAMY (1993) described the subdivision of the cortex of the femora sampled into growth rings (annuli and zones) and observed a connection between increasing age and decreasing spacing of annuli and zones. Generally, deep in the cortex, wider growth rings are deposited than in its periphery. In contrast to the theropod *Syntarsus rhodensiensis*, also studied by her (CHINSAMY 1990), the sampled femora of *M. carinatus* contain no closely spaced resting lines in the periphery of the cortex. Therefore, *M. carinatus* shows no "slowing of growth in its last stages" (CHINSAMY 1993). Between the annuli, the primary bone tissue of *M. carinatus* consists of fibro-lamellar bone with a high vascular density. The annuli themselves consist of nearly avascular lamellar bone. Primary osteons are predominately longitudinally. Secondary osteons are scattered through the whole cortex with a predominance in the mid-cortical to peri-medullary region. Also, cancellous bone tissue is widespread around the medullary cavity, and the transition from compact to cancellous bone is described by CHINSAMY (1993) as abrupt. The histological samples of *M. carinatus* of different individuals vary in number and width of the growth rings. Resting lines seems to occur more frequent in the later stages of bone deposition.

CHINSAMY (1993) interpreted the deposition of fast and slow growing bone areas observed in *M. carinatus* as similar to the growth pattern of crocodilians and other ectothermic tetrapods. Thus, she concluded that the bone deposition of *Massospondylus carinatus* was seasonally cyclical (CHINSAMY 1993). CHINSAMY (1993) found difference between *M. carinatus* and crocodilians in the distribution of secondary osteons. In *M. carinatus* they were scattered throughout the whole cortex as a result of bone resorption and subsequent redeposition, while in crocodilians secondary osteons appear only in the peri-medullary region as a result of cancellous bone formation (CHINSAMY 1993). Therefore, *M. carinatus* shows bone resorption and subsequent re-deposition, which is in this form untypical for reptiles (RICQLÈS 1976, CHINSAMY & DODSON 1995).

Based on the assumption that one annulus and one zone represent one annual growth cycle, CHINSAMY (1993) counted the observed growth rings in the different femur samples of *M. carinatus*. To give a complete age estimate as possible of the sampled individuals, she

added her estimate of resorbed growth rings to the counted visible growth rings. She estimated the total LAG number by using the width of the initial zones of the smallest specimen. This method results in a total age for the sampled *M. carinatus* individuals between 2 and 15 years, at a total femur length between about 12.0 cm and 44.0 cm. A regression analysis of the plot of the number of growth rings versus femur length brought out that the best correlation is reached with a power curve. The implication is that growth rate changes during ontogeny (CHINSAMY 1993). Growth in *Massospondylus carinatus* initially was rapid and slowed down subsequently. On the basis of this growth curve, CHINSAMY (1993) had used a mathematic equation to determine the length increase of the femur in five-year steps. A significant decrease in growth with time could be shown with this method. Based on these mathematical data and bone histology of the femora, CHINSAMY (1993) came to the conclusion that growth clearly decreased in *Massospondylus carinatus* with increasing age but did not really stop. Thus, growth continued "indefinitely", although at a decreasing rate (CHINSAMY 1993). Such an indeterminate growth strategy is typically reptilian, and according to CHINSAMY (1993), the implication is that *M. carinatus* has had a physiology similar to ectotherms. On the other hand, she recognized that the highly vascularized fibro-lamellar bone tissue of *Massospondylus carinatus* indicates very rapid growth during the favorable season. This feature associated *M. carinatus* more closely with endotherms. CHINSAMY (1993) concluded from this that *Massospondylus carinatus* occupied an intermediate physiological level between ectotherms and endotherms.

FOELIX (1999a: figure 4, 5; 1999b: figure 10) illustrated thin sections of *Plateosaurus* ribs from the locality of Frick. He documented growth rings in the outer parts of the rib samples and suggested periodic growth for *Plateosaurus*.

Of quite some interest are the results of the histological examination of *Thecodontosaurus antiquus* (CHERRY 2002). CHERRY studied 17 thin sections made from femora, tibiae, humeri, phalanx, and ribs. All sections showed fibro-lamellar bone, but LAGs occur only in the rib. However, she noted that it cannot be excluded that sampled bones derived only from juvenile individuals, and therefore LAGs in the limb bones were not deposited yet. From the fibro-lamellar bone tissue, CHERRY concluded a relatively rapid growth rate and a physiology intermediate between ectothermy and endothermy for *T. antiquus*. Furthermore, she suggests that similarities in growth rate and pattern between the basal dinosaur *T. antiquus* and more derived dinosaurs may have been inherited from a common ancestor.

3. *Plateosaurus* from Central Europe

3.1 General systematics and occurrence

The genus *Plateosaurus* belongs to the Prosauropoda, which together with the Sauropoda forms the Sauropodomorpha (HUENE 1932). The main features of the Sauropodomorpha are a small head on an elongated, thin neck, a massive trunk and a long tail. The kind of locomotion (bipedally or quadrupedally) varies, depending on body size and body mass. Thus, a quadrupedally walk on columnar legs is assumed for some large prosauropods and all sauropods. Some authors support the view that the prosauropods are a monophyletic sister clade to the sauropods (SERENO 1989, GALTON 1990), while others believe a prosauropod, like the name suggest, was the ancestor of the sauropods (HUENE 1932, COLBERT 1964, BENTON et al. 2000, YATES 2001) and forms the stem-group of the sauropods. In the latter case, the prosauropods would be a paraphyletic group with some taxa more closely related to the sauropods than others. The phylogenetic relationship between the two groups has not really been resolved yet, however (BENTON et al. 2000, WILSON 2002).

Prosauropods are medium to large-sized dinosaurs, with a length from around 2.5 m to a maximum of 10 m. The postcranial skeleton of prosauropods is very uniform in contrast to the complex skull. Prosauropods have been found virtually worldwide. Stratigraphically, they appear in the middle Carnian and disappear at the end of the Toarcian, with a predominance in the fossil record beginning in the Norian (GALTON 1990). *Plateosaurus* itself appears in the upper middle Keuper (Norian) and disappears in the Rhaetian. In Central Europe, the remains of *Plateosaurus* were mainly found in the Stubensandstein and the Knollenmergel Beds of late Norian or early Rhaetian age or in stratigraphically equivalent marls and mudstones (GALTON 2001).

3.2 Anatomical features of *Plateosaurus*

A precise osteological description of the studied bones is unnecessary here, because details can be found in the literature (HUENE 1926; GALTON 1985; 1986, 1990; VAN HEERDEN 1997). Thus, only a brief anatomical description is given here, including bone features observed on the *Plateosaurus engelhardti* material from Trossingen investigated for this study.

Plateosaurus is characterized by a small skull, a long neck, a moderately barrel-shaped trunk, and a long tail. The body mass seems to be concentrated in the pelvic region (VAN HEERDEN 1997). The axial skeleton consists of a proatlas, ten cervical vertebrae, fifteen trunk or dorsal vertebrae, three fused sacrals with the pelvis, and around fifty tail vertebrae. Ribs are

found on the dorsal vertebrae, and thin, pointing backward cervical ribs are found along the neck. A well-developed gastral basket is present. The dorsal vertebrae increase in size gradually towards the pelvis, and the tail vertebrae decrease toward the tip of the tail. The appendicular skeleton consists of a typical dinosaur Bauplan. Only the manus possess a conspicuous feature, a trenchant and raptorial-like ungual on digit I. The femur of *P. engelhardti* is sigmoidal in form, meaning it is curved distally in anteroposterior view (GALTON 2001). This is according to GALTON (2001) one of the main features to distinguish *P. engelhardti* from other *Plateosaurus* species. According to MOSER (2003), the sigmoidal form of some femora as well as other morphological differences in the huge *Plateosaurus* material from Trossingen was caused by paleopedogenetic effects: clay precipitation and swelling processes. Thus, the distally straight or sigmoidal form of femora is the result of their varying position in the sediment during fossilization, respectively paleopedogenesis (MOSER 2003). MOSER (2003) noted that these features are not significant and are not suited to distinguish different taxa.

3.3 Size, body mass, and biology of *Plateosaurus*

Plateosaurus is a medium- to large-sized dinosaur, with a maximum length from snout to tip of tail of around ten meters (WEISHAMPEL 1984). On the other hand, MOSER (2003) thinks that the assumed maximum size of ten meter is too high for *Plateosaurus*, because this size estimates are based on bones which were enlarged by clay swelling. For example, the left femur with a measurable length of 99 cm (98 cm by MOSER 2003: 70) kept in the IFG supposedly increased in length 25-30 % (MOSER 2003). Thus, according to this hypothesis, the maximum body length of *Plateosaurus* must be reduced from ten meters back to around 7.5 meters. However, as the current study will show (section 6, 7), the histological record of *Plateosaurus* bones is quite intact and provides no evidence for any diagenetic changes in bone size, particularly bone length.

SEEBACHER (2001) determined the body mass for an individual of 6.5 m length of *Plateosaurus* of around 1072 kg. SANDER (1992) estimated body mass of *Plateosaurus* by using a scale model and calculated that an individual of 8 m length had a weight of 2179 kg (table 6).

Plateosaurus has small, mostly homodont spatulated teeth, with a coarse marginal serration. On the basis of the teeth, most authors assume a herbivorous diet for *Plateosaurus* (GALTON 1990, VAN HEERDEN 1997). *Plateosaurus* was considered to be at least facultative bipedal (GALTON 1990, UPCHURCH 1997). VAN HEERDEN (1997) discussed the fourth

trochanter of the femur as a rough indication for the usual kind of locomotion in dinosaurs. The position of the fourth trochanter is in bipedal dinosaurs always proximal to the middle of the length of the femur while it is lower down in the heavy, surely quadrupedally walking sauropods. Due to the intermediate position of the fourth trochanter in *Plateosaurus* femora, it was assumed by VAN HEERDEN (1997) that *Plateosaurus* was not as typical a biped as, for instance, the theropods. For a predominately bipedal locomotion also argues the very well developed thumb with its large, trenchant claw. The claw was possibly used in defence when the animal stood on its hindlimbs or as a grasping organ for branches during high browsing. A hand with such a construction appears ill suited as a walking organ (HUENE 1926). GALTON (1990) suggested that the first ungual was held clear above the ground during quadrupedal locomotion. A fully quadrupedal locomotion is excluded by most authors.

In contrast to these previous theories, MOSER (2003), after a detailed study of the skeleton, mainly concerning the pelvis region and the tail vertebrae, came to the result that *Plateosaurus* moves quadrupedally and carries the tail horizontally. MOSER (2003) does not exclude a bipedal carriage, but only when *Plateosaurus* ran fast.

Plateosaurus is usually the most common terrestrial vertebrate in the beds in which it occurs. Many fragmentary to complete articulated skeletons are known. *Plateosaurus* is also found in mass accumulations. However, those do not necessarily represent the mass death of e.g. a herd. Mass accumulations also can be the result of a normal background turnover of a very common animal (WEISHAMPEL 1984, SANDER 1992; UPCHURCH 1997).

At its time, *Plateosaurus* together with other large prosauropods, was the largest animal on land and apparently occurred in high individual numbers. According to GALTON (1990), *Plateosaurus* represents at least 75% of the tetrapod finds from the Knollenmergel of Germany. Therefore it is likely that *Plateosaurus* formed the majority of the vertebrate biomass in its ecosystem. It presumable lived in a variety of environments. Herd life is not documented for *Plateosaurus* until now, and an indication against it may be that *Plateosaurus* lacks crests, frills, or other common display structures which are known from many theropods and ornithischians for which herd life has been suggested (UPCHURCH 1997). Also SANDER (1992) could not find any evidence in the *Plateosaurus* bonebeds of Central Europe which would support or disprove the theory of herd life for *Plateosaurus*. It thus may have lived in loose family assemblages or as single individuals.

WEISHAMPEL & CHAPMAN (1990) had done a multivariate morphometric analyses on femora of *Plateosaurus*. They came to the conclusion that on the basis of the femora, two morphs can be distinguished which may be sexual in nature and may represent a different

locomotory regime in males and females. The main features which led to their results are the relative dimension of the proximal and distal articulations and the varying shape and size of the fourth trochanter (WEISHAMPEL & CHAPMAN 1990). GALTON (1997) discussed more marked differences, probably also indicating a sexual dimorphism, in the appendicular skeleton of two other Upper Triassic prosauropods (*Thecodontosaurus antiquus and Melanorosaurus readi*). GOW et al. (1990) suggested sexual differences in the skull of *Plateosaurus*, but GALTON (2000) contradicted this, because the skull differences do not fit with femoral differences. GALTON (1997, 2000) explains these differences as "probably individual variations". BENTON et al. (2000: 97) noted that HUENE (1908) already had distinguished a robust and a gracile morph in the prosauropod *Thecodontosaurus* from England, explaining this variation as due to two different species. According to BENTON et al. (2000), variation in the postcranial skeleton of *Thecodontosaurus* could also be the result of sexual dimorphism, like GALTON (1997) had suggested before, or of allometry and individual variation.

Differences in morphology were seen by WELLNHOFER (1993) in the *Plateosaurus* finds from Ellingen compared to those from Trossingen. He found the Ellingen specimens to be more robust and massively built in contrast to the more lightly built and slender specimen from Trossingen (WELLNHOFER 1993). GALTON (2000) suggested that these differences are due to a sexual dimorphism, with the larger and more robust form from Ellingen representing the female. According to MOSER (2000, 2003), the massiveness of Ellingen bones is the result of pedogenetic swelling.

Plateosaurus engelhardti bones investigated for the present study show that among the Trossingen material bones of a similar length show some slight morphological variations in size and shape, mainly of the proximal epiphyses and in thickness/wide of the shaft diameter which can be described as a more robust and a more gracile type. These differences cannot be found throughout complete or nearly complete skeletons, only single bones were conspicuous. Due to a similar size range of the studied bones, allometry effects can be ruled out as an explanation. This leaves the possibility of two different species occurring in Trossingen which seems unlikely because there no really significant and clear differences in morphology. Thus, the observation best fit sexual dimorphism or individual variation as explanation.

MOSER (2003) believes that the high morphological variability of *Plateosaurus* bones is the result of diagenetic effects (paleopedogenesis) and not of a biological nature.

Egg clusters are known from prosauropods from South Africa (GRINE & KITCHING 1987). MORATALLA & POWELL (1994) suggest altricial behaviour, at least for the prosauropod

Mussaurus, because of the association in a fossil nest of eggshell fragments and remains of hatchlings. The hypothesis is that hatchlings may have remained in the nest for a certain time, and one or both of the parents may have looked after them (UPCHURCH 1997).

3.4 *Plateosaurus* bonebeds of Central Europe

   Plateosaurus was first described from the Feuerletten (Trossingen Formation) from Heroldsberg near Nürnberg (Germany) on the basis of only a few vertebrae and hindlimb bones as *Plateosaurus engelhardti* (MEYER 1837). Today *Plateosaurus* is known from many skeletons, and from several dozens localities in the Norian beds of Germany, Switzerland, and France (WEISHAMPEL & WESTPHAL 1986: Abb. 4). Several of these skeletons are complete, making this animal one of the best-known Late Triassic dinosaurs. The most important of these numerous localities are Halberstadt in central Germany, Trossingen in southwest Germany, and Frick in northern Switzerland. These three localities were called "*Plateosaurus* bonebeds" by SANDER (1992) due to the same taphonomic processes involved in their origin. Each of these accumulations yielded a large number of fragmentary and complete skeletons.

   In Halberstadt, the fossils were found in vary-coloured mudstones, which due to their similarities in lithology, fossil content and stratigraphical position are correlated with the Knollenmergel Beds (Trossingen Formation) in Southern Germany (SANDER 1992). The main collecting phase for Halberstadt was between 1909 and 1913; during this time the remains of 35 individuals were found (JAEKEL 1914). The fossils were exposed during normal quarrying activities and not by systematic excavation. In the time after 1923, several fossils were recovered again. Since the 1940's, the site is no longer accessible. From Halberstadt came, except for *Plateosaurus*, the early turtle *Proganochelys*, and remains of a few other tetrapods, for example theropod teeth.

   The locality of Trossingen consists of two bone-bearing layers, the lower and the upper bone layer. According to SEEMANN (1933) both bone layers belong to the Knollenmergel Beds. GALTON (2001) assumed that the lower bone bed belongs to the highest level of the Upper Stubensandstein (Löwenstein Formation) and the upper bone bed to the Knollenmergel (Trossingen Formation). The majority of fossils came out of the lower bone layer. The remaining *Plateosaurus* finds of southern Germany all belong to the Knollenmergel (Trossingen Formation) (GALTON 2001). The stratigraphic position of the Trossingen Formation and the uppermost Löwenstein Formation is still discussed. It is not clear yet if they belong to the upper Norian or to the lower Rhaetian (GALTON 2001).

The locality of Trossingen was excavated in three phases. The first excavation campaign was started by E. FRAAS from the Staatliche Museum für Naturkunde in Stuttgart in 1911 and 1912 (FRAAS 1913). Remains of 12 individuals were discovered during this time. F. V. HUENE of the University of Tübingen continued the excavations from 1921 to 1923 with financial support from the American Museum of Natural History; therefore half of the discovered material was later shipped to the USA (HUENE 1928, 1929, 1944). During this second excavation campaign in Trossingen, remains of 12 to 14 individuals were recovered. The third and most productive excavation in Trossingen was in 1932, again initiated by the SMNS, this time under the leadership of R. SEEMANN (SEEMANN 1932, 1933).

In these years, most of the *Plateosaurus* material available today was found, altogether the remains of around 65 individuals, including seven nearly complete and articulated skeletons and around 20 partially preserved skeletons (SANDER 1992). The majority of fossils were isolated bones or small assemblages of disarticulated bones, and represents remains of another 40 individuals. Thus, in total the remains of around 100 individuals were excavated in Trossingen. In addition to *Plateosaurus*, only *Proganochelys* and theropod teeth were discovered.

The fossils of the locality of Frick were embedded in the Upper Variegated Marls, a greenish-grey mudstone, which is stratigraphically and lithologically similar to the Knollenmergel of southern Germany (RIEBER 1985, SANDER 1992). *Plateosaurus* remains from Frick were first discovered in 1961, but detailed investigation and excavation did not start before 1976, by a then preparator of the Paläontologisches Institut und Museum der Universität Zürich, U. OBERLI, in his spare time. From 1977 to 1979, a larger part of the quarry was explored and several incomplete and disarticulated skeletons were found (SANDER 1992). The firm of IMHOF brothers led a second excavation campaign from 1983-1985, again under the coordination of the PIMUZ (RIEBER 1985a, b). Their most important find was a nearly complete skeleton, but more disarticulated and incomplete skeletons were also found. A large-scale excavation with a taphonomic aim in 1988 brought out some incomplete and disarticulated skeletons as well (SANDER & GEE 1989a, b).

Altogether, the excavations at Frick produced five nearly complete and articulated skeletons, around seven articulated posterior halves, and two articulated anterior halves. In Frick, also one bone field of four disarticulated individuals of *Plateosaurus* was excavated.

Today the quarry in Frick (Tonwerke Keller AG) is still accessible, but since 1988 only one excavation was done in 1995, again under the leadership of the IMHOF brothers and with the help of R. FOELIX (NAA) and H. MOOR (Neue Kantonschule Aarau) (FOELIX 1999a).

This excavation resulted in the remains of around 2-3 disarticulated and incomplete individuals. In addition, several isolated bones were found which may partially belong to these excavated individuals. Thus, the fossil remains of *Plateosaurus* in Frick belonged all together to no fewer than 25 individuals.

Beside the *Plateosaurus* remains, some theropod teeth were discovered in Frick, too. Two pleuralia provide evidence for the occurrence of turtles in Frick (KLEIN in prep.). In addition to the rich material and the high number of individuals, which were found at all three localities, there are further similarities according to SANDER (1992). First the large size of the bonebeds is conspicuous. The finds were spread over thousands of square meters, and, with one individual found per 100 m^2, the sites show a loose spacing. The sites are largely monospecific, the only other regular components are *Proganochelys*, and some shed teeth of small theropods. The carcass position is similar in all three localities. Nearly all skeletons lie on their belly, often with the posterior half deeper in the sediment than with the anterior half. The anterior halves are often incomplete or disarticulated.

A further conspicuous point is that in none of these localities were any juveniles found (SANDER 1992, MOSER 2003). The size of individuals of *Plateosaurus* specimens found in the bonebeds ranges between 4.8 and 10 meters total length (figure 1).

The origin of the *Plateosaurus* bonebeds has been interpreted in the literature in different ways. Early authors suggested that *Plateosaurus* got trapped and sank in seasonally wet mud, respectively in a muddy swamp in a deltaic area (FRAAS 1913), or that the carcasses were washed together by fluviatile transport (JAEKEL 1914).

HUENE (1928) thought that the Knollenmergel beds are the result of aeolian deposition and that the mass accumulation of *Plateosaurus* originated by regular seasonal migrations of *Plateosaurus* herds to distant feeding grounds through a desert. On their way, the weakest individuals of the herd died (HUENE 1928).

During his excavation in Trossingen, SEEMANN (1933) analysed the sediment in detail and came to the conclusion that the *Plateosaurus* specimens congregated in an arid area around the last few water holes. Because of incautious behaviour or by other individuals, pushing from behind they got into deeper areas of the waterholes and sank into the mud. Finally they died of thirst. Later WEISHAMPEL (1984) and WEISHAMPEL & WESTPHAL (1986) proposed a mudflow scenario. However, none of these theories have given a fully satisfying answer to all open questions and special features of these localities.

With the relatively recent excavations in Frick, a new interest in the taphonomic background started. SANDER (1992) was the first to recognize that the three localities

Halberstadt, Trossingen, and Frick, have the same origin. He reviewed the old theories and available excavation notes from Halberstadt and Trossingen and added the results of the excavations in Frick. He proposed the hypothesis that the taphonomic origin of the *Plateosaurus* bonebeds is miring in floodplain mud, followed by mummification or carcass disarticulation by theropod scavengers and weathering (SANDER 1992). SANDER (1992) developed his theory about the origin of the *Plateosaurus* bonebeds mainly on the basis of the fact that all complete or nearly complete skeletons were found in a uniform carcass position: They are lying bellies down, with a typical hindlimb position with angled knees. In addition, the hindlimbs were often buried deeper in the sediment than the rest of the individual. Due to this uniform position, a post mortem transport must be excluded and an in situ death has to be assumed (SANDER 1992). Additionally, no preferred orientation of isolated long bones can be observed.

Although, some questions still left open, SANDER'S theory (1992) of miring fits best with the observed facts known today.

3.5 Taxonomy of *Plateosaurus* from Central European bonebeds

Plateosaurus remains are relatively uniform in the postcranial skeleton and obviously distinct features are often missing. Thus, it is difficult to distinguish them without a detailed analysis of the complete skeleton. This led right from the beginning of studying *Plateosaurus* to numerous descriptions of genera and species, often on the basis of incomplete skeletons.

JAEKEL (1913-14), for example, thought that the prosauropod fossils in Halberstadt belonged to several species. HUENE (1932) believed that numerous species and genera occur in Halberstadt and Trossingen. Thus, in this monograph about the order Saurischia, HUENE (1932) described ten species in two genera (*Plateosaurus* and *Pachysaurus*) from Trossingen and also two genera (*Plateosaurus* and *Gressylosaurus*) with nine species from Halberstadt (HUENE 1932).

All more recent workers held the view that the middle Keuper Knollenmergel Beds and sediments of equivalent stratigraphical position, like those occurring at Halberstadt and Frick, contain only one species of prosauropods. This species is *Plateosaurus engelhardti* (GALTON 1985, 1986, 1990, WEISHAMPEL & WESTPHAL 1986; WEISHAMPEL & CHAPMAN 1990, SANDER 1992). Differences in osteology within one locality and between the different localities are small and can be explained by intraspecific variations or possibly by sex differences (see above).

Currently, the discussion is being reopened with several authors working on the taxonomy of *Plateosaurus* from Central Europe (GALTON 2000, 2001, Moser 2003). GALTON (2001), in a detailed analysis of all *Plateosaurus* species ever described found that the holotype of *P. engelhardti* is different in a few features from the material from Trossingen. Thus, he concluded that *P. engelhardti* is only found in the Feuerletten (Trossingen Formation) of Heroldsberg and Ellingen (GALTON 2001). On the basis of his analysis, he referred all "non *engelhardti*"-specimens from the Knollenmergel and equivalent beds of Germany, France, Switzerland, and Greenland to *Plateosaurus longiceps*. This species was first described by JAEKEL (1913-14) from the Steinmergelkeuper (equivalent to the Knollenmergel) of Halberstadt.

On the other hand, MOSER (2003) argues that all morphological differences occurring in the *Plateosaurus* material of southern Germany are the result of diagenetic effects like carbonate and clay precipitation during paleopedogenesis. According to MOSER (2003), only *Plateosaurus engelhardti* is present in the higher Middle Keuper of southern Germany.

According to YATES (personal communication 2002) all finds of *Plateosaurus* from Trossingen belong to a single species. YATES also believes that the species from Trossingen and the material from Halberstadt are very close relatives. *Plateosaurus* remains from the locality of Frick consist also only of one species, but they do not belong to the same species as the Trossingen specimens, due to a few small but consistent differences. They are more similar to the species from Halberstadt than to that from Trossingen.

For the current study the correct specific name is not important, only that the material from Trossingen and Frick belongs each to a single species and that these species are close relatives, if not the same species. All authors agree in this point. Due to *Plateosaurus engelhardti* being the first described species, we use this name for all the species studied.

4. Material

4.1 Specimens studied

Due to their relatively simple appositional growth, predominately long bones like femur, tibia, fibula, and humerus were used for studying growth in general and for skeletochronology. Nevertheless, in the present study, also flat bones like pubis and scapula are included. Other bone types such as vertebrae, ribs, foot phalanges and ischia were sampled in rather limited numbers for comparative purposes.

Plateosaurus material from the localities of Trossingen (southern Germany) and Frick (northern Switzerland) and material kept in the SMNS from other Knollenmergel Beds

localities was considered for the present histological study. Bones from Trossingen and Frick localities were all measured and partially sampled. Bones from other localities were only measured. Their data were used for comparison and to get an overview about the general size range of bones and bone relations. Most of the studied material from Trossingen is kept in the SMNS. Some bones were also sampled and measured in the IFG, where finds from the second excavation period at Trossingen (1921-1923) are stored. The material from the excavations in Frick is mainly kept in the MSF and NAA, some measurements were taken from specimens in the SMA.

4.1.1 *Plateosaurus engelhardti* from Trossingen

The fossils from the first excavation of Trossingen and *Plateosaurus engelhardti* remains from geographically associated localities were fully accessioned in the collections of the SMNS. The material from the third excavation conducted by Seemann in 1932 is only partially accessioned in the collection. Nearly half of the finds from this period are stored in the magazine by their original field numbers (table 1, 2b). The material was prepared mechanically soon after excavation periods. Thus, it mostly prepared out from the surrounding sediment, and if necessary or possible, the bones were glued and partially reconstructed with plaster. But the material was not soaked with any stabilizing liquor or resin.

Field numbers given by SEEMANN during the 1932 excavation range from 1 to 65 and represent the order in which the specimen were discovered (SEEMANN 1933) (table 1). One find number may represent a large bone assemblages of several individuals, a complete or nearly complete individual, or only a few bones (table 1, 2b). During preparation, it became clear that some of the finds of only few bones can be assigned to individuals represented by other find numbers. Find 3, 6, and 54 represent turtle remains. Find 1 and maybe some more are today missing and were lost during World War II (1944) (personal communication R. WILD, ZIEGLER 1986).

Before selection of material for histological examination, all the material surviving in the SMNS and IFG was inventoried. The results are listed in table 2. On the basis of this inventory, the minimum number of individuals (MNI) were determined for each find by counting long and flat bones with a similar size and assigning them to right and left body sides. Thus, finds 8 (only a right tibia does not belong to this individual), 14, 15, 33, 48, and 61 of 1932 probably represent relatively complete individuals. Finds 5, 20, 21, 28, 36, 37, 45, 50, and 53 of 1932 represent presumably single individuals, but always only a few bones were

Table 1: *Compilation of specimens excavated by SEEMANN in 1932 based on his field notes (unpublished documents; stored in the SMNS). The commentary describes the material as interpreted by SEEMANN after a first examination of the unprepared finds in the field. 0 = cannot be found in the SMNS; C = the find is stored in crates in the magazine, M = the find is accessioned to the collections in the magazine.*

find-number	current	original comments of SEEMANN
1	0	complete individual; destroyed in WWII
2	0	tibia, rib, vertebrae
3	M	bone-plate (turtle?)
4	0	tail vertebrae
5	M	nearly complete individual
6	M	bone plates
7	0	single vertebraes
8	C	1-2 incomplete individuals
9	0	claw with phalanges and crushed bones
10	M	1 - ? incomplete individuals
11	0	phalanges
12	0	*unreadable...* complete individual with skull, strongly scattered
13	0	ribs (maybe belonging to find 10?)
14	C	partially preserved individual, presumably posterior part
15	C	parts of a well preserved individual with skull, predominately posterior half
16	0	claw and vertebrae
17	0	large long bone
18	0	pelvis (illium, ischium)
19	0	ribs, vertebrae, tarsale
20	M	foot bones, tail and skull
21	C	humerus
22	0	?
23	0	foot bones
24	0	vertebrae
25	0	femur, single *..unreadable*
26	0	poorly preserved vertebrae; scapula, put in plaster
27	C	2 femora
28	C	scapula, pubis, femur, tibia
29	C	scapula, ribs, large vertebrae, pelvis
29	C	complete: vertebrae, femur, fibula ?, maybe to find 29
30	0	belonging to 28 ?
31	0	vertebrae
32	0	femur
33	M	femur, tibia, *..unreadable…* foot, pelvis with tail vertebrae
34	0	ribs, different foot bones, tibia
35	0	scapula, foot bones
36	M	neck, fore- and hindlimb, nearly complete individual
37	M	foot bones, nearly complete individual
38	0	foot bones, vertebrae, and more. (bad preserved femur)
39	0	foot bones, ischium, tibia ?, vertebrae, femur, scapula
40	0	2 scapulae, coracoid, humerus, femur
41	0	radius,/ulna
42	0	ischium
43	0	foot-bones, vertebrae
44	0	femur, pelvis, tail vertebrae
45	M	illium, vertebrae, foot-bone, and more
46	0	4 vertebrae
47	0	tail vertebrae, single *…unreadable*

48	C	incomplete skull, vertebrae, shoulder girdle
49	0	vertebrae
50	M	both forelimbs, scapula
51	0	compressed vertebrae
52	0	vertebrae
53	M	foot bones, fibula
54	M	turtle shell
55	0	tail vertebrae, single
56	0	plant remains
57	0	vertebrae and foot-bones
58	0	vertebrae and foot-bones
59	0	undefined bones
60	0	tail vertebrae, pelvis, and hindlimb
61	C	nearly complete individual
62	0	tibia and tail vertebrae
63	0	humerus
64	0	vertebrae and ribs
65	M	large assemblage of bones, surely several individuals

preserved. Find 10 is a bone assemblage of at least two relatively complete individuals, but a third one is documented by a femur. Find 27 is composed mainly of hindlimb and pelvic girdle bones and represents at least four individuals. Find 29 seems to be made up of no less than three left body halves. Find 65 is composed of at least five individuals, of which three were relatively complete with regard to the main long- and flat bones (table 2b).

Finds 5, 10, 20, 36, 37, 45, 50, 53, and 65 of 1932 were fully accessioned to the SMNS collection, find 33 was prepared in its original position as found and is on exhibit. Finds 8, 14, 15, 21, 27, 28, 29, 48, and 61 are stored in large crates in the magazine. The original SEEMANN field-numbers together with the total length of the bones are used to uniquely identify the sampled bones in this study. The material in the crates provided the main database for the present histological research, while the fully accessioned material in the magazine was only accessible for measurements.

From the available material in the IFG, also a few bones were sampled. This material excavated by HUENE, was mechanically prepared, like the bones in the SMNS, but in addition it was treated with shellack (WEISHAMPEL & WESTPHAL 1986). To identify the sampled bones in the IFG, the total bone length is combined with the inventory number of the bone, when available.

In contrast to the number quoted in the literature (reviewed in SANDER 1992), the actual minimum number of individuals of *Plateosaurus engelhardti* excavated in Trossingen and still preserved in the IFG and SMNS collections amounts to around 54 individuals (table 2).

Although the count of 54 individuals is only a rough estimate, around the half of the presumed individuals seem to be missing. One cause of the discrepancy between the literature

and actually available material is the shipment of *Plateosaurus engelhardti* remains from the excavation of 1921/23 to the USA. In addition, misinterpretation of the finds, still partially buried in the sediment during and after the 1932 excavation would also have played a role. Further specimens, like find number 1, were lost or destroyed, but their exact number is unknown.

Table. 2: *List of* **Plateosaurus engelhardti** *material available in the SMNS and IFG today:* **Table 2a***: Remains from excavations in Trossingen before 1932 and from other localities in the Knollenmergel Beds from southern Germany. Collection and compactus means the find is inventoried into the magazine of the mentioned museum and possesses an field- or inventory number.*

field or inventory number	repository/collection	number of individuals	notice/remark
SMNS 13200 a-z (Trossingen)	collection SMNS	5	several bones from at least five individuals, excavated in 1911/12; the most complete individual was the base for the osteological description of *Plateosaurus* by HUENE (1926)
SMNS 12949/12950/12951 (Trossingen)	collection SMNS	2	a few bones from at least two individuals, excavated in 1911/12
SMNS 80664 (Stuttgart-Degerloch)	collection SMNS	1	only a few bones
SMNS 4011 (Stuttgart-Degerloch)	collection SMNS	1	left humerus
SMNS 53537 (Stuttgart-Degerloch)	collection SMNS	2	one relative complete skeleton, and maybe one ? humerus
SMNS 6014-6020/ 6047-6050/ 6058-6060/6061 (Trossingen)	collection SMNS	2	skull, a few other bones
IFG 192.1/ 163 (Trossingen)	compactus IFG	1	left femur, left tibia
IFG, uncat. (Trossingen)	compactus IFG	1	scapula
IFG mounted skeleton (Trossingen)	IFG, on exhibit 2002	>2	composite of several individuals
IFG mounted skeleton (Trossingen)	IFG, on exhibit 2002	>2	composite of several individuals
IFG, in situ preparation (Trossingen)	IFG, on exhibit 2002	1	mainly a posterior half
IFG, in situ preparation (Trossingen)	IFG, on exhibit 2002	1	only a few bones
IFG, in situ preparation (Trossingen)	IFG, on exhibit 2002	1	one hindlimb

Table 2b: *List of currently available* **Plateosaurus** *remains from the 1932 excavation in Trossingen* *("nearly complete skeleton" means that only few bones are missing). Collection means the find is inventoried into the magazine of the mentioned museum and possesses an inventory number. Magazine means the find is stored in the mentioned museum, but not inventoried yet (e. g. stored in large crates).*

field or find number	repository/collection	number of individuals	notice/remark
5	collection SMNS	1	only a few bones
8	magazine SMNS	2	one nearly complete skeleton, and one single tibia
10	collection SMNS	3	remains of one smaller and one larger individual; remains of at least one or more other individuals
14	magazine SMNS	1	one nearly complete skeleton
15	magazine SMNS	1	mainly a posterior half
20	collection SMNS	1	manus and pes, a few bones; most remains are on loan to the Heimatmuseum Trossingen
21	magazine SMNS	1	right humerus
27	magazine SMNS	4	mainly hindlimb and pelvic girdle bones
28	magazine SMNS	1	only a few bones
29	magazine SMNS	3	no less than three left incomplete body halves
33	SMNS exhibition	1	in situ preparation of a posterior half
36	collection SMNS	1	right pes and a few other bones
37	collection SMNS	1	only a few bones
45	collection SMNS	1	one manus
48	magazine SMNS	1	one nearly complete skeleton
50	collection SMNS	2	only a few bones, but of two different sizes
53	collection SMNS	1	one Radius
61	magazine SMNS	1	one nearly complete skeleton
65	collection SMNS	5	four relative complete individuals, and remains of one more

Altogether 39 bones were sampled from the locality of Trossingen (table 4), representing a minimum number of individuals of around 16. For some individuals, several bones were sampled, making a comparison of the growth record in different bones of the same individual possible (SMNS F 14, SMNS F 29, SMNS F 48). To check the consistency of the growth record in a single bone, different samples on varying locations were taken.

4.1.2 *Plateosaurus engelhardti* from Frick

The *Plateosaurus* material from the locality of Frick was also prepared out from the surrounding sediment, and if necessary and possible the bones were glued and reconstructed with plaster. The material from the excavations before 1995 is inventoried in the collection of the MSF. The remains of *Plateosaurus* exhibited in the SMA are on loan from the MSF.

The material from the 1995 excavation is not fully prepared yet and is stored in the NAA. None of the material from the locality of Frick was soaked in any stabilizing resin, except for cyanoacrylate glue in the field.

If a collections number is present, mostly consisting of the original field number, it is used in the present study. If the bones lack any number, the total length, body side, and the museum where the fossil is kept is listed to make an unequivocal identification of the specimen possible.

Again, before sampling the available material, mainly concerning long and flat bones was inventoried, and the results are listed in table 3.

Table 3: Plateosaurus engelhardti *finds from Frick kept in the Naturama (NAA), the Sauriermuseum Frick (MSF) and the Sauriermuseum Aathal (SMA).*

field or find number	Repository/collection	number of individuals	notice/remark
GEO 92	NAA	>2	two anterior halves
GEO 93	NAA	to GEO 92 ?	left manus, radius, ulna, and vertebrae
GEO 162	NAA	to GEO 92 ?	vertebrae, gastralia
GEO 94	NAA	to GEO 92 ?	pubes, ribs, and gastralia
GEO ?	NAA	to GEO 92 ?	cranium, ribs, and gastralia
F 88	NAA	1?	caudal vertebrae; femur, humerus, tibia, fibula
Imhof 1986	NAA	1	left hindlimb with pes, cranium, right ischium, femur, fibula, tibia
no number	NAA	1	pes
no number	NAA	1	right humerus
A9	NAA	1	tibia, right scapula-coracoid
A8	NAA	to A9	fibula
B50/B45	NAA	1	ischia
no number	NAA	1	pubis
material from the 1988 bone field (SANDER 1992)	MSF (magazine)	4?	scapula, fibula, tibia, fibula, tibia, fibula, pubis, tibia
MSF 23	MSF, on exhibit	1	completes skeleton
MSF 4	MSF, on exhibit	1	whole posterior half
MSF17	MSF, on exhibit	1	anterior half and fibula
MSF 13	MSF, on exhibit	1	a few bones
MSF 19	MSF, on exhibit	1	partly preserved skeleton
MSF 10	MSF, on exhibit	1	pubis
material from the 1988 bone field (SANDER 1992)	MSF, on exhibit	>1	composite of several individuals, mounted above the door
MSF 5	SMA, on exhibit	2	two anterior halfes exhibited in situ
MSF on exhibition	SMA, on exhibit	1	right pes
MSF on exhibition	SMA, on exhibit	1	left pes

Most of the material from Frick is on exhibit and not accessible for sampling. Thus, only five to six individuals that are represented by seven femora were studied. Figure 1 shows clearly that the Frick bones fit well into the lower range of the medium-sized *Plateosaurus engelhardti* individuals from Trossingen.

The minimum number of individuals is relative large and is about 20. This is due to the presence of more single bones from the bone field and more disarticulated skeletons in Frick than in the locality of Trossingen.

A total of 11 bones was sampled for histological research from the locality of Frick (table 4), representing a minimum number of individuals of around 11, too. Unfortunately, none of the Frick individuals could be sampled from more than one bone. But in some bones, samples were taken at different locations to check for the consistency of the growth record.

Table 4: *Sampled bones of* **P. engelhardti** *from the Trossingen and Frick localities, arranged according to kind of bone and bone length.*

total length	kind of sample	body side	locality	specimen number	repository/ collection
femora					
ca. 50.0 cm	thin-, polish,- and cross section	right	Trossingen	F 29	SMNS
56.5 cm	thin-, polish,- and cross section	right	Frick	F 88-B130	NAA
59 cm	thin- and polish section	left	Frick		NAA
59.5 cm	thin- and polish section	right	Trossingen	F 29 A	SMNS
62.5 cm	fracture surface	right	Trossingen	F 27	SMNS
63.5 cm	thin- and polish section, fracture surface	left	Trossingen	F 14 A	SMNS
72.0 cm	thin-, polish,- and fracture surface	left	Trossingen	F 29 A	SMNS
74.0 cm	fracture surface	left	Trossingen	F 8	SMNS
74.0 cm	thin- and polish section	left	Trossingen	compactus	IFG
76.0 cm	fracture surface	right	Trossingen	F 48-1	SMNS
77.5 cm	thin- and polish section	left	Trossingen	F 48-1	SMNS
81.0 cm	thin- and polish section	left	Trossingen	F 27	SMNS
99.0 cm	thin- and polish section	left	Trossingen	on exhibition 2002	IFG
tibiae					
ca. 51.0 cm	thin- and polish section	right	Frick	MSFM-1	MSF
51.0 cm	cross section	right?	Frick	F 88/B70	NAA
51.0 cm	fracture surface	right	Trossingen	F 15	SMNS
>> 52.0 cm	thin- and polish section	left	Frick	MSFM-2	MSF
53.0 cm	thin- and polish section	right	Frick	A 9	NAA
55.0 cm	thin- and polish section, fracture surface	right	Trossingen	F 14 A	SMNS
59.0 cm	thin-, polish-, and cross section	left	Trossingen	F 29 A	SMNS
66.0 cm	fracture surface	right	Trossingen	F 48-2	SMNS
fibula					
46.5 cm	fracture surface	left	Trossingen	F 29 B	SMNS
52.5 cm	fracture surface	right	Trossingen	F 14	SMNS
53.0 cm	fracture surface	right	Trossingen	F 15	SMNS
57.5 cm	fracture surface	left	Trossingen	F 29 B	SMNS
59.0 cm	fracture surface	right	Trossingen	F 48-2	SMNS
ca.59.0 cm	fracture surface	right?	Trossingen	F 8	SMNS
humeri					
not available	thin section	right ?	Trossingen	11921	IFG
41.0 cm	cross section	left	Trossingen	F 14 A	SMNS

| 43.5 cm	thin- and cross section	left	Trossingen	F 29 A	SMNS
ca. 43.5 cm	cross section	right	Trossingen	F 61 B	SMNS
44.5 cm	thin- and cross section	right	Frick	F 88/B640	NAA
53.0 cm	thin section	right	Trossingen	exhibition 2002	IFG
scapulae					
36.5 cm	thin- and polish section	left	Frick	unnumbered	MSFM
>> 39.0 cm	cross section	right ?	Frick	unnumbered	NAA
>> 42.0 cm	cross section	left	Trossingen	F 29	SMNS
47.0 cm	thin-and polish section, fracture surface	right	Trossingen	F 14 B	SMNS
48.0 cm	thin- and polish section, fracture surface	left	Trossingen	F 29 B	SMNS
49.5 cm	thin- and polish section	left	Trossingen	F 29 A	SMNS
pubes					
not measurable	thin- and polish section	not identified	Frick	unnumbered	NAA
48.0 cm	cross section	left	Trossingen	F 29	SMNS
50.0 cm	thin- and polish section, fracture surface	left	Trossingen	F 14 B	SMNS
52.5 cm	thin- and polish section	right	Trossingen	F 29 B	SMNS
53.5 cm	thin- and polish section, fracture surface	left	Trossingen	F 29 B	SMNS
other bones					
dorsal vertebra (10.8 cm)	thin-, and polish section		Trossingen	RW 12	IFG
dorsal vertebra (10.7 cm)	thin-, and polish section		Trossingen	RW 14	IFG
rib (size not available)	cross section		Trossingen	F 29	SMNS
rib (size not available)	thin-, and polish section		Frick	F88/738	MSF
foot phalange (size not available)	thin-, and polish section		Trossingen	8159	IFG
ischium (43.0 cm)	thin section and fracture surface		Trossingen	F 27	SMNS

4.1.3 Body size in *Plateosaurus* from Frick and Trossingen

Based on skeletal reconstructions (in WEISHAMPEL & WESTPHAL 1986) femur length is approximately one-tenth of overall body length in *Plateosaurus engelhardti* (SANDER 1992). On the basis of this ratio, the *Plateosaurus engelhardti* material from Trossingen consists of individuals with a total body length from around 4.70 meters (left pubis SMNS F 65, 38.0 cm total length, calculated femur length 47.0 cm, see methods section) up to ten meters (left femur IFG: 99.0 cm).

In figure 1a, a size class histogram based on the femora from Trossingen and Frick is given. Two peaks are observable in the large Trossingen sample, one between 57.5 cm and 67.5 cm and a second between 72.5 cm and 80.0 cm femur length. The first peak includes 23 femora from Trossingen (52 %). Additionally six femora from Frick (86 %) fit into this first
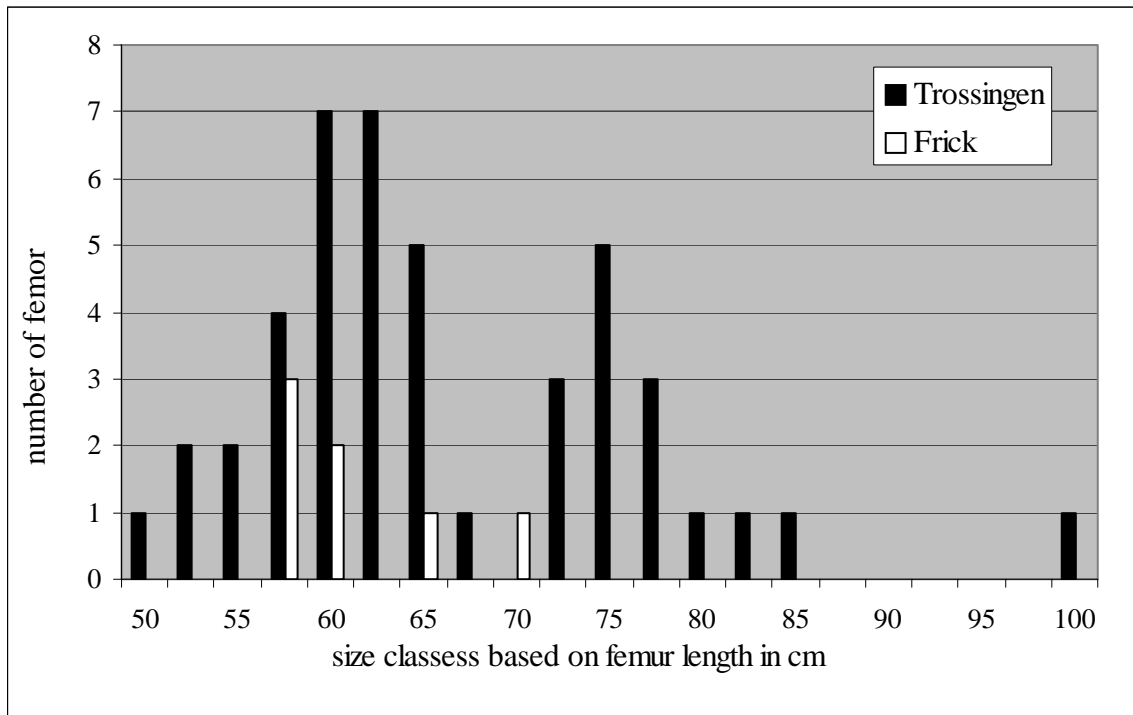
A
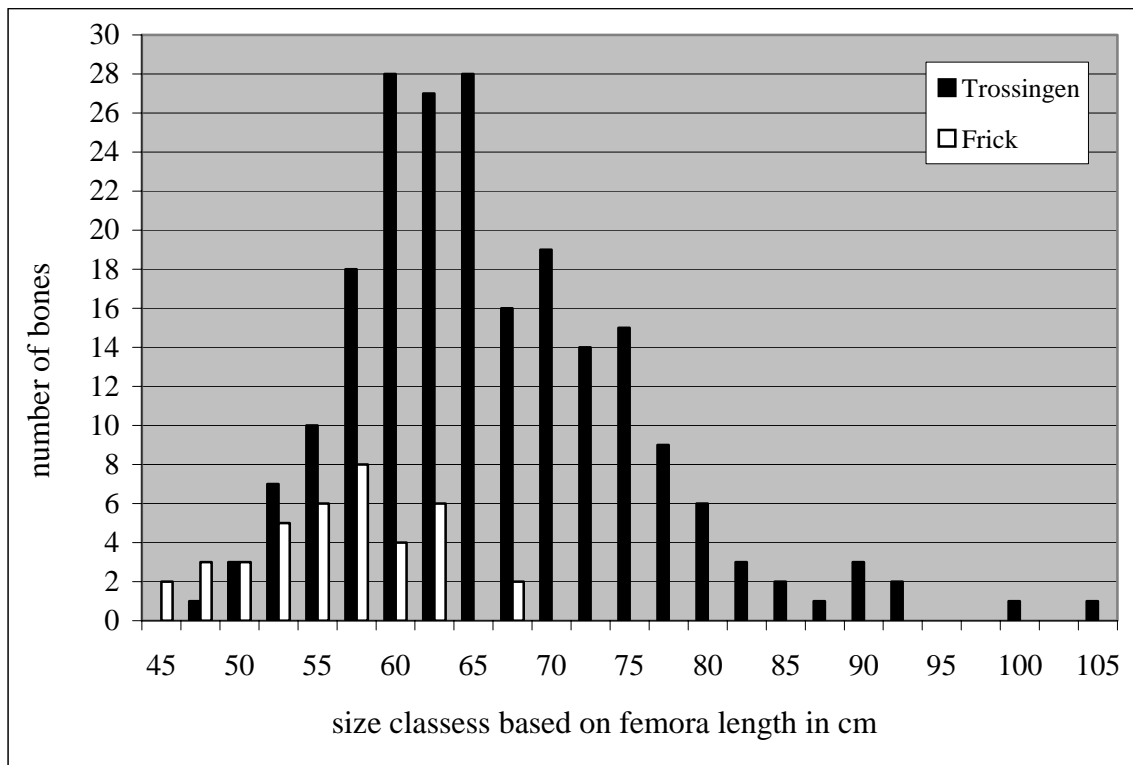
B

Figure 1: *Size class histograms based on femur length for Trossingen and Frick.*
1A: *Size class histogram of femora from Trossingen and Frick. 44 femora from Trossingen that correspond with an estimated minimum number of individuals of 37, and 7 femora from Frick that correspond with an estimated minimum number of 5 individuals are included in this histogram.* **1B:** *Size distribution of all bones of Trossingen and Frick, scaled to femur*

size. All long- and flat bones, altogether 214 bones from the locality of Trossingen and 39 from the locality of Frick are included. The minimum number of individuals in Trossingen is around 54 and in Frick around 20. Scaling to femur length based on bone ratios in table 5 (see method section, section 5.1).

peak. The second peak contains 11 femora from Trossingen (25 %) and one from Frick (14 %). Apart from the higher sample number, the peaks in the present histogram (figure 1a) fit well with the histograms published by WEISHAMPEL & WESTPHAL (1986: figure 11) and SANDER (1992: figure 16). Figure 1a shows that most individuals from Trossingen and all from Frick belonged to medium-sized individuals. Really large individuals of *Plateosaurus engelhardti* are very rare; only four femora (9%) are known from Trossingen which had attained over 80 cm in length, and none is known from Frick.

A second histogram (figure 1b) considers all long- and flat bones scaled to their corresponding femur size. Femora are represented by their actual length. Here 174 bones (81%) from the Trossingen sample and 26 bones (67 %) from the Frick sample fit into the size classes between 57.5 cm and 77.5 cm. The remaining 21 bones (10%) from Trossingen and 13 bones (33%) from Frick are smaller. Only 19 bones (9 %) from Trossingen and none known from Frick are from individuals larger than 80.0 cm femur size.

Nevertheless, the result deduced from both histograms is clear: Medium-sized individuals make up the majority (about 75%) of the *Plateosaurus engelhardti* individuals found in Trossingen. All individuals from Frick represent small- to medium-sized individuals, in relation to the Trossingen individuals. No bone from either locality indicates an individual smaller than 4.70 m. The lack of smaller individuals is surely due to a taphonomic filter (SANDER 1992), and possibly also the lack of the large ones. A second possibility for the large individuals being so rare in Trossingen is a generally more rare occurrence in the living population.

Unfortunately, no juveniles or small individuals of *Plateosaurus engelhardti* are available for sampling because none are known in the fossil record from the bonebeds or any other locality from Central Europe so far. Nevertheless, prosauropod juveniles would be very important for checking the early ontogenetic histology, like the first primary bone tissue deposited and the early growth record in general. The growth record of juveniles is necessary for an exact calibration of the extrapolated part of the growth record of larger individuals. Remains of juvenile *Plateosaurus* specimen with a femur length of 24 cm from the

Feuerletten of Ellingen/Bavaria cited by WELLNHOFER (1993), are now referred to the theropod group (MOSER 2003).

Because of the diagenetic flattening of the *Plateosaurus* bones from Frick, they appear to be thinner and generally smaller than *Plateosaurus* bones from Trossingen. A comparison of the measurements of the specimens from both localities shows that this is not really the case, and the comparison of the total lengths of different bones shows that the individuals from Frick fit into the medium size classes of the Trossingen individual*s*.

Thus, the remains from Frick belonged all to small to medium-sized individuals. The smallest measured femur from Frick is 56.5 cm in length (MSF 23, left), and the largest measured femur is 69.0 cm in length (MSF 13: right). Juveniles are missing in Frick as well as in Trossingen.

4.2 Preservation and diagenesis

Bone is built up of inorganic (hydroyapatite crystallites) and organic material (e.g. collagen, protein). Usually the organic components decay after an animals death. The remaining spaces, for example bone cells, vascular canals, and medullary cavities are re-filled with magnesium or iron oxides (CHINSAMY & DODSON 1995) or simply with sediment. During fossilization, inorganic material is replaced by other crystallites (fluoroapatite) but the original histological structure is often preserved (CHINSAMY 1994).

4.2.1 Trossingen

The fossils from the Trossingen locality are generally well preserved, except for some compaction producing cracks. However, the bones from Trossingen are generally brittle and fragile because of their diagenesis. Main problem here is the missing cementation of the pore-rooms. Additionally, the bones are embedded in clayey sediment. On the one hand clay causes swelling when the bones come in contact with water. On the other hand, the fossils break when the bones get to dry. Due to its brittleness, much damage to the fossil bones happened during or after excavation. This led to many places on the bones having been partially restored in plaster. Today, cracks and fractures are still numerous in the Trossingen material and, in spite of careful handling, often some new ones were added during handling (own experience, MOSER 2003). To preserve and stabilize the fossil bones over time, it is advisable to impregnate them with synthetic varnishes (Zaponlack) or natural varnishes (shelllack). Unfortunately, only some specimens could be treated this way in the past.

Microcracks and fractures are the result of fossilization processes and run through the bones. They do not follow any pattern, running roughly radially, but also parallel to bone surface. They often prefer to follow the LAGs. Enlargement and splitting of LAGs by microcracks is also possible.

Cross-sections show that natural cavities in the bones, like the medullary cavity and cancellous bone regions as well as post mortem cracks, were filled with red mud and clay and occasionally with diagenetic minerals like calcite. Even the very small vascular spaces and microcracks were infilled with fine sediment, which frequently contains iron or manganese oxides. Thus, such infilled spaces appear dark in color. Cementation and precipitation of minerals in pore spaces and cavities is generally rare.

For the bones from the Trossingen locality MOSER (2003) describes a structural change by precipitation of clay. He argues that the bone surface is split in many small pieces, building a mosaic, and clear indicating a regularly welling of bone. He explained that clay precipitation depends on the position of bone in the sediment during paleopedogenesis (MOSER 2003). Thus, sometimes only part of bones were affected which could explain untypically large epiphyses or shaft diameters. Generally, clay precipitation causes a very regular kind of swelling (in contrast to carbonate precipitation) and on the basis of the cracks between the mosaics the original size could be calculated back (Moser 2003).

In spite of this theory of clay precipitation, little diagenetic swelling is observable at the histological level of Trossingen bones. Predominately microcracks, originated from the stresses caused by compaction are observable. Another diagenetic effect is that the primary apatite is sometimes substituted by calcite as can be seen in polarized light. In some regions, the original bone microstructure is destroyed by the growth of crystallites, mostly along microcracks. However, these diagenetic effects do not affect interpretation of bone histology.

4.2.2 Frick

Except for the greater crushing, the material from Frick is generally better preserved than the material from Trossingen because it is not as brittle and fragile. Infiltration of sediment into the bone is as common in Frick as in Trossingen, but the bones from Frick are nevertheless not as sensitive to fracturing. Careful sampling does not cause further damage to the bones, making further preservation and stabilizing with resin or varnish not as necessary as for the Trossingen material.

Natural bone cavities, like the medullary cavity and cancellous bone regions as well as post mortem cracks are filled with sediment, consisting of fine green to grayish clay, and

sometimes also with diagenetic minerals like calcite. Even the very small vascular spaces and the microcracks were filled in with the fine clay. However, in the Frick material microcracks are very rare.

In some specimens the medullary cavity is crushed and/or parts of the cortex were pressed into the medullary cavity. In others, parts of cortex were displaced by crushing. The effects of paleopedogenesis as described by MOSER (2003) are not documented in Frick, too. Bone surfaces are seldom and when only slightly fractured into mosaics.

In Frick bones, little diagenetic effects are observable at the histological level as well. The primary apatite is sometimes substituted by calcite. In some regions, the bone microstructure is destroyed by crushing. However, these diagenetic effects do not affect interpretation of histology and growth record. The Frick samples are very light-colored in thin section.

The Frick material took up a polish much better than the Trossingen material. Thus, lines of arrested growth in the Frick specimen often show up as clear polish lines. On the other hand, without polishing features of the bone tissue and lines of arrested growth are often not as clearly visible as in the Trossingen samples.

5. Methods
5.1 Osteology, measurements, and mass estimates

A detailed osteological study by the author has accompanied this histological research to confirm that in Trossingen as well as in Frick only one species of *Plateosaurus* occurs, and that this species, is very similar in both localities, if not the same. Furthermore, it was searched for hints of a possible sexual dimorphism in bones from both localities. Osteology and measurements from the Frick bones were difficult to judge because of the strong crushing.

Standard measurements like complete bone length, wide and length of the epiphyses, and shaft circumferences were taken from all bones in the SMNS, IFG, MSF, NAA, and SMA to get the largest database possible. Measurements of total bone length provide important information because they also serve to correlate the size of the bones with femur length and therefore with the total body length of the individual. Body length, in turn is important e. g., to construct growth curves and mass estimates. On the basis of these data, possible differences in size and/or shape should be documented. Furthermore, the different measurements from complete bones help in estimating dimensions of incomplete bones.

To determine relative length of postcranial bones, individuals were chosen to determine a percentage value, based on an average length for each of the bones in relation to the length of the femur (table 5). The percentage values for the localities of Frick and Trossingen were determined separated. Values for the Trossingen skeletons are based on several individuals, while for the Frick material only one individual was available (table 5).

Table 5: *Relative lengths of selected postcranial bones in relation to femur length. The data for Trossingen are based on several presumed individuals (SMNS F 5, F 8, F 14, F 37, F 48; 53537) and on the cast of SMNS 13200, exhibited at the SMNS. The mean value resulting from the measurements of the different individuals are used. The data from Frick are based only on a single individual, which is exhibited at the MSF (MSF 23).*

	Trossingen	Frick (MSF 23)
tibia/femur	80%	81,5%
fibula/femur	80%	92%
humerus/femur	62%	68%
pubis/femur	81,5%	not available
scapula/femur	68%	76%

During the acquisition of these data it was conspicuous that the measurements for bones of the right and left body halves of a single skeleton as well as the ratios of bones between different skeletons can differ considerably. This again suggest a high intraspecific variability or, according to MOSER (2003), variation caused by paleopedogenesis.

The data from the Frick material have a greater general margin of error because of the strong crushing of the bones. The percentage values of all bones of the complete skeleton from the Frick locality are slightly higher than the mean values of the bones of the Trossingen locality (table 5).

Mass estimates were done by using the method of developmental mass extrapolation (DME) developed by ERICKSON & TUMANOVA (2000). The cube of femoral length of each specimen was taken, and each value was assessed as a percentage of first the mass estimate of SEEBACHER (2001) and second the mass estimation of SANDER (1992). Then each of the resulting values for the largest femur (IFG, exhibition, 99.0 cm) were set as 100 percent and calculation was done again (table 6).

Table 6: *DME on the basis of the mass estimates available in literature (SANDER 1992, SEEBACHER 2001). Mass in the first column bases on data given by SEEBACHER (2001) who calculated that a* Plateosaurus *individual of 6.5 m body length had a body mass of 1072 kg. Mass in the second column bases on data given by SANDER (1992) who found in a scale experiment that a individual of around 8 m body length had a mass of 2179 kg. Mass in the third column bases on the mean value for the largest femur (IFG 99 cm,left, 3962 kg) of both, SEEBACHER (2001) and SANDER (1992).*

femur length	estimated body mass (kg) based on SEEBACHER (2001)	estimated body mass (kg) based on SANDER (1992)	estimated body mass (kg) on the basis of the mean value for the largest femur
50.0 cm	482,4	522,96	515
56.5 cm	707,5	762,65	753
59.0 cm	804	871,6	832
59.5 cm	825,4	893,39	872
62.5 cm	954,08	1045,92	991
63.5 cm	996,96	1089,5	1030
65.0 cm	**<u>1072</u>**	1176,66	1109
72.0 cm	1457,92	1590,67	1545
74.0 cm	1586,56	1721,41	1664
76.0 cm	1715,2	1873,94	1783
77.5 cm	1811,68	1982,89	1902
80.0 cm	1993,92	**2179**	2100
81.0 cm	2079,68	2266,16	2179
99.0 cm	3784,16	4140	**<u>3962</u>**

5.2 Sampling

5.2.1 Whole bone cross sections

Based on earlier studies on dinosaur long bone histology, the middle of the shaft is the best place to obtain the most complete growth record (RICQLÈS 1983, CHINSAMY 1993, SANDER 2000, ERICKSON & TUMANOVA 2000, HORNER et al. 2000). This is due to the predominately appositional growth of the shaft and the location of the neutral zone in this region (SANDER 2000). To determine the best coring site around the circumference of the mid-shaft region, whole bone cross sections were cut from a femur, a pubis, a scapula, and a rib from Trossingen (SMNS F 29) as well as from a femur, a tibia, a scapula, and a humerus from Frick (single bones from the NAA). All of these bones do not belong to single individuals but represent several specimens. The best coring site is defined by a combination of the thickest available cortex with clear and numerous growth cycles and minimum remodeling, i.e. minimum erosion moving outward from the medullary cavity and minimum

secondary bone tissue. These conditions are largely met around the whole cross sections of the mid-shaft region. Nevertheless, the optimal coring site of each bone type is defined in the histological descriptions by bone in section 6.

Before cutting, the mid-shaft region was stabilized by a girdle of synthetic resin. The sample was obtained by placing two parallel cuts across the shaft, resulting in a slice a few centimeters in thickness. The slice has a proximal and a distal side. After sawing, both sides of the slice were impregnated with a synthetic, low viscosity resin (Araldite 2020) finely ground, and polished to a high gloss.

5.2.2 Coring

A new, rather simple sampling method was developed by SANDER (1999, 2000) and also used for this research. Minimizing damage to the sampled bone, a core of ca. 10 to 15 mm diameter is drilled with a diamond-studded coring bit into the cortex of the mid-shaft area. The drill is generally lubricated with water, but sometimes, depending on the fossil bone material, oil lubriation is used or no lubriation at all (dry drilling). The coring bit is attached to a normal electric drill with adjustable speed. For the brittle *Plateosaurus* material, low speed and very low torque settings were necessary. The method of SANDER (1999, 2000) was improved with regard to lubrication by using a small plasticine dam which was built around the drilling hole and into which the lubricant was poured. This has the effect to protect the *Plateosaurus* bones from excessive moisture, respectively other lubricants, but also guarantees constant lubriation during drilling. The drill was mounted in a simple drill press. The foot of the press is weighted down with a dish of sand in which the bone is supported securely.

The cores so obtained were embedded in synthetic resin (Araldite 2020) and then cut longitudinally, perpendicular to the long axis of the whole bone. One half of the core was processed into a thin section and the other half into a polished section. Thin sectioning followed standard procedures for petrographic thin sections, but specific problems were encountered (see section 5.3).

5.2.3 Existing fracture surfaces

Due to the mode of preservation of the *Plateosaurus* material from Trossingen and Frick, the long bones show many fractures. Most of these fractures run across the narrow mid-shaft region, which is most interesting for histological research, too. The surfaces which, due to the lack of cementation of the fractures are not covered by vein minerals, are similar to the

whole bone cross sections produced by sawing and provide a full overview of the growth record in this bone region. Histological structures can be observed very well in these surfaces, even with the naked eye. Cores sampling problems due to the clayey pore fill of the bones were an added reason for using existing fracture surfaces in this research.

Bones with good fracture surfaces were borrowed from the museums and studied tracing under a binocular microscope with a camera lucida. In addition, the whole fracture surface as well as details were photographed with a digital camera (Nikon D1). Later, the growth record was traced by hand on the digital images by using a computer graphic program. The advantage of these images is that they show the whole cross section, providing an overview about the growth record, without any new damage to the bone. On the down side, due to the limited resolution of these images, histological details, like the bone tissue types cannot be distinguished, and lines of arrested growth cannot be identified with the same certainty as in thin sections. This is predominately a problem in the exterior cortex where growth cycles usually become very close in some adult individuals. Therefore the existing fracture surfaces are best used for complementing the data from thin and polished sections. The number of LAGs counted on only such a fracture surface is commonly too low, and a greater error must be assumed than for physical sections.

5.3 Problems encountered during sampling and thin sectioning

The core sampling method was used before on sauropod bones without any problems (SANDER 1999, 2000, 2003). However, the *Plateosaurus* bones turned out to be more difficult to sample. Due to the predominately fragile condition of the *Plateosaurus* bones, mainly concerning the material from the Trossingen locality, the bones must be generally handled very carefully. In addition, the material in the SMNS, representing the majority of the bones available for sectioning, lacked any impregnation, leading to several problems during sampling.

Problems started while drilling, when many cores fractured or sheared off before the medullary cavity was reached. The fragments of such a core commonly could not be glued back together, and the growth record is quite incomplete in these samples. Several changes in the drilling method gave no fundamentally improved results for the *Plateosaurus engelhardti* material in the SMNS.

It was conspicuous that these problems did not appear during the sampling of material in the IFG collections. As indicated by preparation methods in literature (WEISHAMPEL & WESTPHAL 1986), the IFG specimens from Trossingen were impregnated soon after

preparation with a natural varnish, shelllack. The bones in the IFG today are in a much better condition than the un-impregnated bones in the SMNS. With this background information, the preparators at the SMNS were asked to impregnate two SMNS femora for the present study with zapon varnish. A complete core was drilled from one of these two bones without any problems. Unfortunately, impregnation with zapon varnish is an expensive and time-consuming procedure and could not be done for all the bones to be sampled.

Processing the drilled cores into thin sections also led to some unexpected problems, like some pieces braking out of the cores during grinding of the halves. The thin sections also sometimes show differential impregnation (e. g. figure 5A, C) effects, and later some of the thin sections separated partially from the slides. This was again due to the fragile nature and clayey pore fill of the bones. Problems such as separation of section and slide probably arise as a result of the limited permeability of bones. It could be observed on the basis of the thin- and cross sections that the resin ran into the polished sections only along the microcracks. Although the material seems to absorb the resin completely, the thin sections show that only some areas were really impregnated by the resin. Possibly, these effects originate from different preservation close to the cracks. However, the differential impregnation effects are not clearly understood yet.

5.4 Methods of histological and skeletochronological study
5.4.1 General aspects

The histological data base consists of 50 specimens (33 long bones, 11 flat bones, 6 other bones) from both localities, including fracture surfaces. All sections were examined by standard light microscopic techniques. The thin sections were viewed in a compound microscope in transmitted light, both normal and polarized. At high magnifications, bone cell lacunae, bone type, as well as primary and secondary osteons were visible. To obtain a good overview of the growth marks the distances between LAGs, increase or decrease of vascularization, and type and distribution of remodeling, the cross sections and polished sections were studied under a binocular microscope. A sketch of all sections was made with a camera lucida, and the LAGs were drawn in and counted.

In the Frick material, LAGs were often not as clear as in the Trossingen material but were expressed as polish lines, which can be recorded instead. Polish lines are visible in polished sections to the naked eye or with a binocular microscope by tilting the polished surface to create a reflection but also in the compound microscope using bright field

illumination (SANDER 2000). In the *Plateosaurus* samples, the polish lines correspond generally to the lines of arrested growth and were observed with the binocular microscope.

The current study shows that a combination of various photographic, microscopic, and sectioning techniques are important to get the most complete understanding of the growth record: Due to the mode of preservation and colour of the material, the polished sections often gave better observation results for growth mark than thin sections. Only after close inspection, all LAGs seen in the polish section were also found in the thin sections. The thin sections, on the other hand, are better suited for studying histological features at higher magnifications like bone tissue types or remodeling processes.

5.4.2 LAG counts

Due to the necessity of extrapolation, the current study deals with three LAG counts. The visible LAG count corresponds with the actually LAG count observed in the samples. The extrapolated LAG count is a calculation of the number of LAGs lost by resorption due to expansion of the medullary cavity. The total LAG count is the sum of both, the visible and extrapolated LAG count (for the extrapolation method of estimating resorbed LAG number, see 5.4.3). LAG count corresponds with growth cycles and the latter can be directly transferred into years. For example a count of seven LAGs corresponds with eight growth cycles or years of life.

5.4.3 Extrapolation method

All *Plateosaurus* long bones contain a large medullary cavity which started its activities early in ontogeny. Thus, inner growth cycles were resorbed during the ontogenetic growth of the bone. Additionally, remodeling in most cases affected the edge of the medullary cavity and destroyed the growth cycles, too. LAG counts thus led in sub-adult and adult individuals always to an incomplete number of growth marks. The lack of small, respectively young *Plateosaurus* individuals makes extrapolation of the resorbed growth cycles necessary. However, extrapolation increases the margin of error in the skeletochronological analsis.

RICQLÈS (1983) and CHINSAMY (1993) mentioned that it is necessary to consider the diameter of the inner remodelled region to obtain a rough estimate of the number of resorbed cycles. Both refer to the method of CASTANET & CHEYLAN (1979). REID (1997) referred to FERGUSON et al. (1982) who estimated how many cycles are lost by extrapolation from the thickness of the remaining cycles.

CHINSAMY (1993) estimates the original number of LAGs/growth cycles by using the width of the initial zones of the smallest and therefore presumably youngest specimens. RICQLÈS (1983) also used the diameter of the inner cancellous bone region in relation to the spacing trend between each cycle "to draw a rough estimation of the number of previous cycles first deposited in the younger cortex" (RICQLÈS 1983: 229). ZUG et al. (1986) developed a formula to reconstruct the lost marks of skeleton growth: The total number of marks of skeleton growth is the result of the cross sectional diameter of the sampled bone multiplied with 0.5 because only one side of the bone is considered, and subtracted from the average cross sectional diameter of the hatchling bone. This value is then divided through the average width of preserved marks of skeleton growth.

The extrapolation method used in the current study attempted to incorporate different extrapolation methods discussed above, but they had to be adapted to the specific circumstances of the available *Plateosaurus* material.

On the basis of the assumption that the cycle distances in juvenile individuals were wider than in older individuals, the greatest available cycle distance were here used for extrapolation. Generally, the distance between the centre of the medullary cavity and the first visible LAG (LAG 1) was set in relation to the greatest distance between two LAGs observable in the specimen, i.e. the widest cycle. The result is a calculation of how many LAGs were maximally lost by remodeling and resorption. Generally, the distance between LAG 1 and LAG 2 is the greatest distance in the whole sample. Nevertheless, sometimes some of the outer LAGs show a greater distance than the inner LAGs, due to the relatively irregular growth of *Plateosaurus*.

This method works only for the whole cross section or if the diameter of the medullary cavity is known. Extrapolation in thin- or polished sections faces the problem that the missing part of the medullary cavity needs to be reconstructed. This is done on the basis of the average percentage value of the medullary cavities of the different bone types. The relative size of the medullary cavity is determined by a simple method: The thickness of the cortex of whole bone cross sections was set in relation to the diameter of the medullary cavity at a determinate bone side. Then the mean was calculated from all samples of a single bone type.

From many bones, different histological samples are available and also the fracture surfaces. Polished cross sections supply for each at least four resorbed LAG numbers, due to the four bone sides and their asymmetrical growth of bones during ontogeny. In such a case, the listed data represent an average number of LAGs.

Predominately in the pubis, the ratio of cortex thickness to medullary region diameter varies strongly, depending on which location in the cross section the measurements were taken. Thus, in the pubis it makes sense to measure only at the lateral-proximal edge of the bone because of the great extant of the medullary region in the medial-distal direction.

Thus, except in pubis samples, cross sections and fracture surfaces were measured at four sides of the bone (caudal-median-cranial-lateral), whereas in pubis cross sections, only the dorsal and ventral bone side was measured. Unfortunately, measuring all bone sides is not always possible due to the varying quality of the growth record at the different bone sides. The growth record can be generally unclear, disturbed by resorption and remodeling, or incomplete due to the preservation of the bone. Additionally, the resolution of the fracture surfaces is not of the same quality on all sides of a bone. Thus, the visible and resorbed LAG number differs usually along the circumference of a single bone.

Further source of error is introduced by measuring from the centre of the medullary cavity because the diameter of the hatchling bone has to be subtracted. Due to the lack of *Plateosaurus* hatchlings, an estimate of hatchling femur diameter was done. Estimation based on data of *Mussaurus* (CARPENTER 1999: 206: table 11.3) shows that the femur diameter of a *Plateosaurus* hatchling was very small, only a few millimetres. Thus, the medullary cavity of hatchlings is not considered here because it will have no influence on the extrapolation results.

To summarize there are several problems using extrapolation in *Plateosaurus* histology: Shaft diameters of hatchling and juvenile bones as well as growth rates and cycle distances in juveniles are unknown. Asymmetrical growth of bone (drift) cannot be detected in the cores. Extrapolation from cross sections results in a mean value because it has considered four bone sides. Extrapolation cannot take into account irregular growth spurts or interruptions, growth/enlargement of the medullary cavity, and main direction of resorption. Already REID (1997) mentioned that extrapolation cannot consider growth rates and length of growth periods (continuous or periodic interrupted). Thus, extrapolation is not a very exact method for reconstructing LAGs in *Plateosaurus* bones. The results are only average values of the probable number of resorbed LAGs for each bone sample and should be seen as approximations, and not as exact values. In the current study the extrapolated number of resorbed LAGs in long bones is generally too high due to the very large and active medullary cavities in long bones and the lack of juveniles for calibration.

6. Histological description by bone

Our study began with the determination of the best sampling location by cross sectioning and the analysis of existing fracture surfaces of the mid-shaft areas of each bone type (figure 2, 4). These cross sections were also used for a detailed study of the inner structure (cortex, medullary cavity, remodeling zone). Then the different available bone tissues and types are described, such as kind of growth marks, their appearance and distribution through the cortex. For the sampled material see table 4.

6.1 Long Bones

6.1.1 Sampling location

Based on the study of fractures of broken diaphyses of long bones in the SMNS, cross sections, cores from femora and humeri were usually taken around the most narrow mid-shaft region. The samples from the tibia were taken somewhat distal from the mid-shaft region, and the best sampling location for the fibula is somewhat proximal because the most narrow place in both is not exactly in the middle of the diaphysis (Fig. 2).

Due to damage to the bone surface or a varying shaft morphology, it was not possible to drill the cores always at accurately the same location, respectively bone part. Instead, samples were taken all around the mid-shaft area, wherever the best sampling conditions were available. This is not much of a problem since the sampling of cross sections of the mid-shaft region had shown that the growth record around the circumference differs not as much as at sampling locations more proximal or more distal. A varying growth record in different locations of a bone section results mainly from an asymmetrical growth of the bone during ontogeny. Thus, the most important thing is to sample around the most narrow mid-shaft area of a diaphysis.

To ensure the capture of a maximum growth record the cores in long bones were always drilled through the cortex into the medullary region.

The long bones sampled here show in general a more oval shaft outline in proximal cross sections, whereas the middle diaphysis is more round, and towards the distal end the bone shaft becomes more and more triangular. This is documented, among other bones, by a complete fibula, which is broken into five pieces (right fibula SMNS F 14, 52.5 cm).

The outline of the medullary cavities depends strongly on the outline of the shaft and varies between round, triangular, or oval, mainly depending on sampling location along the diaphysis.

The cortex distribution is always moderately regular around the medullary cavity, but generally with one preferred bone side showing a thicker cortex. The growth record is well preserved at all long bone sides around the mid-shaft region, and in the best specimens lines of arrested growth can often be followed completely around the entire cross sections. In others, LAGs are interrupted by microcracks and micro-faults.
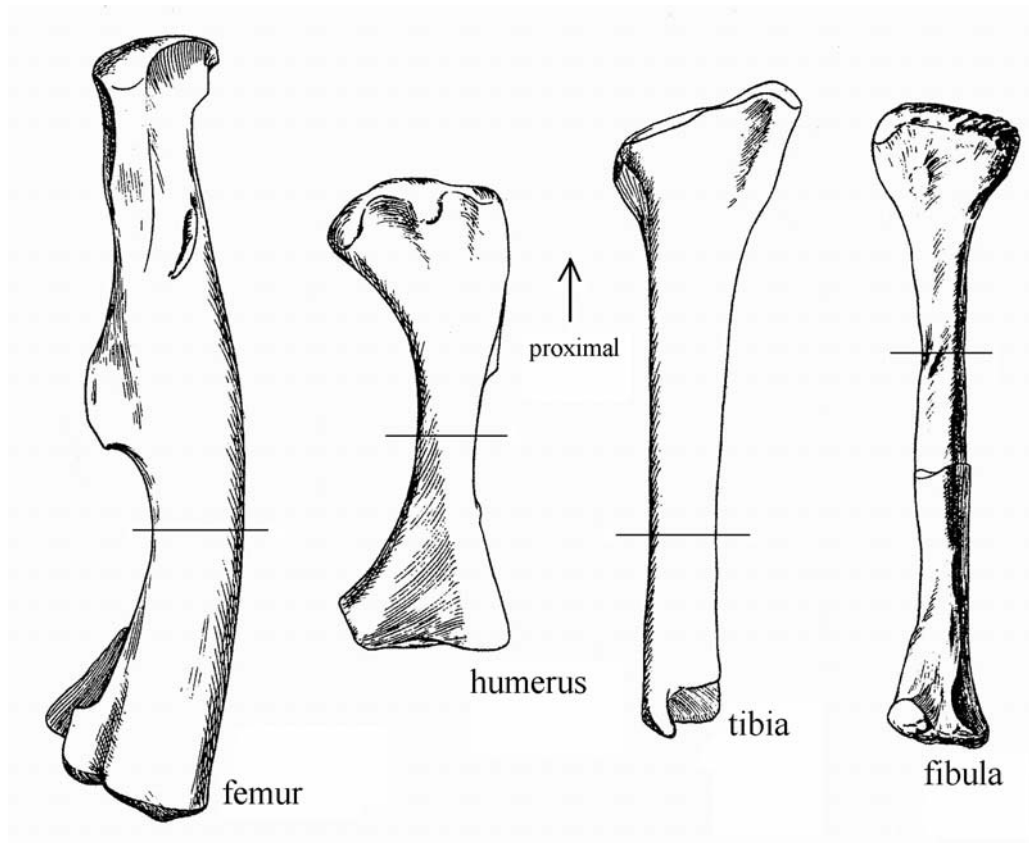

Figure 2: *The preferred sampling location in long bones is around the most narrow mid-shaft region here marked by a line. Right femur and right humerus in posterior view, right tibia and right fibula in medial view. Bone drawings from HUENE (1926). Not to scale.*

6.1.2 Femur

Like in most dinosaurs, the femur is the largest bone in the skeleton of *Plateosaurus*. The cortex is generally thick in the femur, around two to nearly three centimetres at one bone side. The diaphysis diameter, measured from the cranial to the caudal surface, amounts to between 5.8 and 8.9 cm. Most cross sections of femora show the thickest cortex at the caudal side. Thus, at least for the available femur samples, the very best sampling location is at the caudal femur side.

Generally, a small zone of remodeling surrounds the well-defined boundary of the medullary cavity. Only the cross section of left femur SMNS F 14 (63.5 cm) shows a real cancellous bone area around the medullary cavity, followed by an untypically wide

remodeling zone. The medullary cavity is always conspicuously large in the femur and is often partially filled in by cancellous bone. Its average size amounts to around 58% of the shaft diameter. The measurements were taken from the cranial to the caudal side. In the cross section of the femur from Frick, the medullary cavity is only 35% of shaft diameter, surely due to crushing.

The outlines of the cross section of the right femur SMNS F 48 (76 cm) and of the right femur NAA F88/B130 (56.5 cm) are nearly rectangular. In addition the latter contains a protrusion at the medio-cranial edge, and the medullary cavity is pressed together in the middle like a waist. The untypical outline of the shaft cross section of the right femur SMNS F 48 (76 cm) remains unexplained, but also the tibia and the fibula of the same find (individual SMNS F 48) show a similar rectangular shaft outline.

It is noteworthy that neither the cores from the posterior bone side nor the entire cross sections of the femur show any remodeling trace of the fourth trochanter, although the samples were often taken only a few centimetres distal to it.

6.1.3 Tibia

The cortex of the tibia is not as thick as in the femur but nevertheless may reach up to 2.5 centimetres at one bone side. The whole diameter, measured from the medial to the lateral bone surface, amounts to between 3.7 and 5.8 centimetres. Most cross sections show the thickest cortex at the medio-cranial bone side.

Like in the femora, the medullary cavity is relative large in the tibiae. The average percentage of the medullary cavity amounts to around 49% of the shaft diameter. The measurements were taken from the medial to the lateral surface. In the cross section of the tibiae from Frick, the medullary cavity represent only 28% (crushing!).

Generally, the well-defined boundary of the medullary cavity is surrounded by a clear remodeling zone, which in some regions reaches up to the middle of the cortex. However, this remodeling is light and does not completely overprint the primary bone tissue. Extensive regions of cancellous bone were not observed in any tibia cross section.

The main outline of the cross sections of the sampled tibiae is oval, only one showing a more triangular outline (right SMNS F 14A, 55 cm). The outlines of the medullary cavities vary between oval and sometimes more circular. Like the cross section of the right femur SMNS F 48 (76 cm), the outline of the cross section of the right tibia SMNS F 48-2 (66 cm) is more rectangular than oval. The outlines of the cross sections of the tibiae from Frick are

almost rectangular with a protrusion at one bone side. All tibiae from Frick were compressed during the fossilization processes.

6.1.4 Fibula

Cortex thickness in the fibula varies between 0.5 cm and 1.4 cm at one bone side. In most samples, the cranial part of the bone contains the thickest cortex. The whole diameter, measured from the medial to the lateral surface, amounts to between 2.3 cm and 3.5 cm.

The average percentage of the medullary cavity in the fibulae amounts to 52% of shaft diameter and is therefore also large. The measurements were taken from the caudal to the cranial bone surface. The outline of the cross sections of the sampled fibulae varies between oval, triangular, and round. The outline changes clearly along the diaphysis. The outline of medullary cavity varies between oval and round. Like the cross sections of the femur and tibia of SMNS F 48, the outline of the cross section of the right fibula of SMNS F 48-2 (59 cm) is rectangular.

The right fibula SMNS F 14 (52.5 cm), which is fractured along the shaft into five pieces, yields information about the change of bone tissues along the diaphysis. The sections document clearly that the distribution of primary and secondary bone tissue depends strongly on the location on the shaft. The middle shaft region shows the least remodeling, and only the medio-caudal part of fibula shows cancellous bone. A clear boundary of the medullary cavity is developed here. To the proximal and distal extremities, the boundaries become blurred. Remodeling and cancellous bone increases and finally surrounds the medullary cavity completely. Only a thin layer of primary tissue remains in the cortex of the very proximal and very distal shaft region.

6.1.5 Humerus

In comparison to the other long bones, the cortex is relatively thin and amounts to between 0.5 cm to 1.2 cm at one bone side. The whole bone diameter, measured from the cranial to the caudal surface amounts to between 4.0 cm and 5.0 cm. In all humerus samples, the medial part of bone contains the thickest cortex.

As in the other long bones, in the humerus, the medullary cavity is large, and its average size amounts to 55% of the shaft diameter. The measurements were taken from the cranial to the caudal surface. In the cross section of the humerus of Frick, the medullary cavity is only 42%, due to stronger compaction of the bones from Frick.

The outline of the cross sections of the humeri as well as the outline of medullary cavities is triangular with rounded corners. The outline of the cross section and the medullary cavity form of the humerus from Frick is more oval and elongated in the medio-lateral direction.

In most sampled humeri, a relatively large cancellous bone area surrounds the medullary cavity. But in two samples (right humerus SMNS F 61B, 43.5 cm and left humerus SMNS F 29A, 43.5 cm), no cancellous bone is present at the medial bone side.

6.1.3 Bone types in long bones of *Plateosaurus engelhardti*

6.1.3.1 Primary bone tissues and vascular density

The most widespread primary bone tissue in all *Plateosaurus* long bones is the laminar fibro-lamellar complex combined with lines of arrested growth (figure 3A, E). It makes up around 75 % (estimated) of the primary bone tissue in all *Plateosaurus* long bones.

In spite of its cyclical growth, the laminar fibro-lamellar complex with lines of arrested growth shows a relative high vascular density and therefore represents a fast growing bone tissue. The vascular canals build a three-dimensional network. The primary vascularization pattern in *Plateosaurus* long bones is laminar and consists mainly of circular, and longitudinal vascular canals. In some samples, also a few radial and reticular vascular canals occur in the fibro-lamellar complex, mainly in the inner cortex areas. The amount of longitudinal vascular canals increases from the inner to the outer cortex. In general the vascular density decreases gradually within a growth cycle and from the inner to the outer cortex. The osteocytes lacunae in the fibro-lamellar tissue are thick and mainly rounded.

The second regularly appearing bone tissue is the lamellar-zonal bone which occurs in some *Plateosaurus* long bones (figure 3B, F), but except in one sample (right humerus, IFG, 53 cm restricted to the exterior cortex. It consists of lamellar bone with mainly longitudinal vascular canals grading into avascular bone. The osteocytes lacunae in this bone tissue are flattened.

In one femur sample (left, compactus, 74.0 cm), the inner cortex consists of a very highly vascularized bone tissue in a broad cycle and very thick laminae with large vascular canals (figure 3C, G). The individual vascular canals and laminae are much thicker than in the "normal" fibro-lamellar complex of *Plateosaurus engelhardti*. The tissue appears in the second visible cycle. The earlier and later cycles consist of the normal laminar fibro-lamellar complex. Initially, it was assumed that this tissue might represent some kind of juvenile bone, but this could not be verified, because among others, the total size of the femur is 74.0 cm

which excluded a young individual. Thus, this bone type at this location must have another explanation.

A few samples, a femur from Frick (NAA F 88-B130, right, 56.5 cm), a tibia from Frick (NAA F88/B70, right?, 51 cm), a tibia from Trossingen (SMNS F 29A, left, 59 cm), a fibula from Trossingen (SMNS F 14, right, 52.5 cm), and a vertebra from Trossingen (IFG RW 12) show an additional bone type (figure 3D, H). The bone tissue is still the fibro-lamellar complex, but the kind of vascularization is different. It consists of parallel radial vascular canals with a very high density. Although this bone type shows such a high vascularization, which indicates a very rapid growth rate, the tissue is deposited cyclically and delimited by normal lines of arrested growth. It occurs always in the outer cortex areas. Due to the predominance of radial vascular canals in this tissue, it is called in the following radial fibro-lamellar bone tissue (RFB). It is similar to, but much more highly vascularized than, the "radiating" fibro-lamellar bone tissue described by FRANCILLON-VIEILLOT et al. (1990: Fig. 14G).

The cross sections show that RFB is locally restricted. But it appears on different bone sides in the different samples and within the "normal" laminar fibro-lamellar complex as well as in the lamellar-zonal bone. In one femur (NAA F88/B130, right, 56.5 cm), the RFB was deposited at the caudal bone side with three cycles following after a clear cycle of lamellar-zonal bone in an avascular tissue. As in the femur sample, the RFB in both tibia samples (NAA F88/B70, right?, 51 cm; SMNS F 29A, left 59 cm) is restricted to the caudal bone side, and always a few cycles were deposited. It is very untypical for such a highly vascularized bone tissue to occur always in the outer or outermost cortex areas. As documented by the four fracture surfaces along the right fibula SMNS F 14 (52.5 cm), the RFB seems to be restricted to the mid-shaft region and disappears in the proximal and distal diaphysis. It is therefore not evenly distributed along the whole shaft. In the right fibula sample SMNS F 14 (52.5 cm), the RFB is restricted to the lateral bone side. Two cycles are documented here. In the sample of the tibia of Frick (NAA F 88/B70, right?, 51 cm), the RFB is not as high vascularized as in the sample of the Trossingen tibia (SMNS F 29, left, 59 cm). But in this bone it is deposited after a clear layer of avascular lamellar-zonal bone, similar to the femur sample.
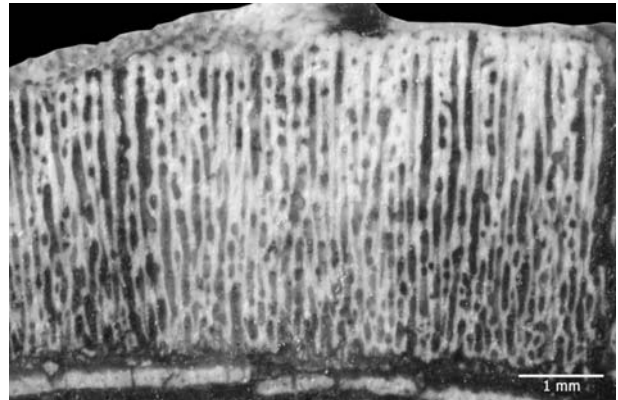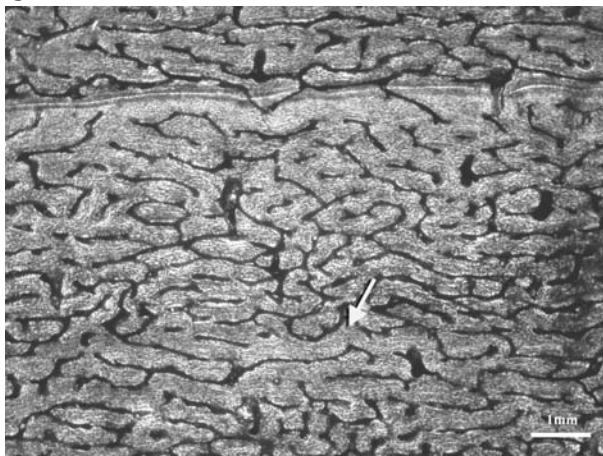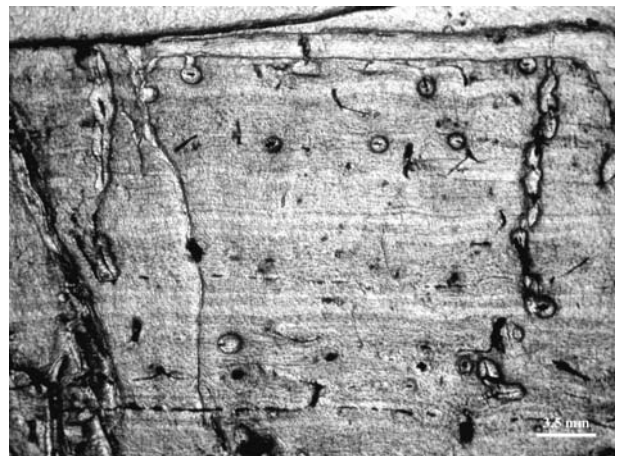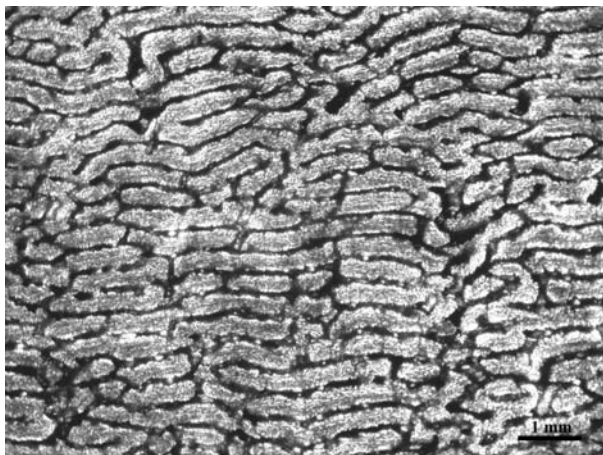
A

B

C

D

E

F

G
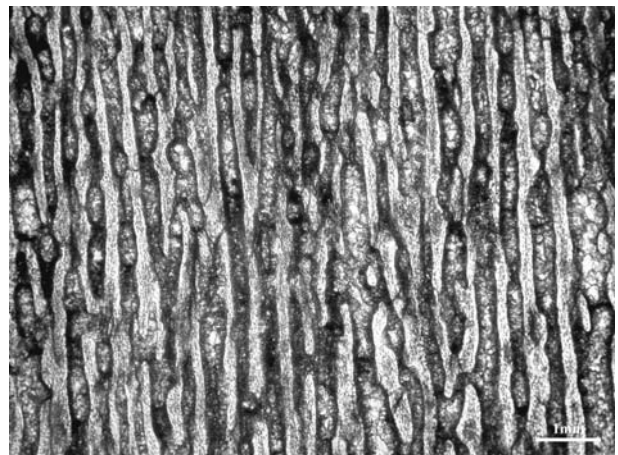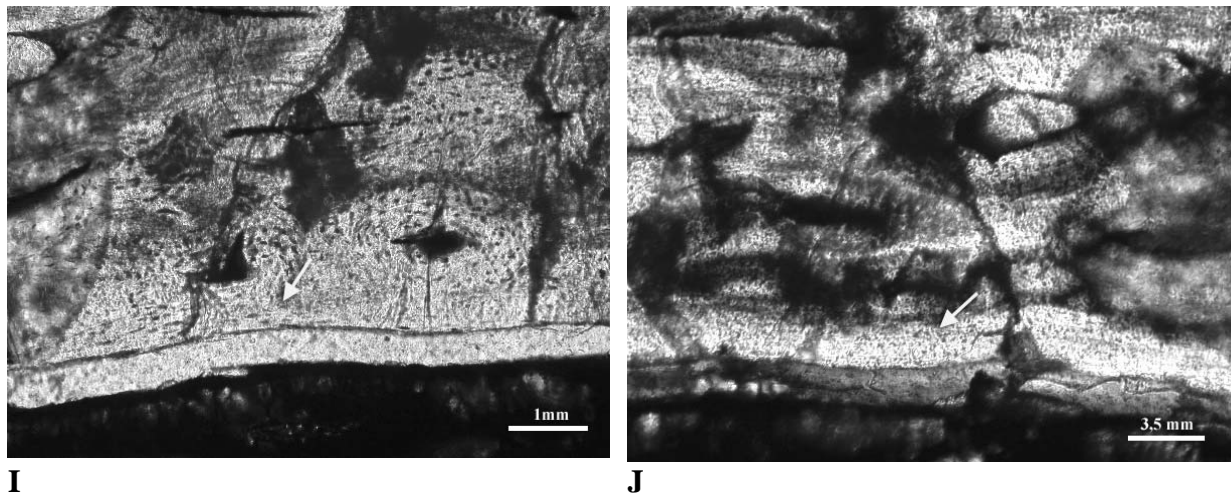
H

I   1mm

J   3,5 mm
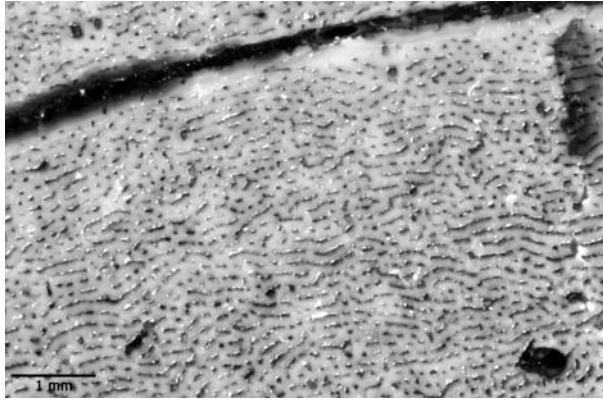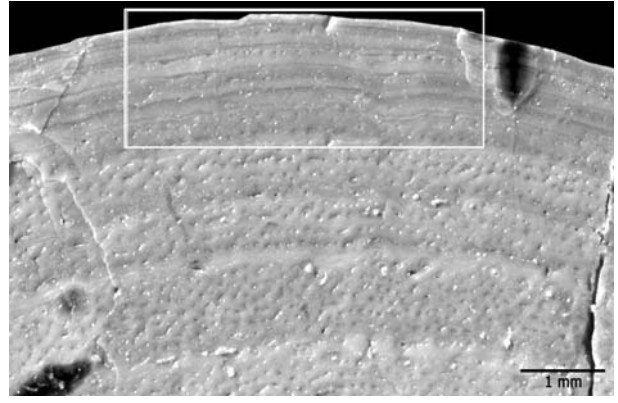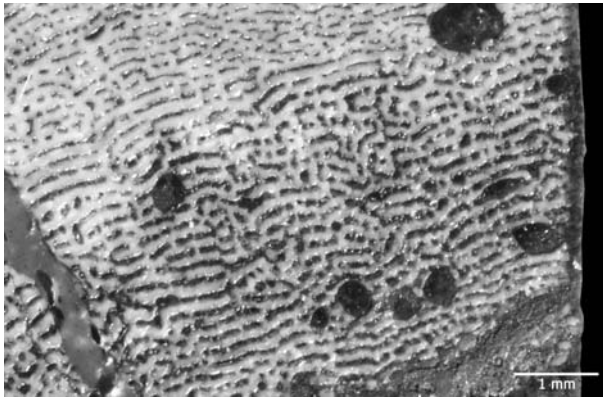
Figure 3*: Bone tissues in* **Plateosaurus engelhardti** *long bones.*

A: polished section of laminar fibro-lamellar bone with LAGs (left femur IFG compactus, 74.0 cm). ***B:*** *polished section of lamellar-zonal bone, marked by a rectangle (right humerus NAA F 88/B640, 44.5 cm).* ***C:*** *polished section of highly vascularized fibro-lamellar bone. Vascular canals and laminae are much thicker than in the normal fibro-lamellar complex (left femur, IFG compactus, 74.0 cm).* ***D:*** *polished section of RFB: Fibro-lamellar complex with mainly radial vascular canal orientation and very high vascular density (IPG RW12).* ***E:*** *thin section of fibro-lamellar bone with a clear LAG in the upper third of section. Arrow marks a second order LAG (left femur 74 cm, IFG, compactus).* ***F:*** *thin section of lamellar-zonal bone (left tibia MSFM-1, 51 cm).* ***G:*** *thin section of highly vascularized fibro-lamellar bone (left femur 74 cm, IFG, compactus).* ***H****: thin section of RFB (IPG RW12).* ***I:*** *thin section showing a thin layer of endosteal bone marked by an arrow (right femur SMNS F 29, 50 cm).* ***J:*** *same sample as before, enlarged.*

This means that after deposition of a bone type indicating that normal growth had nearly stopped, rapid growth had started again and continued with a very high growth rate, at least in restricted areas. In the tibia of the Trossingen bone (SMNS F 29, left, 59 cm), RFB is connected directly to the fibro-lamellar complex, which means that the normal growth rate has accelerated again at a relative late time in growth history.

These RFB cycles seem to correspond with regular growth cycles, because they end in normal lines of arrested growth. At the opposite bone sides of the same cross section, these RFB layers or cycles were deposited as normal cycles of lamellar-zonal avascular bone tissue or of laminar fibro-lamellar complex. Surprisingly, the RFB bone type seems to occur only in single bones of a skeleton and not regularly in all bones of a single skeleton.

6.1.3.2 Remodeling in long bones

All long bone samples of *Plateosaurus* share a generally low rate of remodeling. Real remodeling zones, as seen in pubes or scapulae, that surround the medullary cavity are missing in most long bones. Mainly erosional rooms of varying diameters occur. They were connected to the medullary cavity and were usually concentrated at one bone side. Many erosional rooms show some secondary bone deposition but were also partially filled with surrounding sediment. The transition from cancellous bone, which means the margin of the medullary cavity and the place were most erosional rooms opened up, to the primary cortex is always gradual and irregular in long bones.

Beside erosional rooms, secondary osteons occur in all long bones. If secondary osteons are present in a sample, they are most often sparsely distributed throughout the whole cortex. In some samples, an accumulation of secondary osteons near the medullary cavity could be observed. Nevertheless, in none of the samples does the occurrence of secondary osteons significantly disturb the primary bone tissue or the growth record. The primary arrangement of vascular canals never was fully destroyed during remodeling, and so the secondary vascularization shows mainly longitudinal Haversian canals.

In femora, isolated secondary osteons are generally very rare and completely lacking in many specimen. Only the femur from Frick (NAA F88/B130) shows numerous secondary osteons up to the exterior cortex. Erosional rooms again occur close to the medullary cavities.

The samples of the tibiae show more remodeling than those of the femora but also not as much as in flat bones. Secondary osteons occur close to the medullary cavity as well as scattered throughout the cortex. Erosional rooms are available sometimes up to the middle of cortex, predominately in the region with the thickest cortex. Altogether, the distribution of remodeling is relatively irregular around the tibia cross sections.

As expected, the fibula SMNS F 14 (right, 52.5 cm) broken into five pieces clearly shows along the fracture planes how remodeling increases towards the proximal and distal end of the shaft. Only the mid-shaft region is not significantly disturbed by remodeling processes. Erosional rooms and secondary osteons were observed with a magnifying glass in the fractures but secondary osteons are not visible at this magnification. At the medio-caudal part of the shaft, remodeling extends into the middle of the cortex. In the other parts of the cross sections, remodeling occurs adjacent to the medullary cavity only.

In humerus samples, secondary osteons and erosional rooms are adjacent to the medullary cavity and occur in a moderately wide band around them. Only a few secondary osteons are scattered throughout the cortex and extend to the outer cortex or bone surface.

Although remodeling is relative strong in the humerus, only in the inner cortex the primary bone tissue is sufficiently overprinted to partially destroy the growth record.

6.1.3.3 Endosteal bone

Endosteal bone is documented in one specimen of *Plateosaurus* (right femur SMNS F 29, 50 cm, figure 3I, J). It appears as a thin layer of lamellar bone along the boundary of medullary cavity. Endosteal bone consists of typical lamellar bone structure and is separated from the cortex by a cementing line.

6.1.4 Growth marks in long bones

In the fibro-lamellar complex of *Plateosaurus* long bones, growth cycles can be divided into zones and annuli. The growth cycles in lamellar-zonal bone tissue, on the other hand, mainly consist only of a slow growing part. Nevertheless, a clear line of arrested growth marks the end of each growth cycle. In *Plateosaurus* bones, LAGs occur throughout all documented bone tissues and were not restricted to the slow growing bone types. LAGs run always parallel to bone surface.

A band of dense avascular tissue sometimes accompanies the LAG, appearing as a bright band in some specimen. This bright band is not the same as FRANCILLON-VIEILLOT et al. (1990: 510) described, because a fine line of arrested growth within this bright band can be identified in *Plateosaurus* samples under higher magnifications. LAGs may also appear as polish lines (SANDER 2000), predominately in the material from Frick. Under higher magnification a LAG is always visible in these polish lines.

The density of LAGs is relatively low in the inner cortex but becomes higher in the middle and increases clearly towards the outer cortex regions. This is due to a slower growth rate with increasing age and therefore a closer deposition of growth cycles. However, cycle distance is generally relative irregular in *Plateosaurus* specimen. Irregularities in cycle distances in long bones of *Plateosaurus* are not as frequent as in flat bones, but does occur, too. For example, narrow and poorly vascularized cycles can appear in the inner cortex and wide and highly vascularized cycles can appear in the outer cortex. Such irregularities are independent of bone tissue.

In *Plateosaurus* long bones, bone type and tissue can change from the fibro-lamellar complex into the lamellar-zonal bone type, mainly in the outermost cortex. Once this had happened, LAGs were then deposited extremely close together within the lamellar bone tissue. Then growth cycles are difficult to distinguish from each other and therefore also very

difficult to count. Similar problems were discussed by ZUG et al. (1986: 10) and CASTANET & SMIRINA (1990).

Some wide growth cycle of *Plateosaurus* long bones are subdivided by second-order cycles (fig. 3E). These are mainly indicated by second-order lines of arrested growth. They appear predominately in large growth cycles of the inner cortex where also a slight decrease of vascular density towards the second-order LAG can be observed. A single major growth cycle can be divided in one or two, seldom three second-order cycles. Second-order cycles are the result of short growth decreases during the normal annual growth period. They were probably caused either by seasonal changes of weather or food availability or by individual diseases. Such second-order lines are mentioned relative frequently in literature (ZUG et al 1986, CASTANET et al. 1993).

Sometimes, LAGs are accompanied by small assemblages of second-order lines, most of the time two or three above and below the major LAG. This occurs more often in the outer cortex areas, where cycle distances had become closer than in the inner cortex areas. Such assemblages look similar to closely spaced LAGs in the outermost cortex in lamellar-zonal bone. But in most cases, second-order LAGs could be distinguished from major LAGs by being thinner and less clear in appearance. Usually they can not be followed completely around the entire cross section. Probably these second-order LAGs document remains of zones and annuli which were not fully deposited due to decreased appositional rates in older individuals and low space in the exterior cortex.

6.2 Flat Bones

Although pubis and scapula both bones belong to the category "flat bone", they differ in their histology and in the quality of their growth record.

In contrast to long bones, the diploe structure makes only two main coring sites possible. Thus, the lateral and medial side in the scapula, and in the pubis the dorsal and ventral side are available for sampling. However, remodeling in form of erosional rooms, respectively cancellous tissue, and secondary osteons often disturbs the primary bone tissue at these locations.

In *Plateosaurus* flat bones, the medullary cavity if at all present, is often not clearly separated from the surrounding cancellous bone and remodeling area, so the areas in the center of the bones will be summarized here under the term medullary region. Also, the transition from secondary bone tissue to primary bone tissue is at most times irregular and not clearly delimited. The cortex of the scapula preserves at certain places a relatively good

growth record and that of the pubis provides a very good growth record. However, the scapula is difficult to evaluate due to its bone tissue intermediate between fibro-lamellar complex and lamellar-zonal bone. At least in *Plateosaurus*, it is a bone not very well suited for growth history research.

Like in long bones, flat bones represent only sub-adult and adult individuals, and the growth record of the juvenile phase seems to be lacking as well. This is not due to the enlargement of the medullary cavity but due to strong remodeling. On the other hand, flat bones of *Plateosaurus engelhardti* grew in another way than long bones, as is documented in their histology. Thus, their growth record is possibly more complete, but a correlation with the growth record of long bones remains impossible until histological research on juvenile *Plateosaurus* specimen becomes possible.

6.2.1 Sampling location

The cores and cross sections of the scapulae were taken in the middle of the most narrow mid-shaft region, which contains the least disturbed primary bone tissue (figure 4), as the examination of fractures and cross sections of flat bones had shown. The most complete and undisturbed growth record was found in the cortex of the lateral side of the scapula. The medial cortex also preserves a useful growth record, but shows generally more remodeling. Although the dorsal and ventral edges of the scapula provide the thickest cortex, these areas are usually affected by strong remodeling.

The cores and cross sections from the pubes were usually taken in the proximal to mid-shaft region, as near as possible to the lateral edge of the bone (figure 4). This bone site contains the thickest available cortex and also the thickest primary bone tissue in the pubes cross sections. The most complete and undisturbed growth record was found at the lateral-dorsal part of the pubis. The lateral-ventral part of pubis also preserves a good growth record, but predominately the inner cortex shows much more remodeling than the dorsal side, making the growth record most of the time incomplete there.

Because the scapula as well as the pubis are flat bones, the cores can be drilled through the entire bone to obtain a double growth record. A combination and interpretation of both sides thus resulted in the most complete growth record.
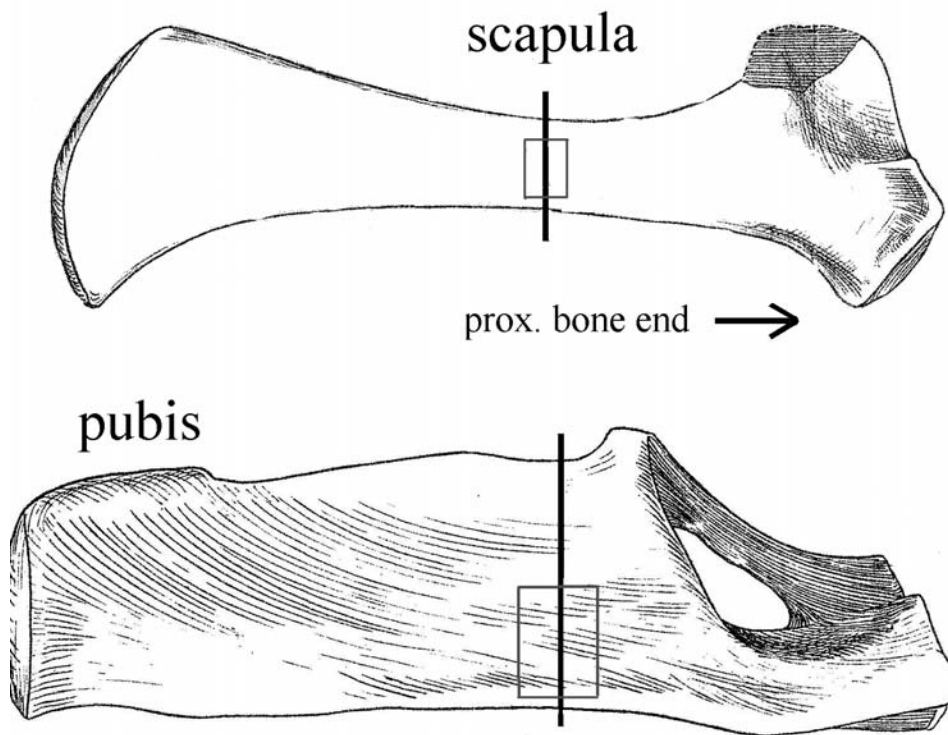
Figure 4: *Preferred sampling location in pubis and scapula, marked by a rectangle.*
Right pubis in dorsal view, left scapula in lateral view. Bone drawing from HUENE *(1926).*
Not to scale.

6.2.2 Scapula

Due to the bone morphology, cortex and medullary region in *Plateosaurus* scapulae
are strongly flattened between medial and lateral bone side. The bone cross-section and also
the outline of the medullary region are similar to a flattened ellipse, tapering towards the
dorsal and ventral edges. The medullary region consists mostly of cancellous bone, but is
completely surrounded by a relatively thin layer of cortex.

The greatest thickness of the cortex is found in the middle of the shaft. Shaft thickness
amounts to two to three centimetres measured from the lateral to the medial bone side. The
average size of the medullary region in the scapula amounts to 37 % of the shaft diameter,
also measured in the middle of the shaft from the lateral to the medial surface.

6.2.3 Pubis

Due to bone morphology, cortex and medullary region of the pubis are strongly
flattened between the dorsal and the ventral side. Thus, the shape of the cross section and
medullary region is generally long and thin whereas the proximal edge is thicker than the

distal end of bone. The form can be described as roughly rectangular, with straight dorsal and ventral surfaces in some specimen and in others more curved dorsal and ventral bone surfaces.

The medullary region starts at the lateral bone edge and extends to the medial edge. From the mid-shaft region to the distal end, the medullary region increases significantly in relative size. Also, the bone becomes thinner in medial direction, and the primary bone tissue disappears and is finally replaced at the medial edge of the bone by purely secondary tissue and cancellous bone.

The greatest thickness of the bone as measured from dorsal to ventral is found near the lateral edge and amounts to two to three centimeters. Thus, the average size of the medullary region is 19 % of the shaft diameter at the lateral edge and nearly 90-100 % at the medial edge.

6.2.4 Bone tissues, vascular density and remodeling in scapula and pubis

The primary bone type in the scapula seems to be a mixture of the typical laminar fibro-lamellar complex known from the long bones and purely lamellar-zonal bone (figure 5A, C). It shows areas with relatively highly-vascularized fibro-lamellar bone which gradually pass into less vascularized lamellar and parallel-fibered bone. Longitudinal vascular canals dominate the vascular system, but their density is considerably higher than in the pubis samples. Additionally a few reticular canals can occur. Thus, the scapula seems to have an intermediate histologic status between fast-growing long bones and the slow-growing pubis.

The primary bone in the pubis is of the pure lamellar-zonal type (figure 5B, D). It consists mainly of lamellar or parallel-fibered bone and is dominated by longitudinal vascular canals. The osteocytes are usually flattened.

Remodeling is generally stronger in scapula and pubis than in long bones. Depending on the location in the cross sections, the primary bone tissue is largely replaced by secondary compact or cancellous bone (figure 12, 13). In the pubis, the lateral part of the proximal bone and in scapula the middle of the mid-shaft region contains only a relative small cancellous bone area, which is surrounded by a moderately broad remodeling zone. The remodeling zone contains a few erosional rooms of predominately rounded shape and secondary osteons, often in several generations. The vascular canals of these follow the primary vascular system and are thus arranged longitudinally. Secondary osteons are in both bones scattered in all regions throughout the primary bone tissue up to the bone surface. The other parts of the section of scapula and pubis show mainly cancellous bone and strong remodeling which resulted in a

relatively high proportion of erosional rooms with varying diameters. In between, often none or only very small parts of primary bone tissue are preserved.
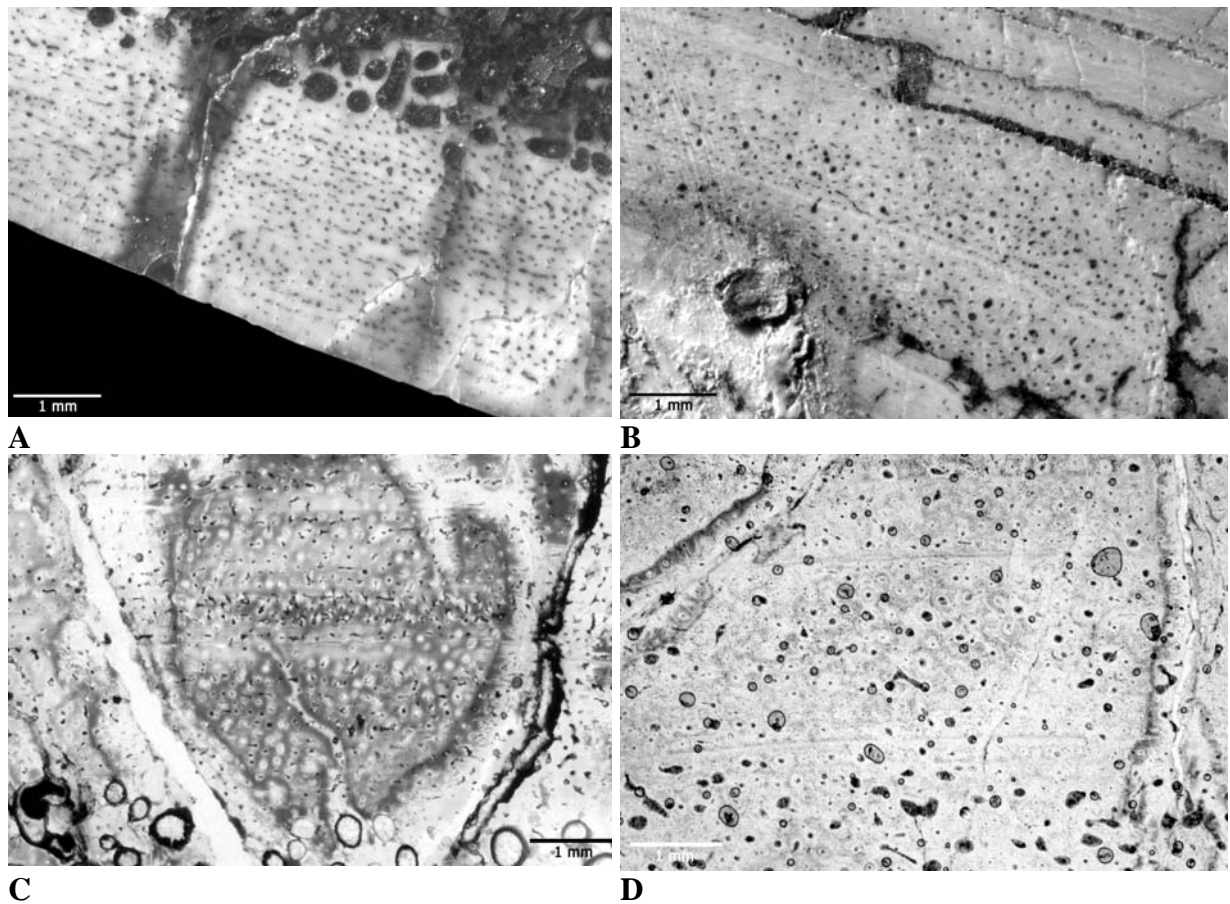

Figure 5: Bone tissues in **Plateosaurus engelhardti** *flat bones*. *A. polished section of a scapula (SMNS F 29, left, 42 cm), lateral bone side. **B**: polished section of a pubis (SMNS F 14B, left, 50 cm), dorsal bone side. **C**: : thin section of the primary bone of a scapula sample (SMNS F 14B, right, 47 cm, thin section I) **D**: thin section of the primary bone of a pubis sample (NAA.).*

6.2.5 Growth marks in scapula and pubis

Growth cycles in flat bones were often not clearly divided into zones and annuli, they consist mainly of zones and LAGs. Nevertheless, each cycle ends in one or more lines of arrested growth. The LAGs are clear where the cortex is thick enough, but following them continuously around the entire cross section is not possible due to the large medullary region in flat bones. Division of growth cycles into second-order cycles are more rare than in long bones, probably again due to the thinness of the cortex and maybe due to a generally slower

growth in the scapula and mainly in the pubis. But close to the main LAGs, before and after, there often occur a few less clear and therefore subordinate LAGs.

In addition to the general decrease in vascular density from the inner to the outer cortex, vascular density decreases within the single growth cycles. Zones of the scapula are generally more highly vascularized than in pubes. Most of the time the LAGs were deposited in small bands of avascular or nearly avascular tissue. Such avascular bands sometimes appear as bright wide bands or as polish lines.

Growth cycle thickness is fairly irregular, but there is a general tendency for cycle thickness to decrease from the inner to the outer cortex. Generally, cycles are quite thinner than in long bones due to the thinner cortex. Finally, the growth cycles disappear in the outer cortex, and only closely spaced LAGs set in a very poorly vascularized or avascular lamellar bone tissue remain. The growth cycle thickness in the scapulae, respectively LAG spacing, decreases in the exterior cortex as in the long bones, but not as sudden as in the pubes.

In contrast to the long bones, medullary regions are small in flat bones. Thus, the resorbed LAG number is low in flat bones. Predominately the pubis shows high visible LAG numbers and very low extrapolated LAG numbers. Thus, it is concluded that the pubis shows the most realistic growth record, whereas the growth record (total LAG count) in the long bones is always an over-estimate due to their large medullary cavities.

6.3 Other bones: vertebrae, ribs, ischia, and foot phalange
6.3.1 Sampling location in other bones

One aim of the current study was to test the suitability of varying bones of the *Plateosaurus* skeleton for bone histology research. Thus, beside typical long bones, scapula, and pubis, some other bones were sampled. Sampling locations were chosen based on general bone morphology and the general principles of bone growth.

Thus, the cores from the dorsal vertebrae (IFG RW 12 and 14) were drilled at the ventral side of the vertebral centra.

The cross section of the rib from Trossingen was obtained from the middle of a long rib of the thorax. The rib from Frick was sampled at two places, one near the proximal middle of the rib and the second sample more distal.

The ischia were rather complete and still articulated but a fracture surface at the most narrow mid-shaft region was available.

The core from the foot phalange was drilled through its shaft from dorsal to ventral, covering its entire thickness.

6.3.2 Bone tissue, vascular density, and remodeling

6.3.2.1 Vertebrae

No cross sections are available for the vertebrae. The thin- and polished sections of the cores show a thick (1 and 1.5 cm length) cortex which consists mainly of primary bone tissue. The primary bone tissue is built up of the fibro-lamellar bone, typical for *Plateosaurus*, with clear lines of arrested growth. However, in these sections only longitudinal vascular canals are visible. Vertebra IFG RW 12 consists in the upper one third of its cortex of RFB. In both vertebrae, only a few secondary osteons are scattered throughout the cortex. The cortex continues inward into cancellous bone with preserved interstitial primary bone tissue. This coarse cancellous bone grades inwards into the medullary region.

6.3.2.2 Ribs

The cross section of the rib from Trossingen shows an outline similar to that of the long bones. The form is generally oval, but in the middle, the rib cross section is slightly waisted. The medullary cavity makes up 39%, the cancellous bone area 36%, and the cortex only 25 % of the dorso-ventral diameter of the rib. The cortex percentage is slightly greater in cranio-caudal diameter (32%). Thus, it is obvious that the medullary region dominates the rib. Only one side of the rib preserves a growth record. The other side shows a relatively high degree of remodeling in form of erosional rooms and secondary osteons. At the dorsal and ventral parts of bone, the cortex is generally thin. As primary bone tissue, the rib contains the fibro-lamellar bone with clear lines of arrested growth in the inner cortex and lamellar-zonal bone in the exterior cortex. Only longitudinal vascular canals are present. Vascular density is intermediate and decreases slightly from the inner to the outer cortex.

The two samples of the rib from Frick show similar features. The cancellous bone area is larger, but more diffuse than in the Trossingen rib, so that measurements make no sense. Remodeling in form of erosional rooms and secondary osteons is very strong, and a true medullary region cannot be marked off. The primary and undisturbed cortex in form of fibro-lamellar bone with clear lines of arrested growth is only preserved in the exterior areas of the more proximal cross section. This section has an elliptical outline and tapers to one side. At the other side of the section, a relative thick cortex is preserved, but it is strongly remodelled. The LAGs are closely spaced and expressed in a nearly avascular lamellar-zonal tissue. The more distal rib sample has a regular elliptical cross section, but no primary cortex is preserved. The sample is totally remodelled, and the tissue can be called secondary compact and cancellous bone.

6.3.2.3 Ischia

The ischia fracture surface has a nearly triangular to oval outline. A real medullary cavity with a clear boundary is missing. The sections contain a large area of cancellous bone, respectively erosional rooms of varying diameters with a diffuse boundary to the cortex. A few secondary osteons are scattered throughout the cortex. The primary bone tissue is of the fibro-lamellar type with clear lines of arrested growth and predominating longitudinal vascular canals. The ischium from Trossingen contains RFB in its exterior cortex.

6.3.2.4 Foot phalange

The centre of the foot phalange shows a large medullary cavity. The rest of the core is built up of cancellous bone, respectively big erosional rooms of varying diameter. Secondary osteons are rare in this sample. Primary bone tissue is present only in the exterior cortex and in small areas between the erosional rooms. It consists in the inner cortex areas of fibro-lamellar bone with a very low, predominately longitudinal vascularization. The exterior cortex is built up of avascular lamellar-zonal bone.

6.4 Summary of the histological record

Long and flat bones can be distinguished well in histological samples due to the development of different bone tissues combined with different vascular systems. Long bones are generally dominated by the laminar fibro-lamellar complex. Lamellar-zonal bone appears only in the exterior cortex of some specimen. A highly vascularized radial fibro-lamellar bone tissue is documented in the outer cortex of six bones. In pubis samples, only lamellar-zonal bone occurs which is dominated by longitudinal vascular canals. Vascular density is almost as low in the pubis. No fibrous bone tissue can be identified in the available pubis samples. The histological structure of the scapula is intermediate between the typical laminar fibro-lamellar complex of long bones and the purely lamellar-zonal bone of the pubis. In the zones the scapula shows predominately fibro-lamellar complex, but in the annuli lamellar and parallel-fibered bone. Like in the pubis, longitudinal vascular canals dominate the vascular system of the scapula, but their density is quite higher than in the pubis samples. In addition, a few reticular vascular canals occur.

Similar to the long bones, the vertebra, the rib, the phalange, and the ischia samples show the fibro-lamellar complex but with mainly longitudinal primary osteons. Some show lamellar-zonal bone, too. But these bones were generally highly remodeled.

6.5 Differences between the Frick and Trossingen localities

Although the histological samples from the two localities can easily be distinguished on the basis of the different color and preservation of the bones, not many histological differences can be observed. The only ones are the more frequent appearance of polish lines and a generally larger amount of secondary osteons in the samples from Frick. These histological differences are not detailed and significant enough to distinguish clearly different taxa of *Plateosaurus* from the localities Frick and Trossingen on the basis of the histology.

7. Results: Bone histology and growth record

7.1. Evaluation of various aspects of bone microstructure

7.1.1 Evaluation of the sampled bones for skeletochronology

As the present study shows, most *Plateosaurus engelhardti* bones contain a well preserved growth record. Mainly long bones and the pubis are bones well-suited for obtaining a good and relative complete growth record, similar to many other dinosaurs (Ricqlès 1983, Varriccho 1993, Chinsamy 1993, Curry 1999, Sander 1999, 2000, Erickson & Tumanova 2000, Horner et al. 2000, Sander & Tückmantel 2003). Other bones, like ischia, vertebrae, phalanges, and ribs are not as well suited for bone histological studies due to high remodeling which leads to an incomplete growth record. The scapula is difficult to judge because of its intermediate type of bone tissue and growth rate, and a relatively strong degree of remodeling in comparison to long bones. Nevertheless, the scapula also consists of areas where the growth record is well preserved. Somewhat unexpectedly, the pubis contained a good and relatively complete growth history.

A difficulty in using *Plateosaurus engelhardti* long bones for life history research is the large medullary cavities, which accounts for around 50% of the entire cross-section. Flat bones, in contrast, do not have such large medullary cavities but contain instead highly remodeled and cancellous bone areas, which can resorb or disturb the inner growth cycles. These and the lack of smaller, i.e. younger individuals make extrapolation of the resorbed growth cycles necessary. (see section 5.4.2).

7.1.2 Secondary osteons and remodeling

The size of the remodeling zone and cancellous bone area, respectively the expanding medullary cavity, can possibly give some information about the age of an individual. Strong remodeling, indicated by much substitution of primary bone tissue by secondary bone tissue and unclear boundaries between the cancellous bone region and the remodeling zone,

indicates a greater age than a bone with clearly delimited and small medullary region and little remodeling.

7.1.3 Endosteal bone

The meaning of endosteal bone is not really clear yet. CASTANET et al. (1988) describe it from young individuals from the tuatara. REID (1997b) mentioned that endosteal bone is formed in marrow-filled limb bones after active growth has ceased or is formed and resorbed during pauses in medullary expansion. This bone type can also appear when bone drift occurs to one bone side (REID 1997b). It is clear that the endosteal layer in the *Plateosaurus* specimen (fig. 3I, J) is locally restricted to the cranial bone side. It is not documented in the core from the caudal bone side and also not in the caudal bone side in the more distally located cross section of the same specimen (right femur SMNS F 29, 50 cm). According to skeletochronology, the bone belonged to a relatively young individual in which growth had not ceased yet.

7.2 Qualitative growth record
7.2.1 Bone tissues

Like in other dinosaurs, the main bone tissue in *Plateosaurus engelhardti* bones is the fibro-lamellar bone. Three types of it were observed (fibro-lamellar bone with clear LAGs, fig. 3A, E; highly vascularized fibro-lamellar bone with clear LAGs, fig. 3C, G; RFB, fig. 3D, H). These three types differ mainly in vascular density and in the arrangement and kind of vascular canals. All three types have in common a subdivision in growth cycles, indicated by regularly appearing lines of arrested growth. Unfortunately, they do not represent an ontogenetic series as in some other dinosaurs (VARRICCHO 1993, CURRY 1999, SANDER 2000; ERICKSON et al. 2000, HORNER et al. 2000).

The two additionally appearing bone types, the radiating fibro-lamellar bone and the very high vascularized bone type represent surely special features/circumstances, due to their rare occurrence. They are neither important for the interpretation of the growth record nor the typical bone types in adult *Plateosaurus* bones.

7.2.1.1 Laminar fibro-lamellar complex with LAGs

In the long bones of *Plateosaurus engelhardti*, the laminar fibro-lamellar complex with clear LAGs represents the usual bone tissue of young, still growing but matured adults. The term adult is used here with reference to the body size, because all bones sampled in this

study belonged to individuals that had reached at least half of the known possible maximum body size (5m). Most individuals are larger (figure 1).

The laminar fibro-lamellar complex with LAGs documents that long bones of *Plateosaurus engelhardti* individuals still grew, as adults at a relative high growth rate, despite cyclical interruption. Nevertheless, a general decrease in vascular density and growth cycle distance from the inner to the outer cortex can be observed in all long bones sampled. The increase in the number of deposited LAGs is accompanied by a change in the spatial organization of bone tissue. This indicates that growth rate decreased gradually with time and size.

Although, the laminar fibro-lamellar complex with LAGs in *Plateosaurus engelhardti* consists of a similar construction than the laminar fibro-lamellar complex described in sauropods (SANDER 2000) and mammals, in *Plateosaurus engelhardti* bones it has a conspicuously smaller distance between the single laminae, and the vascular canals are also distinctly smaller and more rare. This suggests that *Plateosaurus engelhardti* long bones, in spite of a similar bone tissue to mammals and sauropods, still had lower growth rates. The difference in distances between the single laminae in mammals and prosauropods was already documented, but not discussed, by CURREY (1962). See for bone lamina thickness also SANDER & TÜCKMANTEL (2003).

7.2.1.1.1 Growth of juvenile *Plateosaurus engelhardti*

Presumably bones of juveniles grew at least with the same rate, producing a similar tissue as the bones of the adults. On the other hand, it seems to be very likely, based on the results of bone histological studies in other dinosaurs (VARRICCHO 1993, CURRY 1999, HORNER et al. 2000, SANDER 2000, ERICKSON et al. 2000, SANDER & TÜCKMANTEL 2003) that the bones of juveniles grew with higher rates than the bones of the adults. The ability of *Plateosaurus* of growing with higher growth rates than those of the typical laminar fibro-lamellar complex with LAGs is suggested by the two additional types of fibro-lamellar bone tissue described in section 6.1.3.1 and discussed in 7.2.3.

7.2.1.2 Lamellar-zonal bone and determinate growth in *Plateosaurus engelhardti*

The second type of regularly appearing bone tissue in *Plateosaurus engelhardti* is the lamellar-zonal bone. In the pubis it represents the main primary bone tissue. The growth rate in the pubis decreases from the inner to the outer cortex, as in long bones and scapula. This is expressed by a generally decreasing vascular density and cycle distance, accompanied by an

increasingly closely spaced LAGs and a generally increasing spatial organization. Deposition of lamellar-zonal bone makes it clear that *Plateosaurus engelhardti* pubes have lower growth rates apposition than long bones and scapulae.

Lamellar-zonal bone also occurs in the outermost cortex of some long bones and scapulae. Decreasing vascular density the laminar fibro-lamellar complex first initiates the transition from fibro-lamellar bone to lamellar-zonal bone. The lamellar-zonal bone is here deposited in a poorly vascularized or nearly avascular tissue and is characterized by closely spaced lines of arrested growth. The appearance of this tissue in long bones and scapulae is very important because it indicates, in comparison to the fibro-lamellar bone deposited before, a strong decrease of growth, respectively a full growth stop in some samples. In some pubis samples, there is also a dramatic slow down of growth in the outermost cortex, indicated by a clearly decreasing vascular density.

Closely spaced LAGs deposited in a very poorly vascularized to avascular lamellar bone tissue in long bones as well as in flat bones record the time the individual lived after bone growth in thickness and largely in length had decreased or finally stopped. Growth thus was surely determinate in *Plateosaurus engelhardti*.

7.2.1.3 Bone tissue change

The transition from laminar fibro-lamellar bone to lamellar-zonal bone in long bones can be interpreted in at least two ways. One is that sexual maturity occurred at this time (VARRICCHIO 1993, CHINSAMY 1994, REID 1997, HORNER et al. 2001, ANDRASSY 2004). This would mean that sexual maturity was reached late in *Plateosaurus engelhardti* ontogeny and not before nearly maximum body size was attained. A similar situation is known in recent birds and mammals, where in most species sexual maturity is reached at nearly maximum body size. Applied to *Plateosaurus*, this would sugges, that many of the individuals, especially those from Trossingen, had not reached sexual maturity at time of death, although some of them had already reached very large body sizes. In this interpretation, laminar fibro-lamellar bone would be the characteristic tissue of immature individuals and the lamellar-zonal bone that of sexually mature individuals. In the pubis, the lamellar-zonal bone would be typical of immature as well as of mature individuals, and only decreasing vascular density would indicate transition to maturity.

A second possibility is that sexual maturity was reached well before laminar fibro-lamellar bone by lamellar-zonal bone in long bones and scapulae, and before the dramatic decrease in vascular density in the pubis. This would mean that this moment, which is so
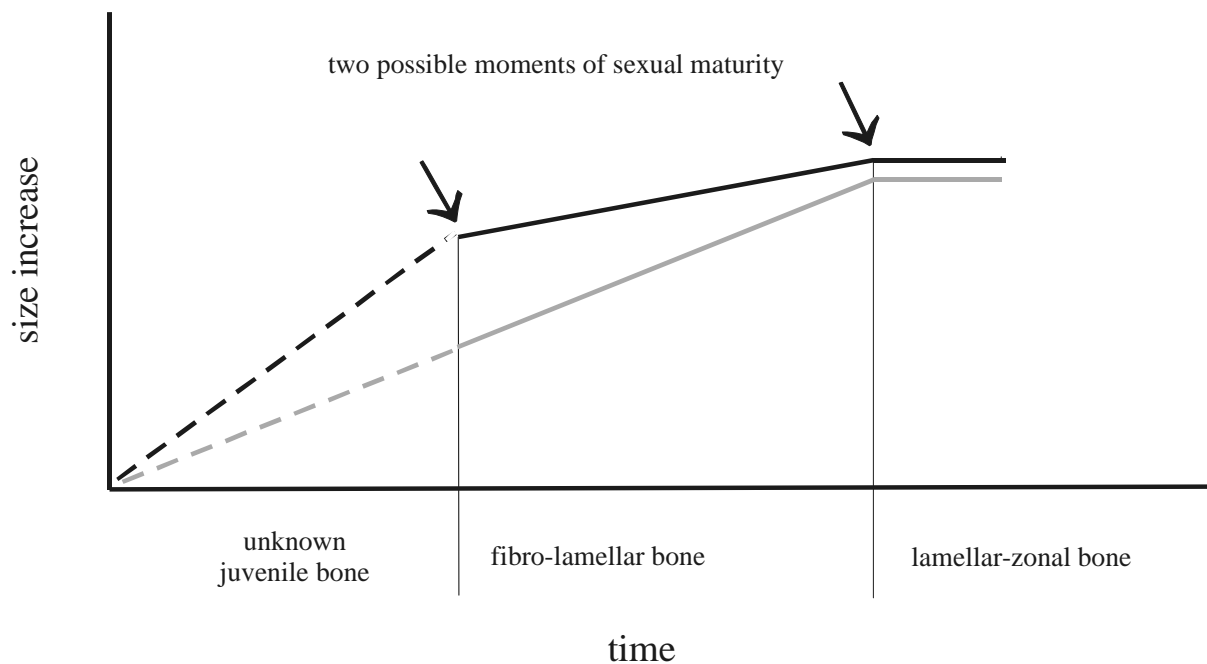
two possible moments of sexual maturity

size increase

unknown
juvenile bone   fibro-lamellar bone   lamellar-zonal bone

time

Figure 6: *Alternative qualitative growth curves based on changes in bone tissue and vascular density. It depicts the two alternative interpretations of the growth strategy of* Plateosaurus engelhardti. ***The first interpretation is represented by the black curve which is divided in three stages of ontogeny***. *The first section represents the unknown juvenile stage which is not preserved in the sampled bones but it is assumed that juveniles of* Plateosaurus engelhardti *grew with higher growth rates than bone tissue of adult individuals suggest. The juvenile stage ends with the change from the unknown juvenile bone tissue to the laminar fibro-lamellar bone with clear LAGs. This change possibly reflects sexual maturity, too. The adult stage is documented by the laminar fibro-lamellar bone in long bones, by relatively highly vascularized lamellar-zonal bone in the pubis, and by the combination of fibro-lamellar bone in the zones and lamellar bone in the annuli of the scapula. The last stage is documented in the histological record by poorly or non-vascularized lamellar-zonal bone in both, long and flat bones. It indicates additionally determination of growth. **The second interpretation is represented by the gray curve.** Here* P. engelhardti *grew with laminar fibro-lamellar bone with clear LAGs from the juvenile stage (the growth rate of juveniles is again assumed as higher than in adults) to adulthood and final body size. When maximum body size is reached, bone tissue changes to lamellar-zonal bone, sexual maturity is reached and growth largely stops.*

important in the life history, is not recorded in the available histologic record of the sampled *Plateosaurus engelhardti* individuals. Either sexual maturity was generally not recorded in the histology of *P. engelhardti*, or it simply was resorbed by expansion of the medullary cavity. Only in the pubis samples a relatively sudden decrease in vascular density and cycle distance can be observed which possibly records the onset of sexual maturity (see section 7.2.4).

According to this second interpretation the laminar fibro-lamellar complex with LAGs in long bones and scapulae would be the typical bone tissue of still growing adults which were sexually mature but continued fast growth for several years after. Lamellar-zonal bone in long bones would only indicate the attainment of final size. In the pubis, the lamellar-zonal bone would represent also, still growing bones of adult individuals. Not before the bone tissue became avascular, maximum size was reached. This interpretation represents a more "reptilian" life history. In living reptiles, sexual maturity is reached long before maximum body size and, in contrast to mammals and birds, growth continues after the first reproduction for several years, however with a clearly decreased growth rate. In many reptiles, size and age at first reproduction vary in relatively wide limits, depending on climate and food availability and quality. Thus, it would also not be easy to determine average age and size at sexual maturity for an extinct taxon that has a similar life history to reptiles.

On the basis of the available data, the second interpretation including an early onset of sexual maturity seems to be more likely.

7.2.3 Discussion of other fibro-lamellar bone types
7.2.3.1 Radial fibro-lamellar bone (RFB)

In some samples, fibro-lamellar bone with dense radial primary osteons (RFB) occurs. It represents very rapid growth with high rates of bone deposition. There are six samples with RFB from both localities. Bones include long and flat bones as well as a vertebra and an ischium. The RFB is bounded by "normal" LAGs and was always deposited for one or a few growth cycles, at most three, of the middle or exterior cortex (figure 3D, H, 14G).

ERICKSON & TUMANOVA (2000) described a similar tissue as "highly porous radially vascularized bone" in three large long bones of *Psittacosaurus mongoliensis*. Like in *P. engelhardti* this tissue is locally restricted and is deposited in the exterior cortex of older individuals (ERICKSON & TUMANOVA 2000). They describe this special tissue as unusual for dinosaurs. In extant vertebrates, highly vascularized radial bone is only formed in bony calli or is associated with substantial shape changes. It is deposited very fast with 1mm/day (ERICKSON & TUMANOVA 2000). These authors discussed if this radial bone tissue in *P.*

mongoliensis bones could have a pathologic cause, but no calli were observed. Another possibility is rapid ontogenetic migration of muscle insertions, but this could also not documented. A third hypothesis is that it reflects a loading change perhaps associated with a shift from facultative bipedally to quadrupedally locomotion (ERICKSON & TUMANOVA 2000).

Several hypothesis about the meaning and origin of RFB in *P. engelhardti* are discussed, but a satisfactory explanation is still lacking. The hypothesis that RFB is pathologic is disproven by the normal and intact bone surface underlain by RFB. The bones with RFB also show no other conspicuous differences in morphology.

Another hypothesis is that the RFB is an expression of sexual dimorphism. It is very likely that one of the sexes, as it is common in recent tetrapods, had had a faster growth rate up to sexual maturity than the other. Thus, this faster growing sex would have had to grow with a correspondingly higher bone growth rate, expressed by higher vascularity. However, RFB is only seen in selected and different bones and not in the complete skeleton of a single individual, as this hypothesis would predict. On the other hand, its occurrence in the middle and outermost cortex of apparently nearly full grown individuals indicates a strongly localized growth spurt in a late stage of ontogeny, when slower growth is usually initiated. Thus, a correlation with sexual maturity or sexual dimorphism seems unlikely, unless sexual maturity is reached late in ontogeny (see above).

The fact that the RFB is known from Trossingen as well as from Frick shows that it is indeed a rare but consistently appearing feature in *Plateosaurus* histology and not a feature which is restricted to a single population. RFB can also be observed in other prosauropods, e.g. in a *Sellosaurus* pubis (SMNS 5715, locality of Stuttgart–Herlach, Southern Germany) and in a *Thecodontosaurus* bone of England (IPB R 555).

In a few samples, an intermediate stage between laminar fibro-lamellar bone and radially fibro-lamellar bone can be observed, marked by a clear increase of radial vascular canals within the laminar fibro-lamellar complex. This suggest that most (if not all) bones have the possibility of growing with RFB, but the trigger for growing with RFB is until yet unknown.

7.2.3.2 Highly vascularized laminar fibro-lamellar bone
The highly vascularized fibro-lamellar bone is only known from one femur from Trossingen (IFG compactus, left, 74 cm, figure 3C, G). Although the area where it occurs in the sample is influenced by diagenetic processes, this does not seen to be the sole explanation. Vascular density is considerably higher than in the normal fibro-lamellar bone of

Plateosaurus engelhardti, and the single vascular canals and laminae are thicker, reminiscent of sauropod tissue (SANDER & TÜCKMANTEL 2003). Therefore this tissue suggests a very high growth rate. In contrast to the radial vascular canals in the RFB, this bone tissue shows "normal" laminar vascularization.

The isolated occurrence of this tissue cannot be explained satisfactorily. Due to the total length of the femur of 74.0 cm, and due to the fact that the cycle in which this tissue appears represents the 5th total growth cycle, juvenile tissue must be excluded. Nevertheless, it is possible that the original juvenile bone tissue of *Plateosaurus* had had a similar appearance to the tissue observed in this femur.

A possible explanation could be that this tissue only represents very fast growth during a restricted period, maybe due to optimal environmental conditions.

7.2.4 Possible onset of sexual maturity recorded in pubis specimens

In comparison to other bones, the pubis has a relatively high number of visible LAGs, and in contrast the resorbed LAG number is very low. Due to this and its exclusively lamellar-zonal bone, the pubis seems to be a bone with a slow ontogenetic growth, possibly indicating negative allometry. This may be the reason why sexual maturity is possibly preserved in the pubis and not in the growth record of any other sampled bone. All other sampled bones had a higher growth rate and faster medullary resorption resulting in earlier cycles having been destroyed.

Sexual maturity can be possibly documented in the pubis by the decrease of vascular density in the lamellar-zonal bone and the general decrease in cycle distance. Growth cessation, a decrease in vascular density, and a decrease in cycle distance appears in all sampled pubes after LAG 5 or 6 (figure 7). In the other bones, sometimes also a similar growth decrease can be observed, but not as clearly regularly as in the pubis samples.

The growth decrease in the pubis in conjunction with the relatively low total LAG number would fit well with the onset of sexual maturity, at least better than the largely complete growth stop occurring later in ontogeny marked by the bone tissue change.

7.3 Quantitative growth record (skeletochronology)
7.3.1 Single bone types

The quantitative analysis of growth is based on the count of growth marks combined with observed differences in vascular density. Two forms of growth marks were used: Lines of arrested growth and, primarily in the Frick samples, polish lines. Although the annual

nature of LAG deposition has not been tested in extinct vertebrates, it is a general assumption in growth history research, and annual deposition of LAGs is the rule in recent vertebrates (CASTANET et al. 1993).
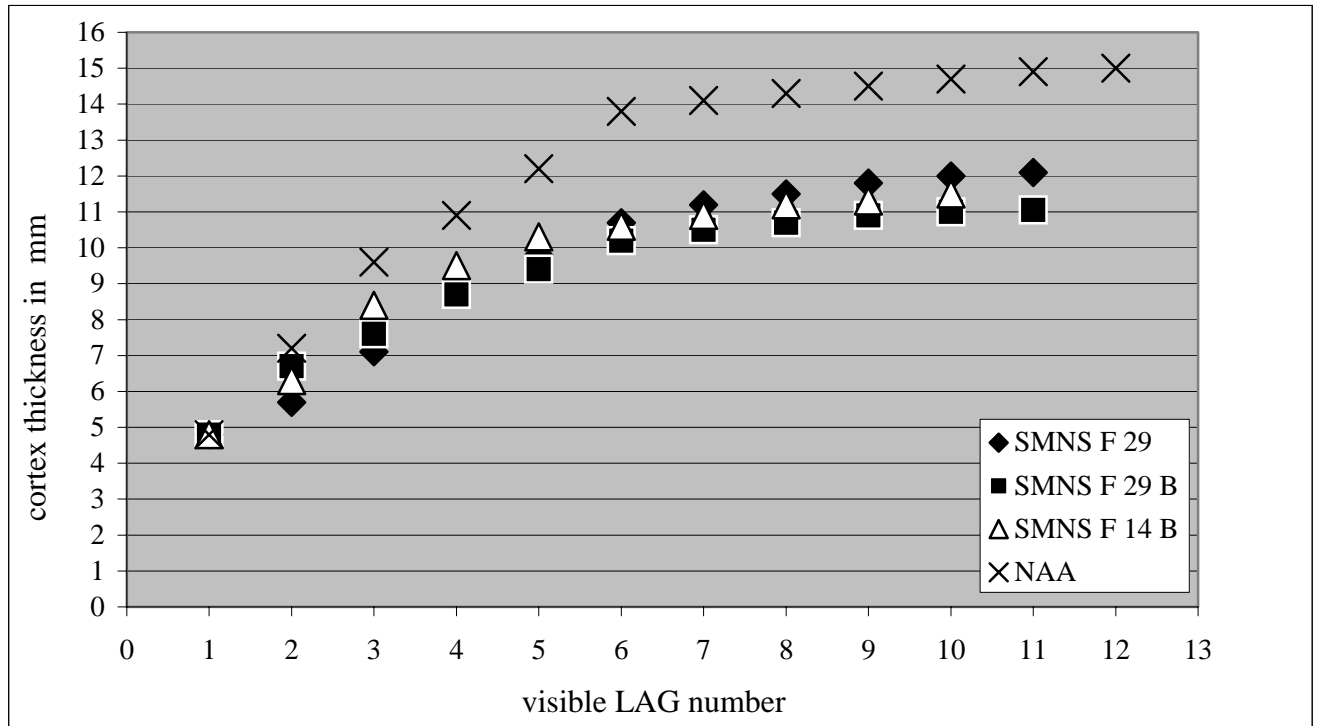

Figure 7: *Cortex thickness plotted against visible LAG count in pubis samples. A decrease in cycle distance occurs in all samples at around visible LAG 5 or 6.*

In the *Plateosaurus engelhardti* samples, LAGs are spaced regularly throughout the whole cortex. They are not restricted to a special bone type and appear in all kinds of fibro-lamellar bone as well as in lamellar-zonal bone. Sometimes LAGs are even partially preserved in secondary bone tissue. LAGs usually indicate the end of a growth cycle and are always accompanied by decreasing vascular density. LAG counts always give a minimum age due to resorption of primary bone during ontogeny. This and the lack of juvenile specimen makes extrapolation of the resorbed LAGs necessary (see methods section, which discusses various kinds of error). Thus, the following age estimate based on LAG counts should generally be seen as approximations and not as exact data.

Due to the large number of single bones sampled for the current study, quantitative analysis starts with their growth record.

7.3.1.1 Femur

The total count of visible LAGs in the femur samples from both localities varies between 5 and 14 LAGs, averaging 8, with a total femur length ranging from 50 cm to 99 cm (table 7). This LAG count corresponds to 6 to 15 growth cycles. The resorbed LAG number is between 3 and 14 LAGs and also averages 8. The total LAG number varies between 12 and 24 LAGs, with an average value of 16 to 17 LAGs.

Table 7: *Femur growth records based on different LAG counts. FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone. Ts = thin section, ps = polished section, cs = cross section, fs = fracture surface.*

sample	visible LAGs	exterior cortex	resorbed LAGs	total LAGs	femur size	kind of sample
SMNS F 29	6	FBLC, high vascular density	6-7	12-13	ca. 50.0 cm	ts, ps, cs
NAA F 88-B130	14	LZB in an avascular tissue, at caudal side RFB	9	23	56.5 cm	ts, ps, cs
NAA unnumbered	6	deposition of closely spaced LAGs in an avascular LBZ has started	6	12	59.0 cm	ts, ps
SMNS F 29A (right; incomplete sample)	5	growth continued with FBLC	-	-	59.5 cm	ts, ps
SMNS F 27	7	not visible in the fracture surface	7	14	62.5 cm	fs
SMNS F 14 A	7	deposition of closely spaced LAGs in a nearly avascular LBZ has started	7-8	14-15	63.5 cm	ts, ps, fs
SMNS F 29 A (left)	8	deposition of closely spaced LAGs in a nearly avascular LBZ has started	10	18	ca. 72.0 cm	ts, ps, fs
SMNS F 8	11	not visible in the fracture surface	5	16	74.0 cm	fs
IFG compactus	12	relative closely spaced LAGs, but still in a FBLC	15	15	74.0 cm	t, p
SMNS F 48-1	5	growth continued with FBLC	9	14	76.0 cm & 77.5 cm	ts, ps, fs
SMNS F 27	11	cycle distance becomes closer, but still FBLC	8-9	19-20	81.0 cm	ts, ps
IFG, exhibition	10	LZB in a nearly avascular tissue	14	24	99.0 cm	ts, ps

As table 7 shows, the femur samples represent a wide size range from small to large individuals. However, no individuals with a femur length of less than 50.0 cm were sampled. Only two specimen are from Frick, and both belong to individuals with a femur length smaller than 60 cm but both show a clear growth stop in the outer cortex.

Individuals with a femur length of 50.0 cm (right, SMNS F 29, figure 8), 59.5 cm (right, SMNS F 29), 74.0 cm (left, IFG compactus, figure 14A), 77.5 cm (left, SMNS F 48), and 81.0 cm (left, SMNS F 27, figure 14B) were still rapidly growing as indicated by "normally" vascularized fibro-lamellar bone. Nevertheless, in some other samples already a decrease in vascular density can be observed, which indicates that a growth decrease was initiated. Some individuals had clearly stopped growth, indicated by deposition of nearly or completely avascular lamellar-zonal bone. This growth stop is preserved in individuals with a femur length of 56.5 cm (right, NAA F 88/B-130, figure 14D), 59.0 cm (left, unnumbered/Frick), 63.5 cm (left, SMNS F 14), 72.0 cm (left, SMNS F 29), and 99.0 cm (left, IFG, figure 14C).

Some femora (right, 50 cm, SMNS F 29; left, 74.0 cm, IFG; left, 77.5 cm, SMNS F 48) show fast growth with fibro-lamellar bone at least up to total LAG 14. After that, growth often starts to decrease and stops completely in some femur samples (right, 56.5 cm, F 88-B130; right, 59.5 cm, SMNS F 29A; left, 99 cm, IFG) at around total LAG 18/19. One femur sample (left, 81 cm, SMNS F 27) continued growth with fibro-lamellar bone to about total LAG 19/20, and another two samples (left, 59 cm, unnumbered Frick; left, 63.5 cm, SMNS F 14) had already stopped growth around total LAG 12 and 14/15.

To summarize, *Plateosaurus engelhardti* femora grew with high rates up to around the 15th total growth cycle. They show at this point a broad size range. Afterwards, growth rate decreases and growth stops finally in most individuals after total growth cycle 19/20. After growth had stopped, *Plateosaurus engelhardti* individuals continued to live for several years, like femur IFG 99.0 cm shows. This individual reached its full body size of around ten meters after visible LAG 5 which corresponds with the total LAG 19. Five closely spaced LAGs deposited in lamellar-zonal bone mark the life span after rapid growth had stopped. An important point is that the femur samples indicate clearly that growth stopped or slowed down at variable body sizes.
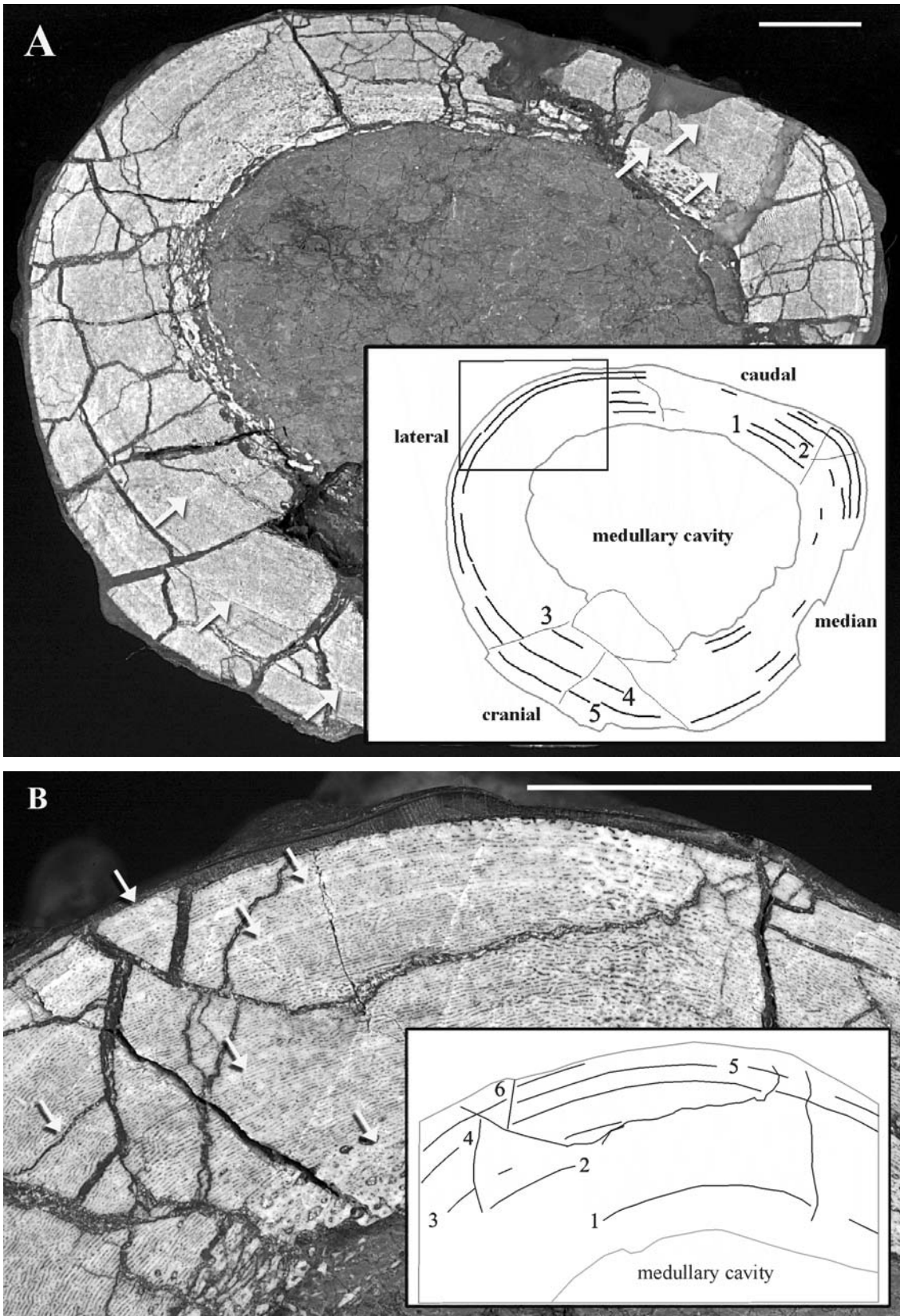
Figure 8: 8A: *Fracture surface and drawing of right femur SMNS F 29 (~50 cm).*
Arrows mark the visible LAGs (Note: some LAGs are not visible at the present

magnification). The rectangle marks the enlargement of the lateral bone section figured in

8B. **8B***: Enlargement and drawing of lateral cortex of right femur SMNS F 29 (~50 cm).*

Due to the higher magnification, one more LAG is visible in the exterior cortex. Scale 1 cm.

7.3.1.2 Tibia

The total number of visible LAGs in the tibia varies between 5 and 11, averaging 8, with a total tibia length of around 51 cm to 66 cm, or a corresponding femur size of tibiae of 63 cm to 77.5 cm (table 8). The visible LAG count corresponds to 6 to 12 growth cycles. The resorbed LAG number is between 4 and 15 and amounts on average to 9. The total LAG number varies between 10 and 26 with an average value of 17 LAGs. Considering the relative small size range of the tibiae sampled, they show a high range in total LAG numbers (10-26) and therefore in age distribution.

Table 8: *Tibia growth records based on LAG count.* *Tibia length is calculated to its corresponding femur size. FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone. Ts = thin section, ps = polished section, cs = cross section, fs = fracture surface.*

sample (tibia length)	visible LAGs	exterior cortex	resorbed LAGs	total LAGs	corresponding femur size	kind of sample
MSFM-1 (ca. 51.0 cm)	6	growth continued with FBLC	4-5	10-11	63.0 cm	ts, ps
NAA F 88/B70 (51.0 cm)	9	deposition of closely spaced LAGs in a nearly avascular LZB has started. At the caudal bone side RFB.	14-15	23-24	63.0 cm	cs
SMNS F 15 (51.0 cm)	7	growth continued with FBLC, but with a lower vascular density	6	13	64.0 cm	fs
MSMF-2 (>> 52.0 cm)	11	LZB in an avascular tissue, with closely spaced LAGs	12	23	>> 64.0 cm	ts, ps
NAA A 9 (53.0 cm)	11	LZB, with closely spaced LAGs, but still a few longitudinally vascular canals	14-15	25-26	65.0 cm	ts, ps
SMNS F 14 A (55.0 cm)	6	growth continued with FBLC but very low vascular density	5	11	63,5	ts, ps, fs
SMNS F 29 A (59.0 cm)	5	two or three cycles of RFB at the caudal bone side, the other bone sides not easy to judge but growth seems to be	12	17	74.0 cm	ts, ps, cs

		continued with FBLC				
SMNS F 48-2 (66.0cm)	7-8	growth continued with FBLC	7	14-15	77.5 cm	fs

As table 8 shows, the tibia samples derive only from medium-sized individuals. Fifty percent of the tibia samples are from Frick. As mentioned before these, individuals are generally smaller than the Trossingen individuals. The Frick tibiae all belonged to the same size class, between 51 to 53 cm, corresponding to a femur size between 63 cm and 65 cm. Nevertheless, one of these tibiae shows continued growth with laminar fibro-lamellar bone, whereby the others of the same size had dramatically decreased or stopped growth. In the Trossingen samples, growth had decreased in one relatively small tibia, but the other tibiae continued growth, including the largest one (right, 66 cm, SMNS F 48-2). Thus, there are individuals of around 6.30 m to 6.50 m in which growth had decreased greatly after a total LAG number of 23/24 (right?, 51 cm, NAA F88/B70), 22 (left, 52 cm, MSFM-2, figure 14F), and 22/23 (right, 53 cm, NAA A9). Tibia MSFM-2 had deposited, after growth had stopped, two more LAGs, and tibia NAA A9 three more LAGs. On the other hand, there are tibiae of about the same size in which growth continued with laminar fibro-lamellar bone at a total LAG number of 10/11 (right, 51 cm, MSFM-1), 11 (right, 55 cm, SMNS F 14, figure 14E) and 13 (right, 51 cm, SMNS F 15, figure 9). The larger tibiae, belonging to individuals of around 7.40 m and 7.75 m, also continued growth with laminar fibro-lamellar bone at a total LAG number of 17 (left, 59 cm, SMNS F 29A) and 14/15 (right, 66 cm, SMNS F 48-2).

There are thus individuals of around 6,5 m body length which show fibro-lamellar bone up to the 20 and 23 LAG followed by lamellar-zonal bone and a dramatically growth rate decrease in some specimens. In other individuals growth continued at a size of 6.40 m (right, 55 cm, SMNS F 14A; right, 51 cm, SMNS F 15), 7.40 m (left, 59 cm, SMNS F 29A), and 7.75 m (right, 66 cm, SMNS F 48-2) and a LAG number of 11, 13, 17, and 14/15. These examples show a significant lower LAG number at a clearly greater body length. Therefore, the tibia samples indicate that growth stopped at variable final sizes in *Plateosaurus engelhardti*.

Unfortunately, none of the really large individuals are represented by a tibia. The tibiae that grew to larger sizes show a generally lower total LAG number and they may have reached their maximum size around the same time, at around LAG 23, as the smaller individuals.
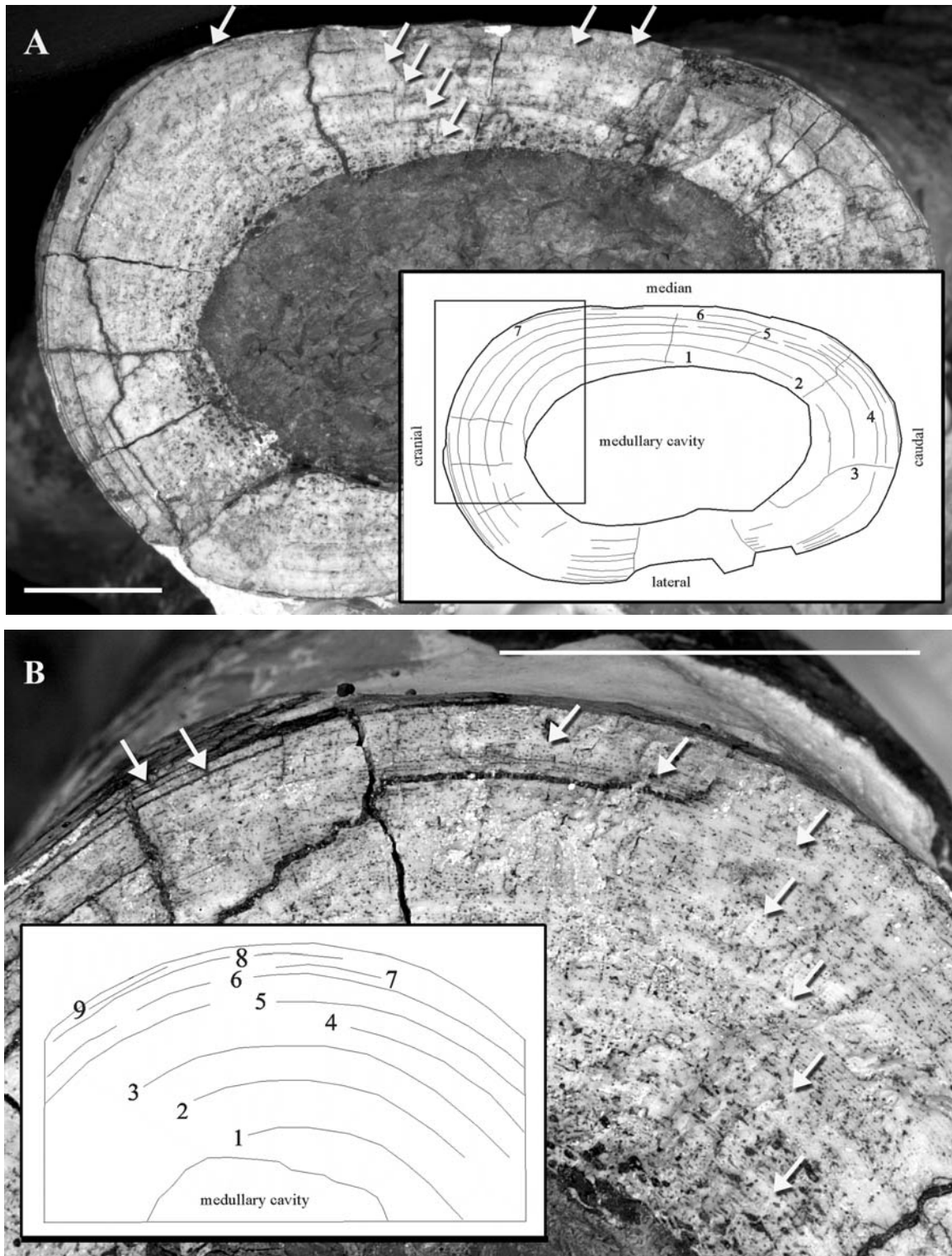
Figure 9: 9A: *Fracture surface and drawing of right tibia SMNS F 15 (51 cm).*
Arrows mark the visible LAGs (Note: some LAGs are not visible at the present
magnification). The rectangle marks the enlargement of the lateral bone section figured in
9B. **9B***: Enlargement and drawing of cranial cortex of right tibia SMNS F 15 (51 cm).*
Scale 1 cm.

7.3.1.3 Fibula

Fibulae were only sampled among the Trossingen material and only in fracture surfaces. These samples offer not as much detail as cross- polish-, and thin sections. Nevertheless, is clear that the fibulae possess the same histology as the other long bones, but counting LAGs is more difficult, and not all may have been identified, predominately in the exterior cortex. Thus, it is possible that the visible LAG number is generally to low. Additionally, in the fibula samples no growth stop could be identified, due to the lack of clearly visible lamellar-zonal bone in the exterior cortex. However, in some samples a clear decrease of vascular density in the fibro-lamellar bone is observable.

The total count of visible LAGs in fibula samples varies between 4 and 8, averaging 6 LAGs. The size range of the sampled fibula is between 46.5 cm to 59.0 cm, corresponding to a femur size of around 58 cm to 77.5 cm (table 9). The visible LAG count corresponds to 5 to 9 growth cycles. The resorbed LAG number is between 5 and 15 and amounts on average to 8. The total LAG number varies between 12 and 20 with an average value of 14 LAGs.

Table 9: *Fibula growth records based on LAG count.. Fibulae length is calculated to its corresponding femur size. FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone. Fs = fracture surface.*

sample (fibula length)	visible LAGs	exterior cortex	resorbed LAGs	total LAGs	corresponding femur size	kind of sample
SMNS F 29 B (46.5 cm)	7	very low vascularized FBLC	6	13	58.0 cm	fs
SMNS F 14 (52.5 cm)	6-7	growth continued with FBLC, but vascular density starts to decrease	6	11-12	63,5 cm	fs
SMNS F 15 (53.0 cm)	5-6	low vascularized FBLC	10	15-16	66.0 cm	fs
SMNS F 29 B (57.5 cm)	4-5	low vascularized FBLC	15	19-20	72.0 cm	fs
SMNS F 8 (59.0 cm)	7-8	very low vascularized FBLC	6	13-14	74.0 cm	fs
SMNS F 48 (ca. 59.0 cm)	7-8	difficult to judge: in some areas growth seems to have stopped, in others growth seems to have continued with FBLC but low vascularization.	5	12-13	77.5 cm	fs

As table 9 shows, the fibula samples represent medium-sized individuals which also have intermediate total LAG numbers. A possible growth decrease or stop is not well seen due to insufficient resolution of the images. All sampled fibula seems to have continued
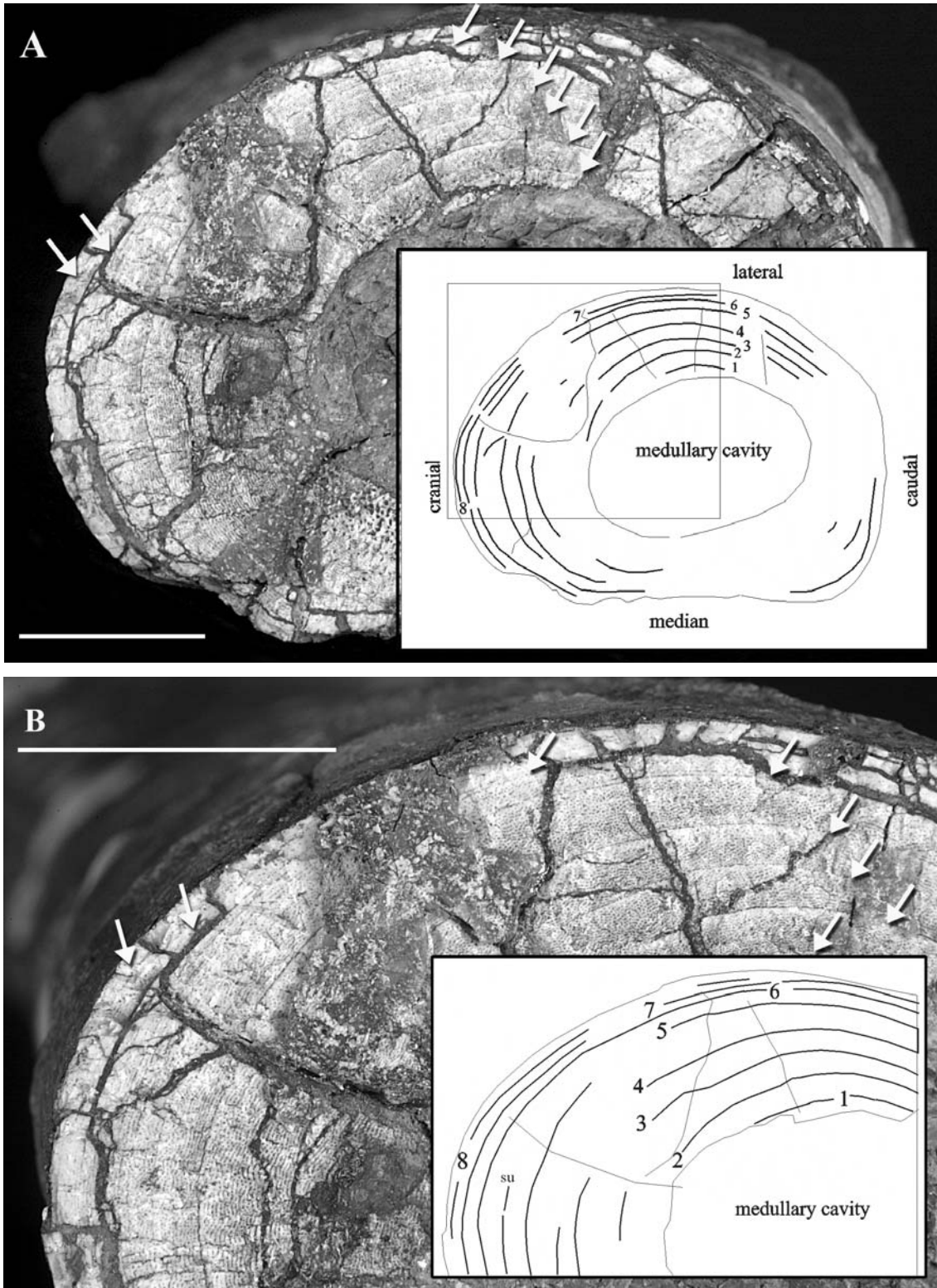
Figure 10: 10A: *Fracture surface and drawing of right ? fibula SMNS F 8 (~59 cm).* Arrows mark the visible LAGs (Note: some LAGs are not visible at the present magnification). The rectangle marks the enlargement of the lateral bone section figured in 10B. **10B:** *Enlargement and drawing of cranio-lateral cortex of right ? fibula SMNS F 8 (~59 cm).* Scale 1 cm.

growth with the laminar fibro-lamellar bone, but with a clearly decreasing vascular density in the outer cortex, which may foreshadow a bone tissue change. A total LAG number of 13 is relatively frequent. This total LAG number is shown by the smallest specimen (left, 46.5 cm, SMNS F 29 B), by a medium-sized fibula (right, 63.5 cm, SMNS F 14), as well as by the largest specimen (right?, 59 cm, SMNS F 8, figure 10; right, 59 cm, SMNS F 48). Two other medium-sized fibula show a somewhat (right, 53 cm, SMNS F 15: 15/16) and a significantly (left, 57.5 cm, SMNS F 29 B: 19/20) higher total LAG number without a clear cessation of growth. To generalize, growth in the fibula continued with laminar fibro-lamellar bone at least somewhat after LAG 13. Then growth decrease is initiated and growth stops around LAG 19/20 or slightly later.

The highest total LAG number (19-20) is shown by a fibula which belonged to a medium to large individual of 7.2 m body length (left, 57.5 cm, SMNS F 29 B).

7.3.1.4 Humerus

The total count of visible LAGs in humerus samples varies between 4 and 10, it amounts in average 7, with a total length of humerus ranging between 41 cm to 53 cm. The humerus length corresponds with a calculated femur length from around 63.5 cm to 85.0 cm in length (table 10). The resorbed LAG number is between 3 and 13 and amounts in average 7 to 8. The total LAG number varies between 7 and 20 LAGs with an average value of 15 LAGs. This total LAG count corresponds to 8 and 21 growth cycles.

The size range of the humeri is relative great, at least based on corresponding femur size. Medium-sized individuals are represented as well as one large individual. Except for sample NAA F 88/B640 (figure 11), which had stopped growth and changed its bone tissue from laminar fibro-lamellar into lamellar-zonal bone, growth had continued with laminar fibro-lamellar bone in all other samples, although in some with a clearly decreasing vascular density. The samples SMNS F 14A (left, 41 cm), SMNS F 29A (left, 43.5 cm), and SMNS F 61B (right, 43.5 cm) were only studied in fracture surfaces. Thus, it is well possible that a growth decrease had been initiated in some of these samples but remains undetected.

Humerus NAA F 88/B640 (right, 44.5 cm) belongs to a medium-sized individual of around 6.5 m body length which had stopped growth after total LAG 14, with deposition of closely spaced LAGs in the outermost cortex continuing to total LAG 18. Another medium-sized humerus (left, 41 cm, SMNS F 14 A) shows a total LAG number of 19/20. In the fracture surface a clearly decreased vascular density can be observed, and the exterior cortex seems to be nearly avascular. Thus, maybe a bone tissue change had been initiated.

Nevertheless, in comparison with sample NAA F 88/B640 (right, 44.5 cm), the growth decrease or stop occurred late in ontogeny in the humerus sample SMNS F 14 A (left, 41 cm).

Table 10: *Humerus growth records based on LAG count. Humeri length is calculated to its corresponding femur size. FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone. Ts = thin section, ps = polished section, cs = cross section, fs = fracture surface.*

sample (humerus length)	visible LAGs	exterior cortex	resorbed LAGs	total LAGs	corresponding femur size	kind of sample
IFG 11921 (not available)	4-5	continued growth with a slightly lower vascularized FBLC	3	7-8	---	ts
SMNS F 14 A (41.0 cm)	8-9	continued growth with a slightly lower vascularized FBLC	11	19-20	63,5 cm	cs
SMNS F 29 A (43.5 cm)	7	continued growth with a slightly lower vascularized FBLC	6	13	70.0 cm	ts, cs
SMNS F 61 B (ca. 43.5 cm)	7	continued growth with a slightly lower vascularized FBLC	13	20	70.0 cm	cs
NAA F 88/B640 (44.5 cm)	10	deposition of closely spaced LAGs in a nearly avascular LZB	8	18	65.0 cm	ts, cs
IFG exhibition (53.0 cm)	8	continued growth with FBLC	4-5	12-13	85.0 cm	ts

A large difference in LAG number is seen in samples SMNS F 29A (left, 43.5 cm) and SMNS F 61B (right, 43.5 cm). Both represent individuals of around 7.0 m body size, but SMNS F 29A show a total LAG number of 13 whereas SMNS F 61B contains 20 LAGs. In the fracture surface of SMNS F 29A high vascular density and the fibro-lamellar bone can be observed up to the exterior cortex. This humerus was surely still in its fast growing stage. Thus, it can be concluded that this humerus would have grown to a large individual. Sample SMNS F 61B seems to belong to a large medium-sized individual. The image of the fracture surface show that growth decrease had started, due to a clearly decreased vascular density. Possibly bone tissue change was initiated in the exterior cortex.

The largest humerus (right, 53 cm, IFG exhibition) sampled belongs to an individual of around 8.5 m body size and shows a low total LAG number of only 11/12 LAGs. In its exterior cortex this sample shows growth continued with laminar fibro-lamellar bone and high vascular density. However, after visible LAG 3 (total LAG 7/8), in the outer part of the middle cortex two cycles of lamellar bone in a nearly avascular tissue and two closely spaced LAGs were deposited. After this, growth had continued again with high vascular density and laminar fibro-lamellar bone. It is not really clear if these two cycles containing lamellar-zonal bone are major cycles or subordinate cycles within visible growth cycle 4. They were here counted as major cycles, based on the generally low total LAG number of this large humerus. However, this is a very interesting observation because it suggests the possibility that *Plateosaurus engelhardti* could had stopped growth fully before final size was reached, maybe due to bad environmental conditions or individual disease, and started again with growth when conditions became better.

For the humerus sample IFG 11921 no bone length is known because the sample was taken from an incomplete bone before the current study started and this bone seems to be lost now. Nevertheless, its total LAG number is the lowest of all samples from *Plateosaurus engelhardti*.

The humerus samples indicate that growth stopped or decreases at a variable size in *Plateosaurus engelhardti* individuals. However, the timing of growth stop appears not as clear as in the long bones described before, possibly due to the lack of thin sections of the outer cortex. Growth stop was initiated in some samples at around total LAG 19/20 and at a body size between 6.35 m and 7.0 m, whereas in one sample growth had stopped at total LAG 14 and at a maximum body size of only 6.5 m. On the other hand, growth had continued with fibro-lamellar bone at a total LAG number of 7/8, 11/12, and 13 and at a body size of 7,0 m and 8,5 m. Thus, on the basis of these data, it is quite possible that maximum body size in humerus is reached around LAG 20.
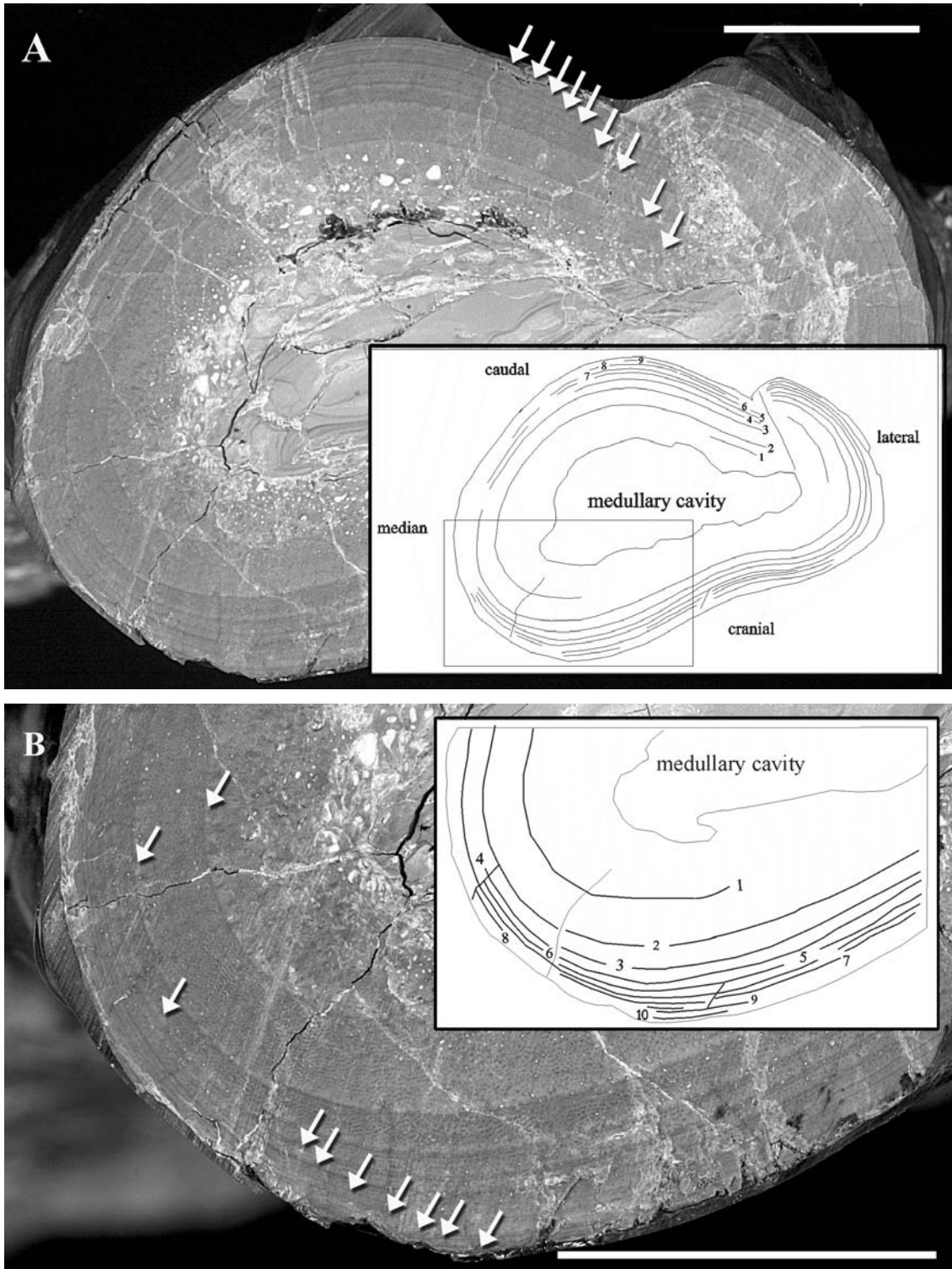
Figure 11: 11A: *Fracture surface and drawing of right humerus NAA F88/B640 (44.5 cm). Arrows mark the visible LAGs (Note: some LAGs are not visible at the present magnification). The rectangle marks the enlargement of the lateral bone section figured in 11B.* **11B***: Enlargement and drawing of cranio-medial cortex of right humerus NAA F88/B640 (44.5 cm). Scale 1 cm.*

7.3.1.5 Scapula

The total count of visible LAGs in the scapula samples varies between 5 and 11, on average 7, with total scapula length ranging from 36.5 cm to 49.5 cm. The scapula length corresponds with a calculated femur length of around 48 cm to 73 cm (table 11). This LAG count corresponds to 6 and 12 growth cycles. The resorbed LAG number is between 3 and 10, with an average value of 6 LAGs. The total LAG number varies between 8 and 18 with an average total LAG number of 13 LAGs. This corresponds with 9 to 19 growth cycles.

Table 11: *Scapula growth records based on LAG count. Scapula length is calculated to its corresponding femur size. FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone. Ts = thin section, ps = polished section, cs = cross section, fs = fracture surface.*

sample (scapula length)	visible LAGs	exterior cortex	resorbed LAGs	total LAGs	corresponding femur size	kind of sample
MSFM (36.5 cm)	11	closely spaced LAGs in LZB	5-6	16-17	48.0 cm	ts, ps
NAA (>> 39.0 cm)	8	closely spaced LAGs, in LZB but still low vascularization available	10	18	51.0 cm	cs
SMNS F 29 (>> 42.0 cm)	5	continued growth	3	8	>>62.0 cm	cs
SMNS F 14 B (47.0 cm)	6	the last two LAGs were deposited little closer, still a few vascular canals	8-9	14-15	63.5 cm	ts, ps, fs
SMNS F 29 B (48.0 cm)	7	continued growth	3-4	10-11	71.0 cm	ts, ps, fs
SMNS F 29 A (49.5 cm)	5	continued growth	5-6	11-12	73.0 cm	ts, ps

In spite of a relative small medullary cavity, the remodeling zone in the scapulae is broad and active and sometimes half of the primary cortex is remodelled. In comparison to the long bones and the pubis, scapula samples therefore show an intermediate resorbed LAG number. Due to its combination of bone tissues, the scapula, although a flat bone, takes up an intermediate position between long bones and the pubis. This is expressed by a lower visible LAG number and a higher resorbed and therefore total LAG number in contrast to the pubis samples. Thus, the scapula grows not as slowly as the pubis, but also not as fast as femur, tibia, fibula, and humerus. The size range of scapula is relatively great, representing small to medium-sized individuals. As the other bones, small scapulae can show high total LAG numbers and large ones lower or similar LAG numbers as the small scapulae samples.

The scapula samples MSFM (left, 36.5 cm) and NAA (right?, 39 cm) contain a few closely deposited LAGs in an avascular bone tissue in the exterior cortex which indicates a

complete growth stop at 4.8 m and 5.1 m body length. The total LAG number in these samples is 16/17 and 18. Growth had decreased strongly after total LAG 14/15 (MSFM, left, 36 cm) and after LAG 16 (NAA, right?, 39 cm). The samples from Trossingen belong to larger individuals, and only in sample SMNS F 14B (right, 47 cm), a growth decrease had been initiated, at a total LAG number of 13/14 and a body size of 6.35 m. The samples SMNS F 29 (left, 42 cm), SMNS F 29 B (left, 48 cm, figure 12), and SMNS F 29A (left, 49.5 cm) would have continued to grow with a total LAG number of 8, 10/11, and 11/12 and a body size of >> 6.2 m, 7.1 m, and 7.3 m at the time of death.

The scapulae from Trossingen represent medium-sized individuals. Very large individuals are not documented in the scapulae from Trossingen. At around 5 m, the scapulae from Frick represent very small individuals when growth had stopped. In the scapula samples, it is conspicuous that the larger individuals have a generally lower total LAG number in comparison to smaller individuals.
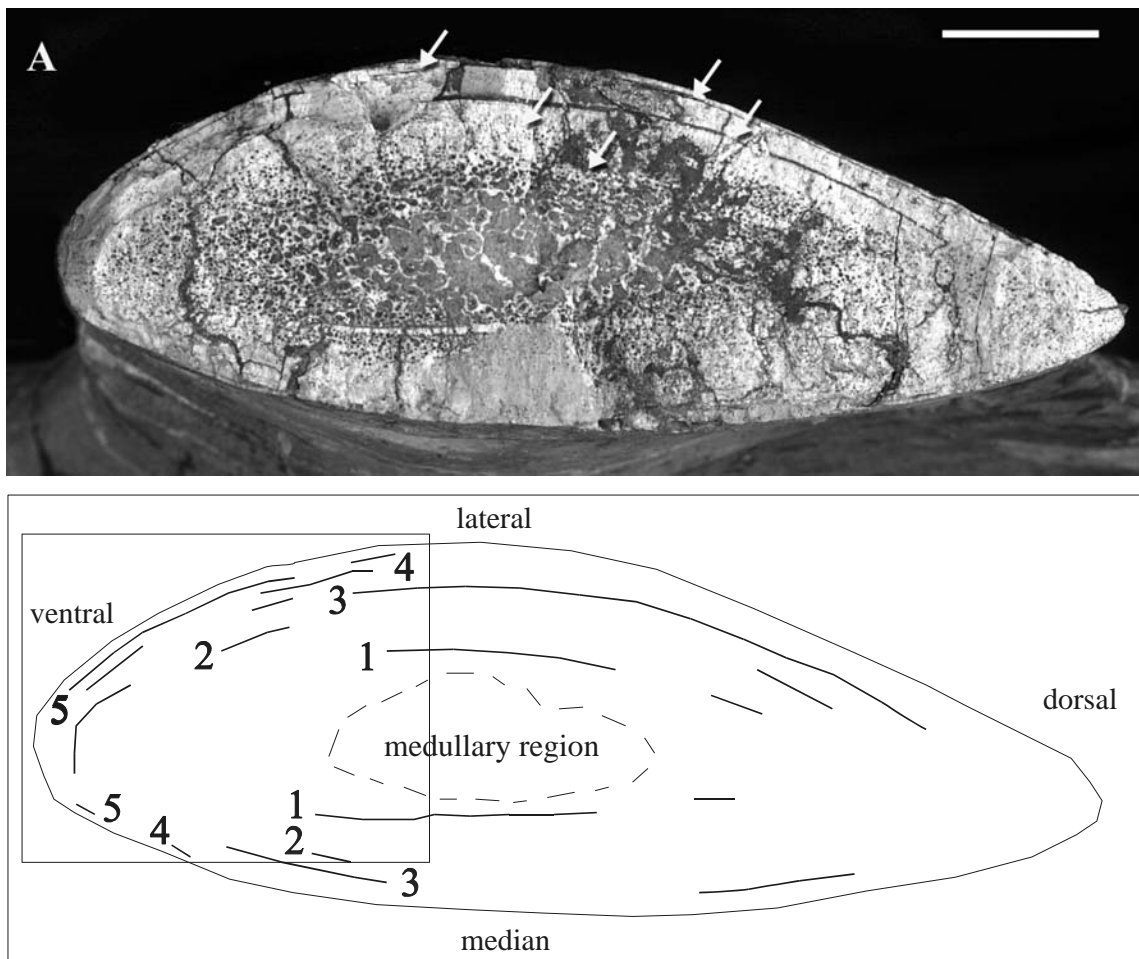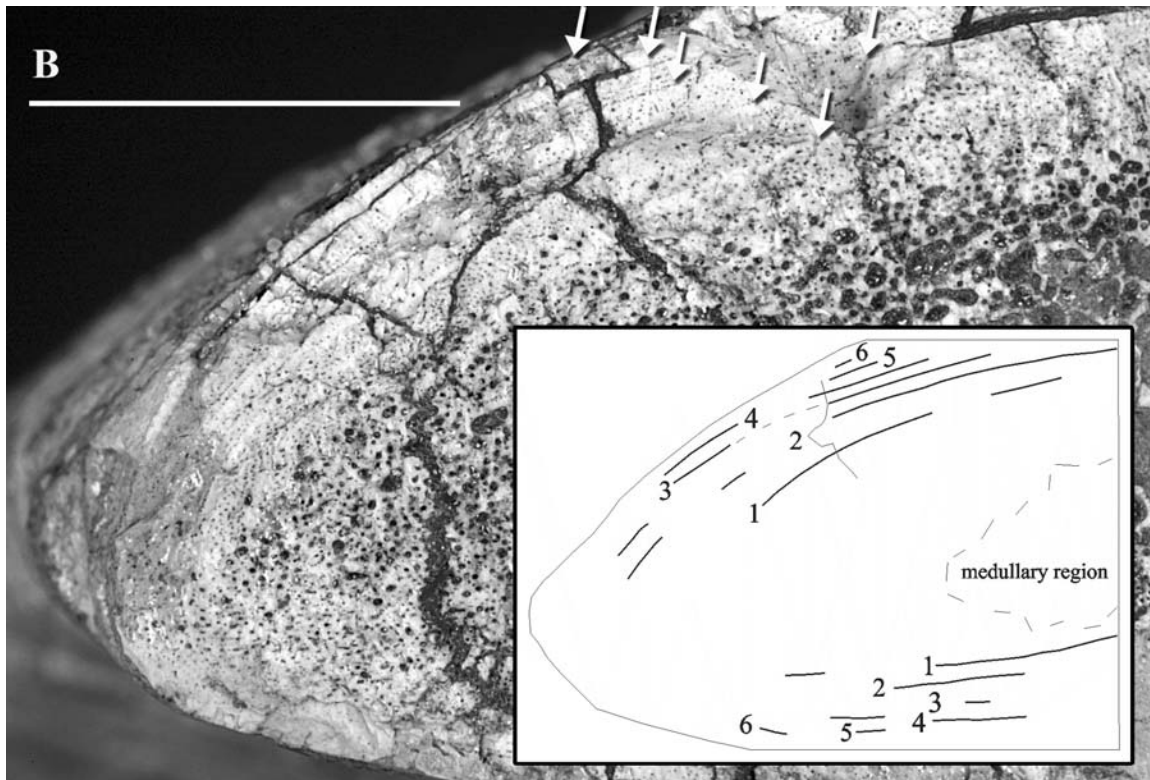
Figure 12: 12A: *Fracture surface and drawing of left scapula SMNS F 29 B (48 cm). Arrows mark the visible LAGs (Note: some LAGs are not visible at the present magnification). The rectangle marks the enlargement of the lateral bone section figured in 12B.* **12B***: Enlargement and drawing of ventral cortex of left scapula SMNS F 29 B (48 cm). Scale 1 cm.*

7.3.1.6 Pubis

The size range differences and the range of LAG numbers are very low in the sampled pubes. The total count of visible LAGs in pubis samples varies between 9 and 11, and it amounts on average to 10. Pubes size range is between 48 cm to 53,5 cm. These pubes length corresponds to a calculated femur length of around 59 cm to 66 cm (table 12). The resorbed LAG number is between 2 and 4 and amounts on average to 3. The total LAG number varies between 11 and 13 LAGs with an average value of 13 LAGs. This total LAG count corresponds to 12 to 14 growth cycles.

Among the studied bones, the slowest growing bone in the skeleton of *P. engelhardti* is the pubis due to its purely lamellar-zonal bone tissue. The pubis shows the lowest resorbed LAG number, whereas the visible LAG count is the highest in all bones. The total LAG number is low to intermediate in comparison with the long bones. This also fits well with the observed small medullary region in pubis samples, at least at the lateral bone side. Thus, it

can be assumed that the growth record in the pubis is the most realistic and complete of all *P. engelhardti* bones.

Table 12: *Pubis growth records based on LAG count. Pubis length is calculated to its corresponding femur size. First decrease indicates possible onset of maturity. The number in parentheses indicates the total LAG number of this first decrease. FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone. Ts = thin section, ps = polished section, cs = cross section, fs = fracture surface.*

sample (pubis length)	visible LAGs	first decrease	exterior cortex	resorbed LAGs	total LAGs	corresponding femur size	kind of sample
NAA pubis (without No.) (not available)	11	6 (8)	closely spaced LAGs, but with low vascularization	2	13	---	ts, ps
SMNS F 29 (48.0 cm)	10	6 (8-9)	closely spaced LAGs, but with low vascularization	2-3	12-13	59.0 cm	cs
SMNS F 14 B (50.0 cm)	9	5 (9)	closely spaced LAGs in an avascular tissue	4	13	63.5cm	ts, ps, fs
SMNS F 29 B (right, 52.5 cm)	10	6 (9)	closely spaced LAGs, in an avascular tissue	3	13	65.0 cm	ts, ps
SMNS F 29 B (left, 53.5 cm)	9	6 (8)	closely spaced LAGs in a partially avascular tissue	2	11	66.0 cm	ts, ps, fs

As table 12 shows, the pubis samples represent only medium-sized individuals between 5.9 and 6.6 m body length. LAGs are always relatively closely, due to the thin cortex, and no bone tissue change is present because only still vascularized lamellar-zonal bone was deposited in pubes. However, in the samples SMNS F 14B (left, 50 cm) and SMNS 29B (right, 52.5 cm), the LAGs were deposited in an avascular tissue, indicating that these two samples had stopped growth. Growth decrease was initiated in both specimen after total LAG 9, and the total LAG numbers at time of death amounts to 13 in both samples. In addition, sample SMNS F 29B (left, 53.5 cm, figure 13) and sample NAA (without No.) show at least a partially avascular tissue, respectively a clear decrease in vascular density in the exterior cortex, so growth stop was initiated at a total LAG number of 11 and 13. Only sample SMNS F 29 (left, 48 cm) had continued with slow growth, but vascular density had already decreased at a total LAG number of 12/13. Thus, on the basis of the pubis samples, maximum size is detected at between 6.35 m and 6.5 m body length, due to a clear growth stop there. At

9 LAGs, the total LAG number when growth definitively had stopped is conspicuous lower as in the long bone samples.

The other pubes also show a decreased vascular density around the same total LAG number. It cannot be detected, due to the lamellar-zonal bone tissue and a generally low vascular density in pubis, if slow growth continued or if they would have stopped growth soon. The comparison of the pubes data with that of the long bones is difficult because the resorbed LAG number in long bones is generally overestimated as result of their large medullary cavities. Thus, the extrapolated LAG number seems to be more realistic in pubes.
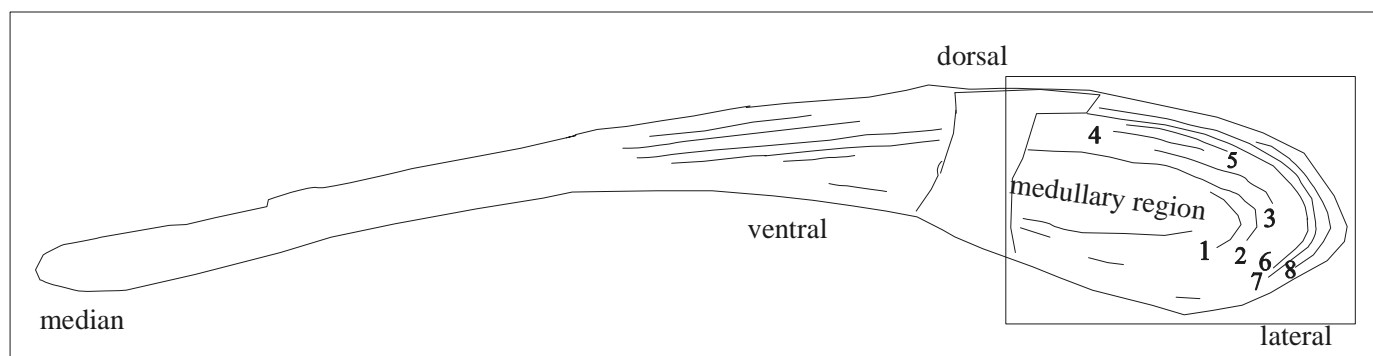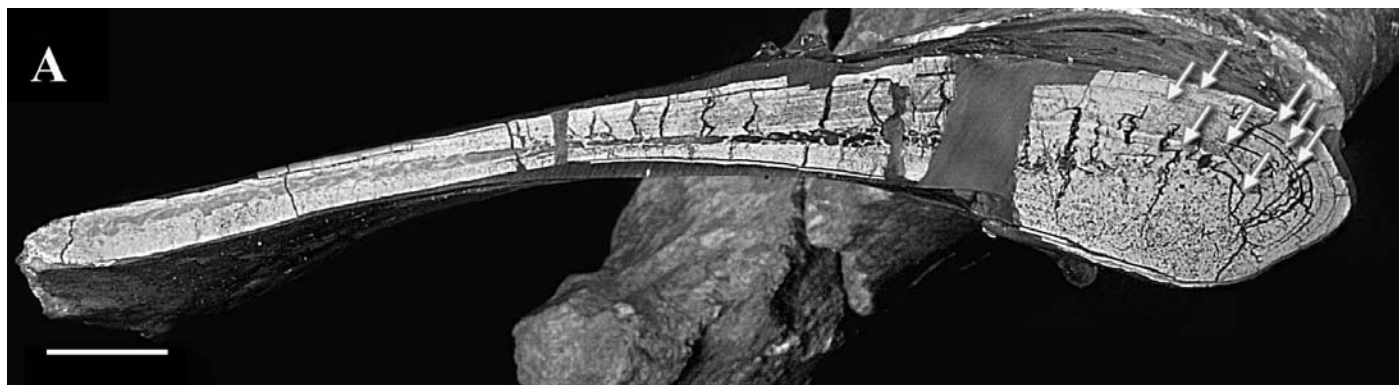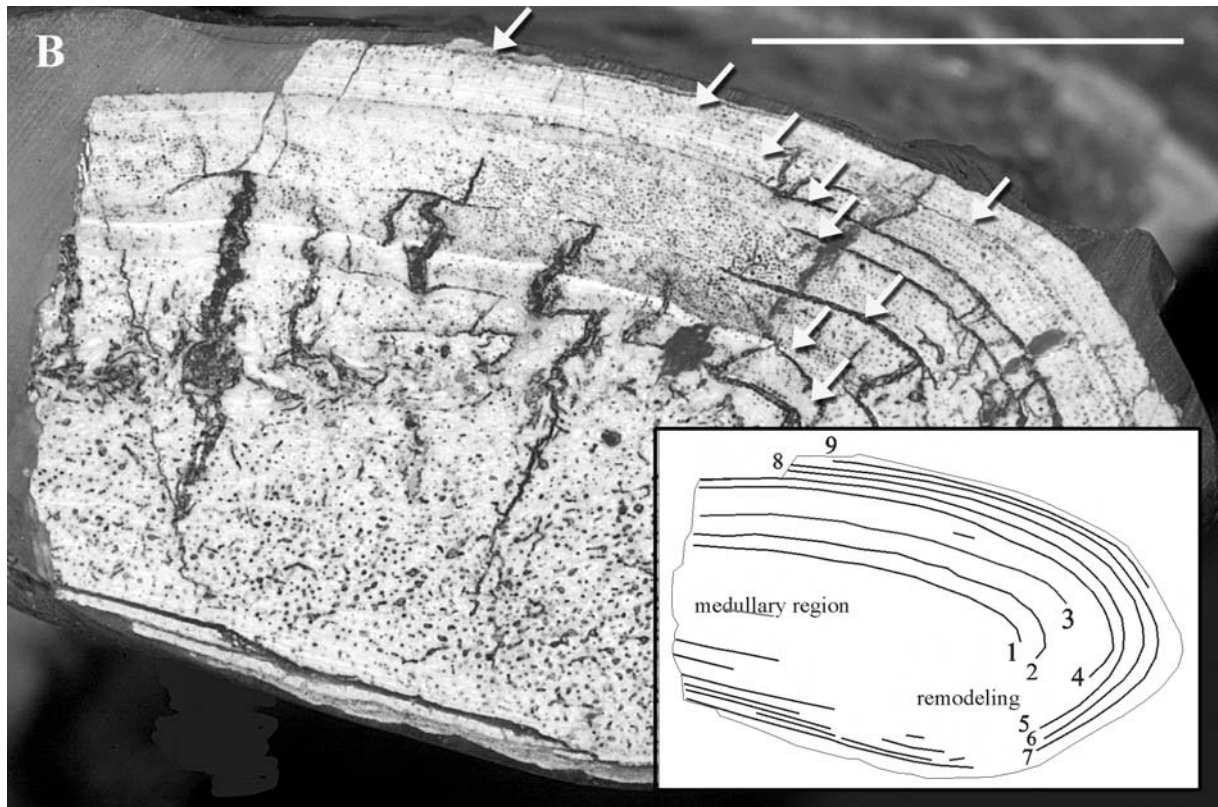
Figure 13: 13A: *Fracture surface and drawing of left pubis SMNS F 29 (48 cm).* *Arrows mark the visible LAGs (Note: some LAGs are not visible at the present magnification). The rectangle marks the enlargement of lateral bone section figured in 13B.* **13B***: Enlargement and drawing of lateral cortex of left pubis SMNS F 29 (48 cm). Scale 1 cm.*

7.3.1.7 Other bones

Table 13: Growth record on the basis of the LAG count in various other bones.

FBLC = fibro-lamellar complex with LAGs; LZB = lamellar-zonal bone.Ts = thin section, ps = polished section, cs = cross section, fs = fracture surface.

sample	visible LAGs	resorbed LAGs	total LAGs	exterior cortex	kind of sample
vertebra IFG RW 12	7	7-8	14-15	a thick layer of RFB in the outer cortex	ts, ps
vertebra IFG RW 14	7	2-3	9-10	bone surface is partially disturbed but the visible tissue shows no indications of a decrease in growth, in contrast the exterior most growth cycle is more highly vascularized than the inner ones	ts, ps
rib SMNS F 29	5-6	7-8	12-14	the outer cortex consist of closely deposited LAGs, but it is still high vascularized with longitudinal canals	cs
rib	4-5	makes no	not	closely deposited LAGs in lamellar-	ts, ps

F88/738		sense	possible	zonal tissue	
rib F88/738	not possible	makes no sense	not possible	remodeled	ts, ps
foot phalange IFG 8159	5-6	makes no sense	not possible	closely deposited LAGs in lamellar-zonal tissue	ts, ps
ischium SMNS F 27	3	7-8	10-11	thick layer of RFB in the exterior cortex	fs

7.3.1.7.1 Vertebrae

Growth cycles are clear in the vertebrae, and each ends in a LAG. Zones and annuli are not as clearly set off as in other bones sampled. The vascularization is generally high, but decreases clearly within each growth cycle and from the inner to the outer cortex. Growth cycle thickness also decreases gradually from the inner to the outer cortex. In both samples, 7 LAGs are visible (IFG RW 12, fig. 14G).

7.3.1.7.2 Ribs

In the rib, growth cycle thickness is generally low and decreases little from the inner to the outer cortex. At least 5-6 LAGs are visible, and extrapolation suggests a total LAG count of around 12-15, depending on bone side (fig. 14H).

The two samples of ribs from the Frick locality show similar features, and only in the exterior cortex around 4-5 LAGs can be counted. The LAGs are closely spaced and developed in a nearly avascular lamellar-zonal tissue. The more distal rib sample preserves no growth marks due to high remodeling.

7.3.1.7.3 Ischia

Only the lateral part of the ischia shows limited remodeling, and a relative good growth record is present with 3 clear LAGs. Extrapolation suggests a total of 10-11 LAGs, or 11-12 growth cycles.

7.3.1.7.4 Foot phalange

Only in the exterior cortex, where the primary bone tissue is lamellar-zonal, closely spaced LAGs are seen. Around 5 to 6 LAGs can be counted (fig. 14I).
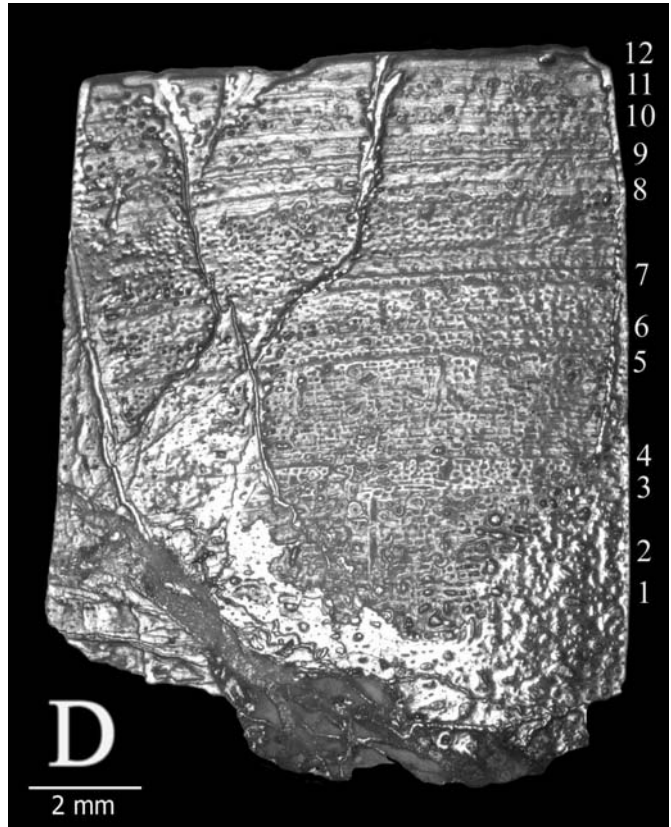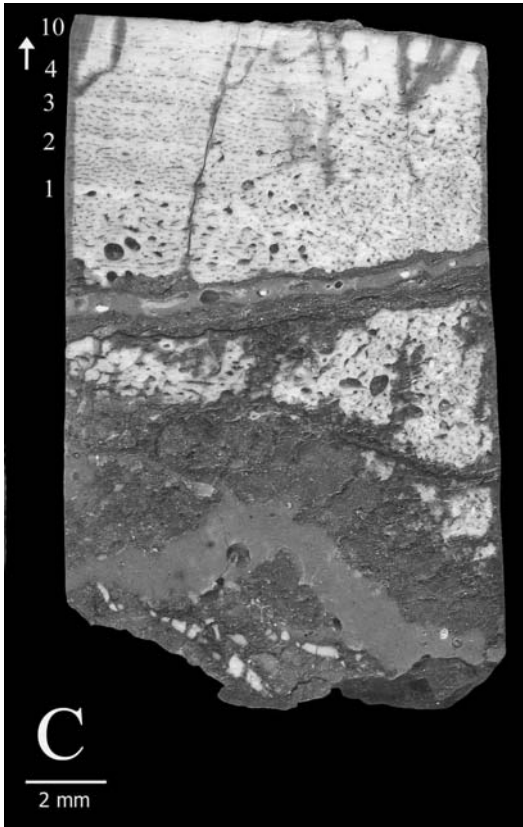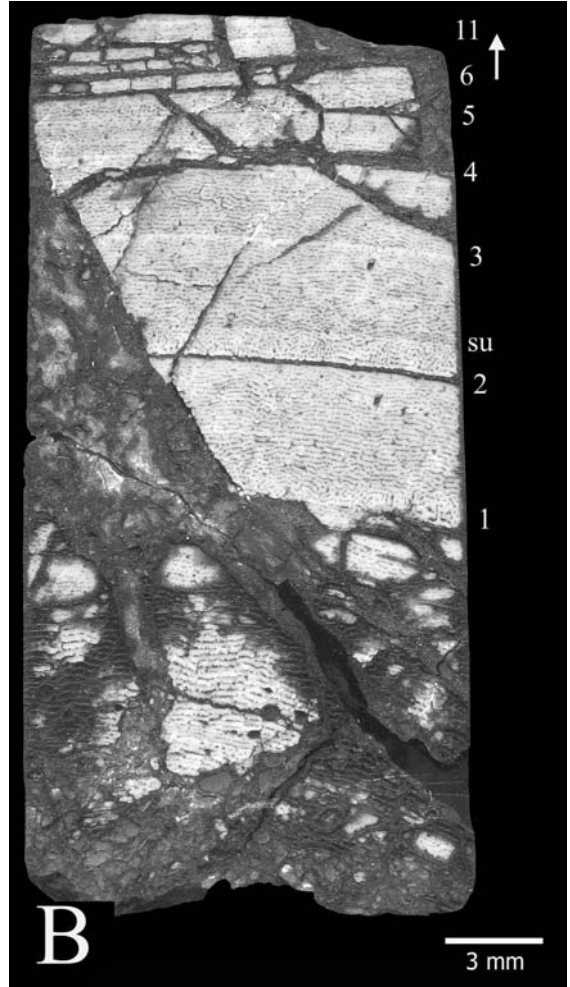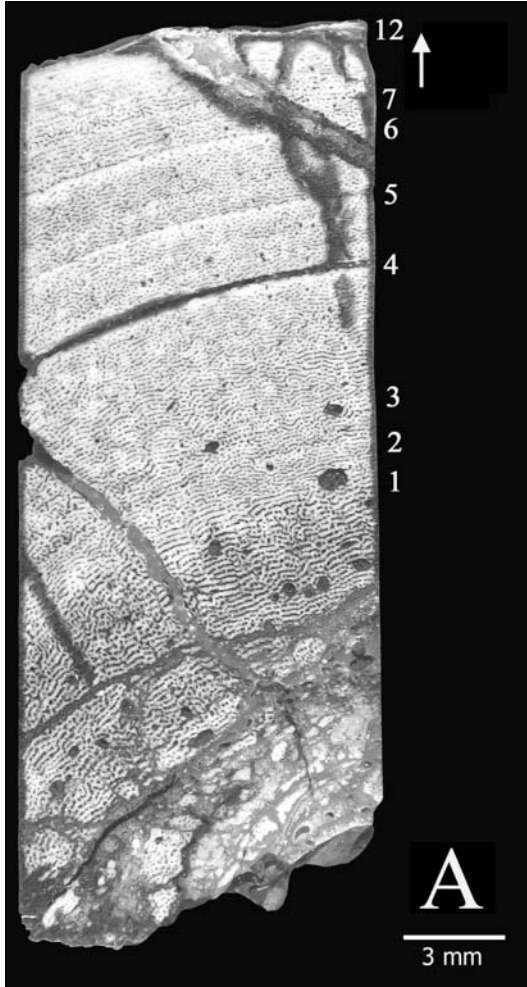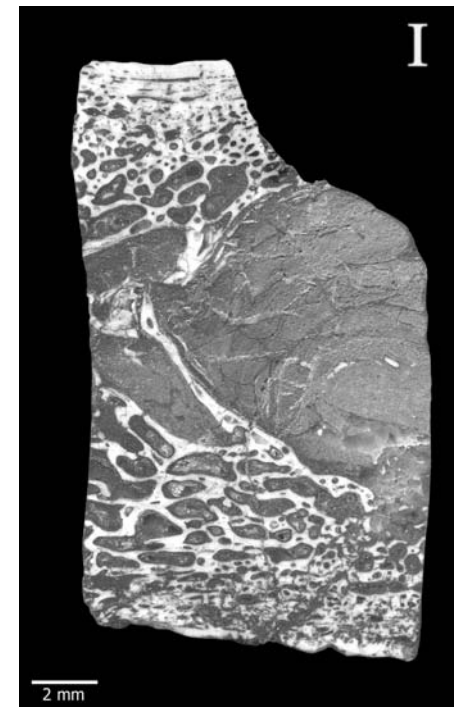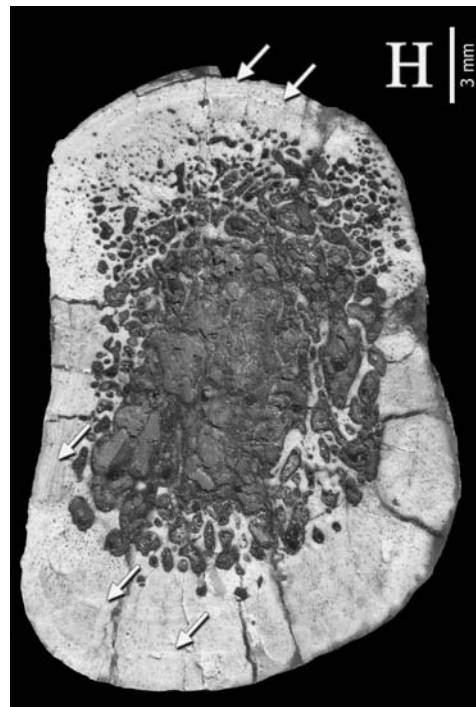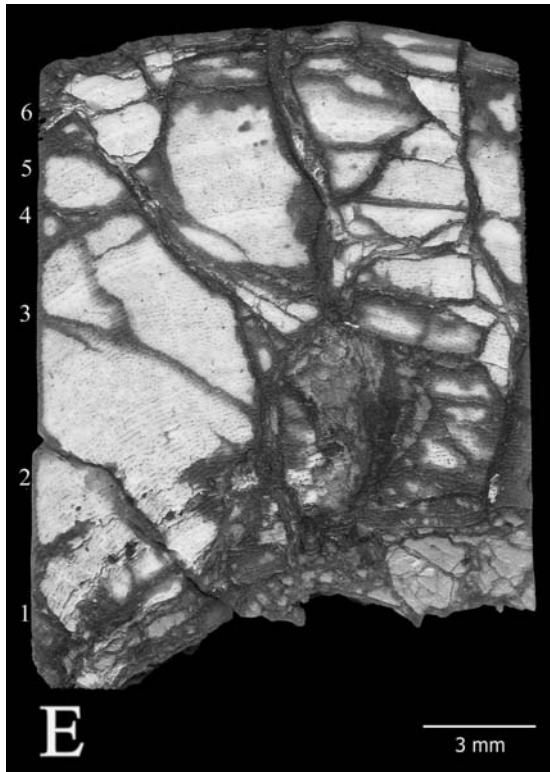
Figure 14: *Selection of polished sections of different kind of bones.* **14A***: Polished section of left femur IFG compactus (74 cm).* *LAG 8 to LAG 12 are not visible under the present magnification.* 14**B***: Polished section of left femur SMNS F 27 (81 cm).* *SU means subordinate cycle.* **14C***: Polished section of left femur IFG (99 cm).* *LAG 5 to LAG 10 are not visible under the present magnification.* **14D***: polished section of right femur NAA F 88-*

B130 (56.5 cm). **14E***: Polished section of left tibia SMNS F 14 A (55.0 cm).* **14F***: polished section of left tibia MSFM-2 (52.0 cm). LAG 6 to LAG 10 are not visible under the present magnification.* **14G***: polished section of vertebra IFG RW 12. Note the thick layer of RFB in the outermost cortex.* **14H***: cross section of the median part of a rib (SMNS F 29). The arrow at the left side marks an area with dense lamellar-zonal bone with several LAGs deposited.* **14I***: polished section of a foot phalange (IFG 8159). No growth cycles are visible under the current magnification.* **Numbers mark visible LAGs.**

7.3.2 Single individuals sampled by several bones

Skeletochronological correlation between different bone types is always an interesting thing due to varying growth rates and varying activities of the medullary cavity in the different kind of bones during ontogeny. An additional source of error is the determination of LAG numbers for the single bones. It thus is not easy to reconstruct the growth history of a single individual on the basis of several bones. The results of such a study, mainly time data given in years, should always be seen as approximation and not as an exact value.

Two individuals from the Trossingen locality were sampled from several bones (table 14). Individual SMNS F 14 is represented by six bones: a femur, a tibia, a fibula, a humerus, a scapula, and a pubis. Individual SMNS F 48 is represented by three bones: a femur, a tibia, and a fibula. Probably a left and a right pubis of find SMNS F 29 B also belong to a single individual, due to their similar size and shape. The bones and their histology have already been considered in previous sections, namely those covering the analysis of the single bones. In the following section, the main focus lies on how the growth record of the single bones fits together to yield the growth record of a single individual.

7.3.2.1 SMNS F 14

On the basis of its isolated position in the quarry (unpublished field notes of SEEMANN, stored in the SMNS) and due to the proportions and form of the bones, find SMNS F 14 belongs to a single individual. The femur length amounts 63.5 cm, which indicates a medium-sized individual in the Trossingen population.

Although only the femur sample shows a clear growth stop in its exterior cortex, as indicated by the beginning of deposition of lamellar-zonal bone, the other sampled long bones of SMNS F 14 also show a clear decrease of vascular density within the laminar fibro-lamellar complex of the outer cortex, but no lamellar-zonal bone was deposited. The scapula shows high vascular density up to the bone surface, and only at the lateral side a slight

decrease in vascular density can be observed. The pubis shows in its exterior cortex that growth had nearly stopped, indicated by nearly avascular bone tissue. All together, the growth record of all bones indicate that this individual had undergone a clear growth decrease, respectively growth stop, and had therefore nearly reached its final size. However, the differences in histology mean that bones of a single individual not only grew at different growth rates but also stopped growing in diameter at a varying time.

Table 14: LAG counts in different bones of the single individuals SMNS F 14, SMNS F 29B, and SMNS F 48.

sample	visible LAGs	resorbed LAGs	total LAGs
SMNS F 14 femur length: 63.5 cm			
femur	7	7-8	14-15
tibia	6	5	11
fibula	6-7	6	12-13
humerus	8-9	11	19-20
scapula	6	8-9	14-15
pubis	9	4	13
SMNS F 48 femur length: 77.5 cm			
femur	5	9	14
tibia	7-8	7	14-15
fibula	7-8	5	12-13
SMNS F 29 corresponding femur length: ca. 65.5 cm			
pubis F29 B (right)	10	3	13
pubis F 29 B (left)	9	2	11

The visible LAG number varies not much in the bones of individual SMNS F 14, being between 6 and 9 LAGs. In addition, the observed growth decrease or stop in the exterior cortex occurs in all sampled bones quite consistently after visible LAG 5. But when the resorbed LAG number is added, differences in the total LAG number between the bones result, due to the various sources of error discussed earlier.

Thus, the total LAG number for this individual lies between 11 and 20. Most frequent are total LAG count of 13 to 15, but at a total LAG number of 11, the tibia shows as well as the humerus, at a total LAG number of 19-20, a great deviation from this average. Growth stop was initiated between total LAG 9 to 13/14. The onset of sexual maturity is possibly recorded by the growth decrease in the pubis after total LAG 9.

To summarize, it is hypothesized that on the basis of the majority of values, this individual grew at high rates up to around its 12th year of age. Afterwards growth started to decrease significantly. The individual stopped growing completely after the 15th year (figure 15).

The maximum possible age for this individual is suggested in the humerus at around 20/21 years. This is in strong contrast to the pubis growth record with the maximum LAG number amounting to only 13. This discrepancy is again the result of an overestimated resorbed LAG number in the long bones. More realistic is the total LAG number of the pubis. Using the resorbed LAG number of the pubis (4 resorbed LAGs) for the other bones the total LAG number ranges only between 10 and 13. Note that than the pubis shows the highest total LAG number. As different growth patterns of each single bone must take into account, it seems unlikely to get the exact same total LAG number for all bones.

7.3.2.2 SMNS F 48

Again on the basis of its isolated position in the quarry (unpublished field notes of SEEMANN, stored in the SMNS) and due to the proportion and form of the bones, find SMNS F 48 belonged to a single individual. The length of the femora is 76.0 cm (right), respectively 77.5 cm (left), representing a fairly large individual.

In the femur, tibia, and fibula of SMNS F 48, growth had continued with laminar fibro-lamellar bone up to death. It thus can be concluded that this individual had not reached its maximum size and would have continued growth. The differences between the visible LAG numbers in the different bones are relatively high. In the femur, there are only 5 visible LAGs, but in the tibia and fibula, 7-8 are visible. However, the total LAG number is less variable and amounts in all three sampled bones to between 13 and 15 LAGs, suggesting an age at death of about 16 years (figure 15). The less variable total LAG count here can possibly be explained by the relatively wide visible growth cycles of this still fast growing individual. Maybe an indication for an relatively younger individual where extrapolation did not result in such an overestimate as in other/older specimens.

7.3.2.3 SMNS F 29

Find SMNS F 29 is composed of mainly left body sides of at least three individuals. Due to the proportion and form, a left and a right pubis are assumed to belong to a single individual. Unfortunately, no other elements of this individual can be identified. The corresponding femur length for the pubes amounts to around 66 cm, indicating a medium-
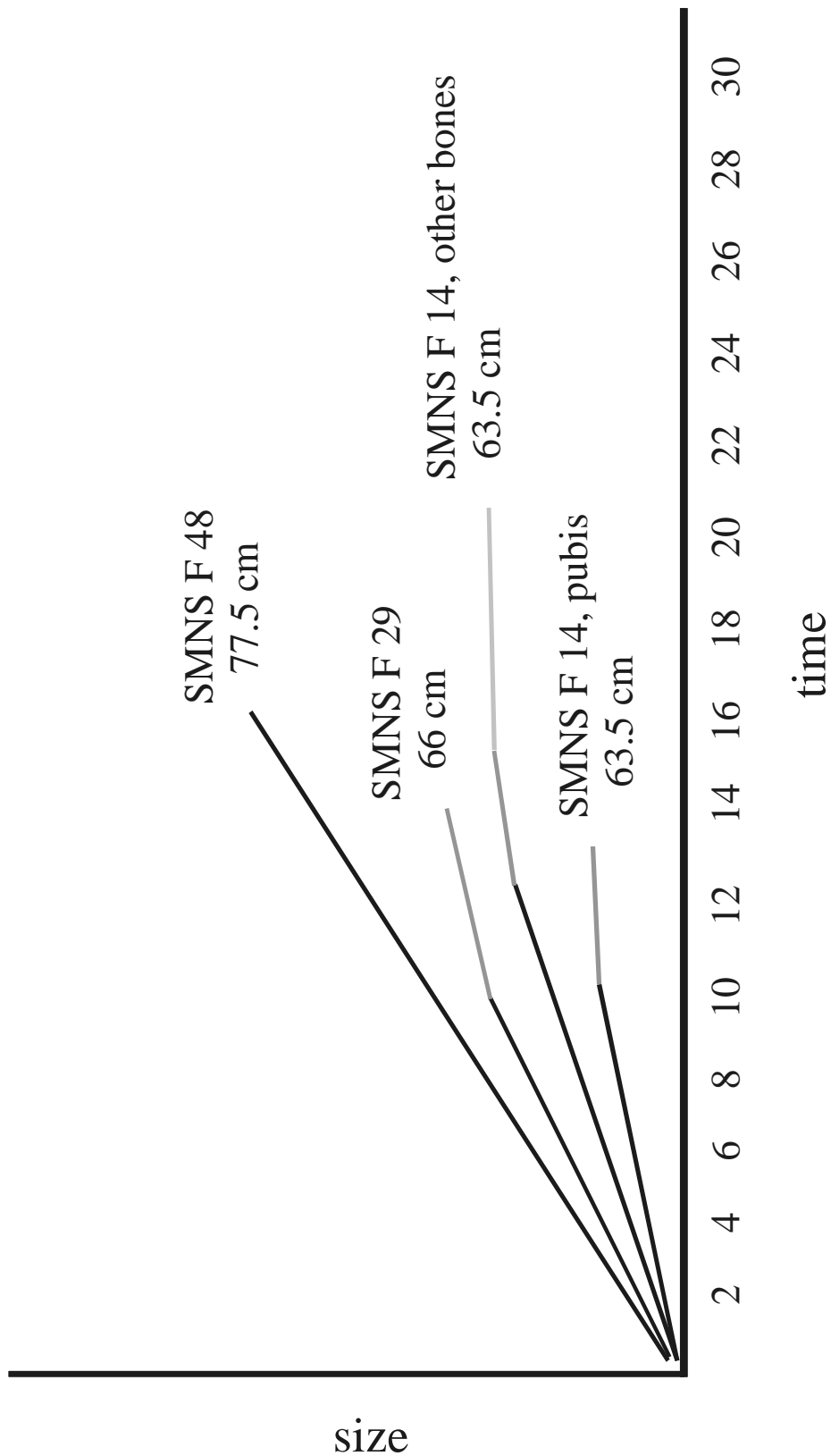
Figure 15: *Average growth curves of individuals SMNS F 14, SMNS F 48, and SMNS F 29.*
Black line represents fast growth with fibro-lamellar bone, gray line represents slowed down
growth, but still with fibro-lamellar bone, bright line represents growth with lamellar zonal bone.
Note the high variability of growth patterns.

sized individual.

In their exterior cortex both pubes show a clear decrease in growth as indicated by closely spaced LAGs in a nearly (SMNS F 29 B, right, 52.5 cm), respectively partially (SMNS F 29B, left, 53.5 cm) avascular bone tissue. Thus it can be concluded that maximum size was nearly reached and growth had nearly stopped in the pubes.

Visible LAG number differs only by one, and growth decreases in both pubes after visible LAG 6 which corresponds to total LAG number of 8 and 9, respectively. This is the most likely time of reaching sexual maturity. Total LAG number differs by two cycles between the left and right pubis, but considering the possible error sources, this is also not very much. Thus, the individual from which these two pubes originated had reached its maximum size of around 6,6 m after 12 to 14 years. Sexual maturity was reached earlier in life, after the 9th or 10th year (figure 15).
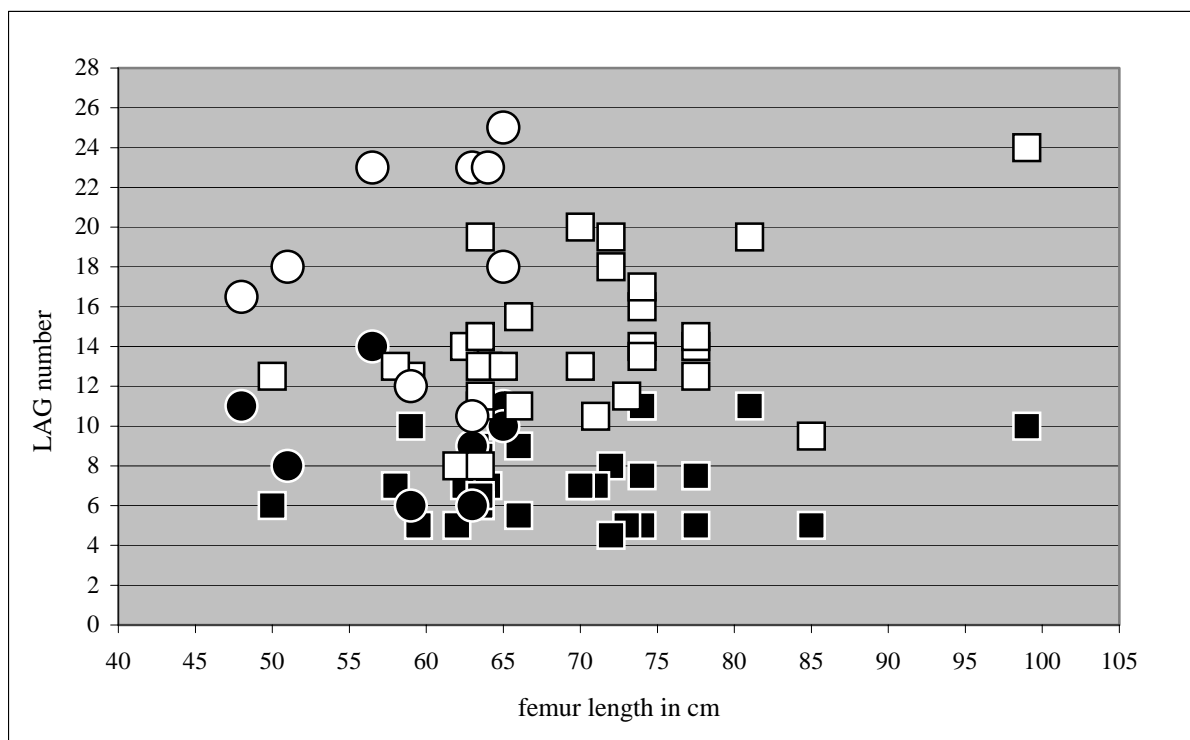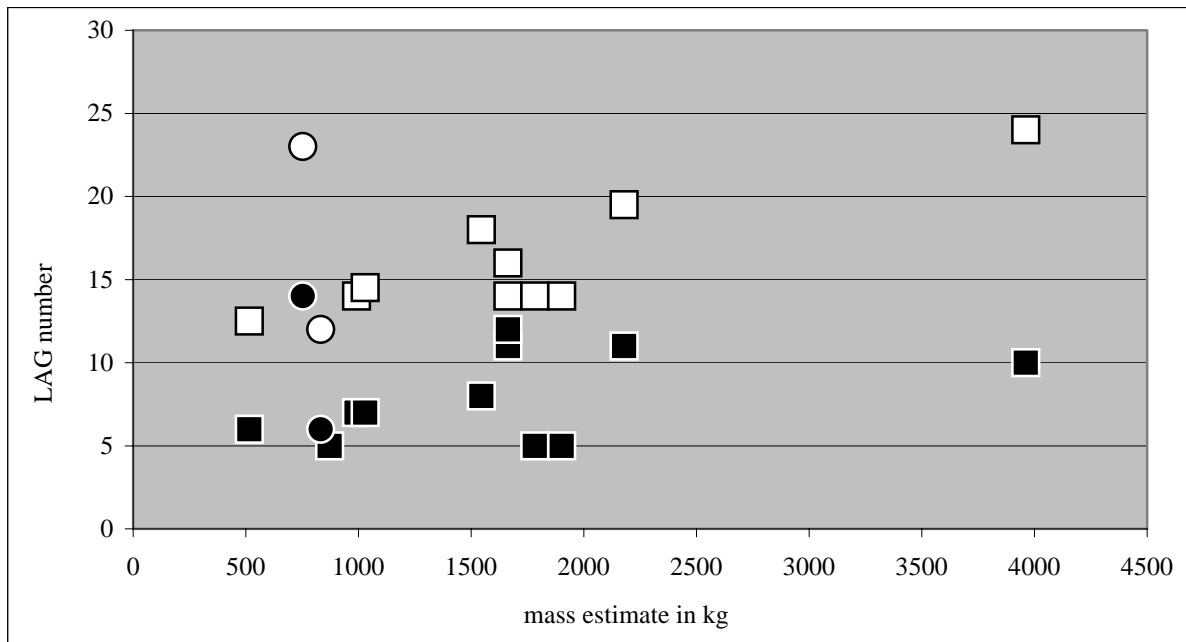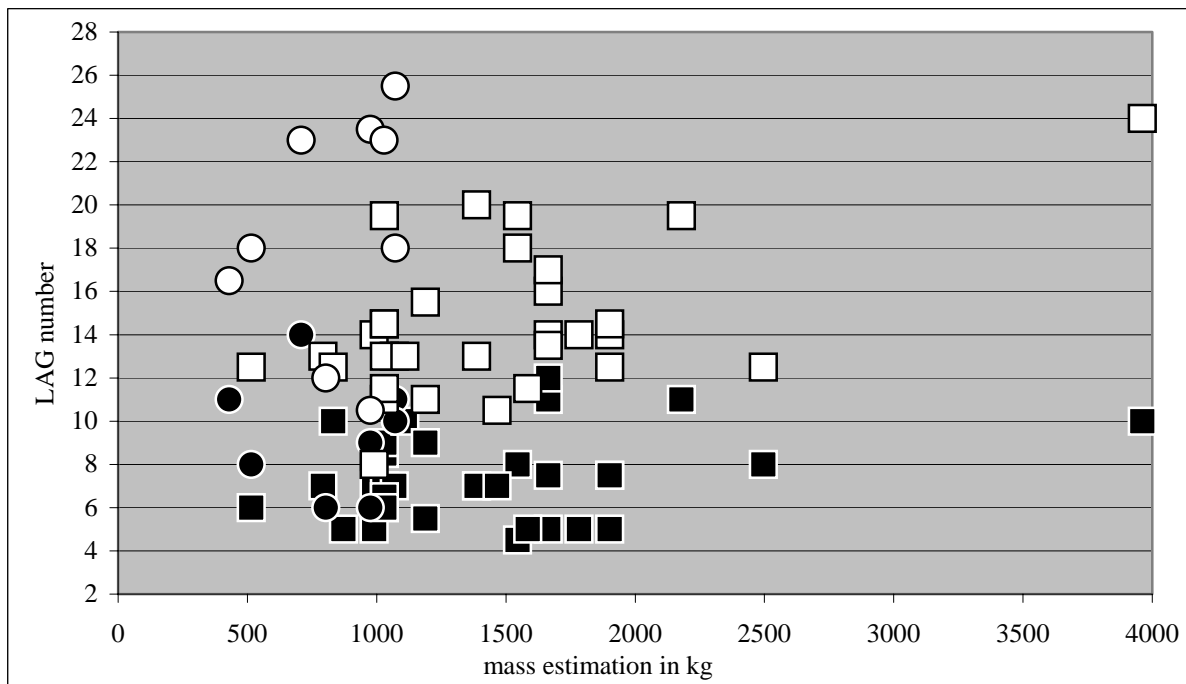

Figure 16: *Femur length plotted against visible and total LAG number. Note that there is no correlation possible between LAG number and size. Black symbols mark the visible LAG number, and white symbols mark the total LAG number. Circles represent Frick specimens, squares the Trossingen specimens. All bones were scaled to their corresponding femur length.*

A

B

Figure 17: *LAG count plotted against mass estimate. 17A: LAG count plotted against mass estimate only for the femora. 17B: LAG count plotted against mass estimate for all sampled bones, scaled to their femur length.* Mass estimates for the specimens is based on the mean value for the largest femur (left, 99 cm, IFG exhibition) of data given by SEEBACHER (2001) and SANDER (1992) (see table 6). Black symbols represent visible LAG number and white symbols total LAG number. Squares mark the Trossingen specimens, and circles mark the Frick specimens. All bones scaled to their femur length.

7.3.3 Results from LAG count

On the basis of the LAG counts some figures were constructed to check several questions. In figure 16 and figure 17 visible and total LAG number are plotted against femur length and mass estimate to see if there is a correlation between LAG number and bone length or body mass. Figure 18 shows the relationship between deposited bone tissue in the exterior cortex (= growth stage) and femur length (= body size). In this figure the main difference to other dinosaurs comes out, that is a very high size range of maximum size.
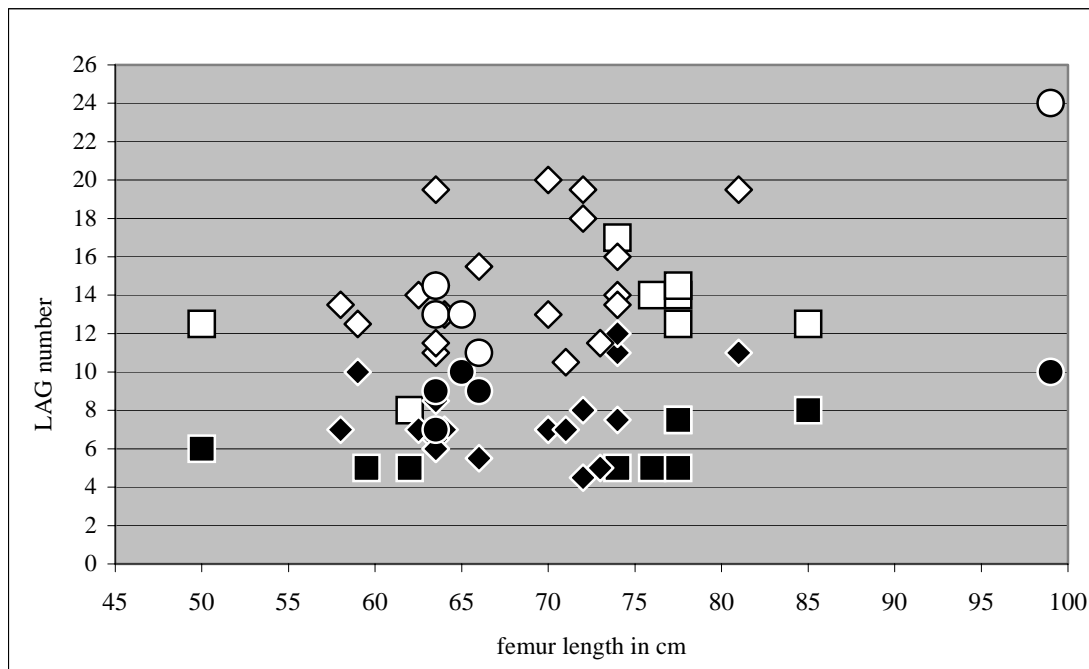
A
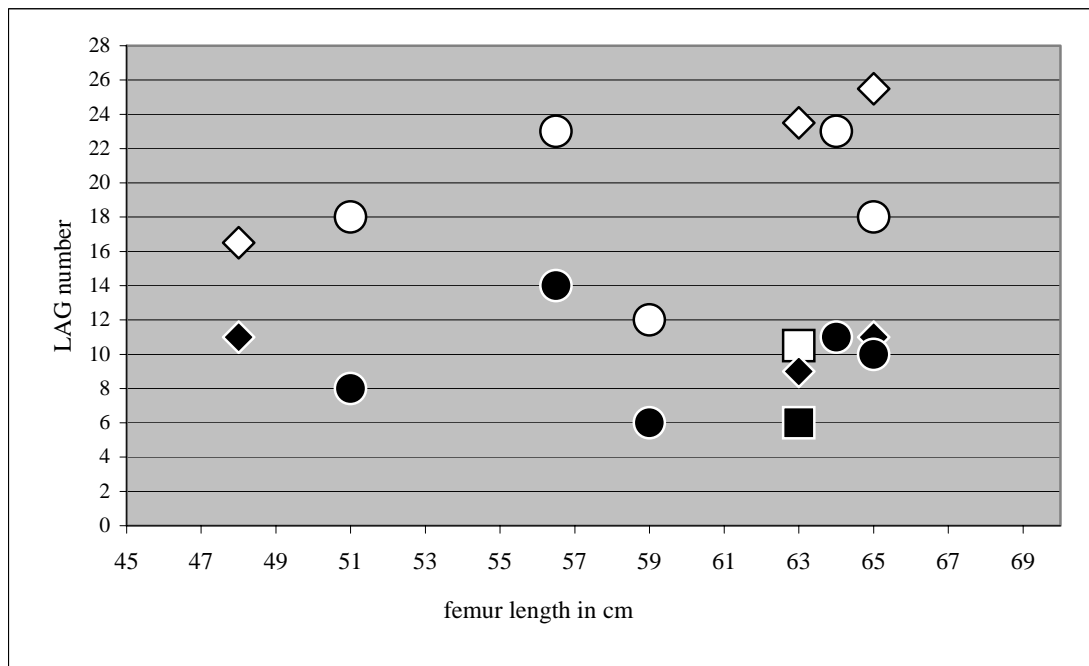
B

Figure 18: *Relationship between growth stage and body size. Bones separated in the categories: „continued growth", slowed down growth", and "stopped growth". Continued growth means that growth had continued with laminar fibro-lamellar bone, without any significant growth decrease. Slowed down of growth means that vascular density becomes very low in the fibro-lamellar complex and bone tissue change was initiated or lamellar-zonal bones, which is relatively high vascularized, is deposited. Stopped growth means that lamellar-zonal bone had been deposited with several closely spaced LAGs in avascular bone tissue in long bones as well as in flat bones .18A: Relationship between growth stage and body size in Trossingen. 18B: Relationship between growth stage and body size in Frick. Black symbols represent the visible LAG number, white symbols represent total LAG numbers. Squares represent continued growth, diamonds slowed down growth, and the circles stopped growth. All bones scaled to femur length. Note that this distribution represents no clear line but a very broad range.*

8. Discussion
8.1 Qualitative growth record
8.1.1 Varying growth in different bone types during ontogeny

Studying different kind of bones of the skeleton of *Plateosaurus engelhardti* confirms that every bone has its own ontogenetic history and therefore its own growth record, as several authors have concluded before (CASTANET & SMIRINA 1990, RICQLÈS 1983, REID 1990, CHINSAMY 1993). In *Plateosaurus* bones, this is especially evident in the different growth speeds of long and flat bones and additionally in the histological differences between pubis and scapula. Although they both belong to the category flat bone (FRANCILLON-VIEILLOT et al. 1990), they show different bone tissues and growth rates.

Thus, even bones from single individuals (SMNS F 14, SMNS F 48) show different counts of lines of arrested growth (table 14, figure 15). Extrapolation of the resorbed LAGs also did not give a uniform result for these individuals, but the differences are not quite as great. They can mainly be attributed to a general error of the extrapolation method.

8.1.2 Differences between Frick and Trossingen locality

As mentioned before, in contrast to Trossingen, the locality of Frick contains only small to small-medium-sized individuals (figure 1), all sampled bones from Frick representing a size range of between 4.8 m and 6.5 m body length. Most samples had decreased or completely stopped growth, only one shows continued growth at a size of 6.30 m (figure 18).

Thus, the generally smaller size of Frick bones does not represent younger individuals but the Frick population consists in general of smaller individuals than that in Trossingen. The maximum size may have been around 6.5 m in Frick, with some individuals having stopped growth earlier. Maximum size in Trossingen is around 10 m, but most individuals stay clearly smaller, somewhat around 6.0 m to 7.5 m

Two hypotheses may explain the lack of larger individuals in Frick: Either large specimens were less common in Frick than in Trossingen, and simply have not been found yet or the *Plateosaurus* population from Frick consists beside a basically similar growth strategy of generally smaller individuals than that from Trossingen. If the population consists generally of smaller individuals, again two explanations are possible. One is a biological cause, like a different habitat, or the Frick specimens belonged to a different species then those from Trossingen.

8.1.3 General patterns and metabolism

The analysis of the histological data results in a contradictory picture of the life history of *Plateosaurus engelhardti*. On one hand, *Plateosaurus engelhardti* grew at least as adult with the laminar fibro-lamellar complex, representing fast growth similar to that of birds and mammals, and also to extinct sauropods. But in contrast to sauropods, birds, and mammals, periods of fast growth were regularly interrupted in *Plateosaurus engelhardti* throughout the whole recorded life time by cyclical growth marks, expressed by the regular deposition of LAGs. This cyclical interruption of growth, together with a lower vascular density and a smaller distance between the single laminae in the bone tissue compared to birds, mammals, and sauropods indicates a generally lower growth rate than sauropods and mammals show, but a higher one in comparison to extant wild reptiles. Like in sauropods, birds, and mammals, the deposition of lamellar-zonal bone and closely spaced LAGs in the outermost cortex shows that *Plateosaurus engelhardti* had determinate growth (SANDER 2000). Indeed, growth stop occurred at a variable body size and age.

Nevertheless, *Plateosaurus engelhardti* must have had a relative high metabolic rate to maintain these periods of fast growth during three-fourth of its ontogeny. Another possibility is that these periods of fast growth were supported by periods of optimal environmental conditions in the past. The generally irregular distances between the growth cycles, as well as small and/or poorly vascularized cycles in the inner/younger cortex and large and/or highly vascularized cycles in the outer cortex lead to the conclusion that *Plateosaurus engelhardti* growth was strongly influenced by environmental factors, similar to extant reptiles. Such

environmental factors concern mainly climate and food availability and quality. However, illness, and starvation or poor quality of food could also affect growth of endotherms.

8.1.4 Sexual dimorphism

CARPENTER (1999) describes use and function of possible sexual display organs and dinosaur behavior during courtship. Additionally he gave attention to the possibility that many display structures, like traces of dinosaur skin, are only rarely fossilized (CARPENTER 1999). He also warned against an over-rating of display organs like crests and frills, and preferred the method of sexing dinosaurs on the basis of the robustness of the skeleton (CARPENTER 1999). Based on many examples in extant tetrapods, CARPENTER (1999) believes that in most dinosaurs the more robust form represents the female.

Looking at extant reptiles, no general principle of which sex is the larger one, can be established. For example, in crocodiles the male is always the larger form, in contrast to turtles and tortoises where in most taxa (not in all !) females grow generally larger than males. The sexes of the largest extant lizard, the Komodo monitor (*V. komodoensis*) are generally of around the same size, but most females stay smaller than males (AUFFENBERG 1980). Similar contradictionary patterns are seen in extant birds. While in most raptorial birds the female is the larger form, males and females of most songbirds are of around the same size. Sex differences are expressed here predominately in color. In many taxa of large mammals, males are larger than females, but in smaller mammals, again no size difference occurs.

Sexual dimorphism in dinosaurs documented only by size differences is rare until yet. The before mentioned histological study of *Syntarsus rhodiensis* (CHINSAMY 1990) leads to the conclusion that the robust specimen, which shows erosional cavities possibly formed during formation of eggshell, represents the female (CARPENTER 1999). Another example is the increased angle between the ischium and tail (possibly for a better accommodation of the eggs through the cloaca, CARPENTER 1999) in the robust form of *Tyrannosaurus rex*.

As mentioned before, prosauropods lacked clear display structures. Thus, a sexual dimorphism expressed in body size and robustness seems possible and reasonably for prosauropods and has already been suggested by many authors (WEISHAMPEL & CHAPMAN 1990, GOW et al. 1990, GALTON 1997, 2000, BENTON et al. (2000), but unequivocal documentation has remained exclusive. GALTON (2001) had suggested the less numerous and more robust and larger morph being the male in Trossingen.

Sexual dimorphism expressed in variable body size and robustness in females and males is expected to be represented in the bone microstructure (e.g. deposition of different

bone tissues, different growth rates expressed by the degree of vascularization), because it represents different growth strategies/patterns of the sexes. This can be realized in recent reptiles in two ways (ANDREWS 1976): One possibility is that the juveniles of both sexes grow at similar rates until the individual of the smaller sex reach its final size. Individuals of the larger sex continue to increase in size. The second possibility is that juveniles of both sexes start to grow with different growth rates. The larger sex grows faster, and sexual maturity is reached at nearly the same age but at different sizes.

SANDER (1999) on the basis of his bone-histological research of the Tendaguru sauropods, discussed sexual morphs in *Barosaurus* bones. SANDER (1999: 109) interpreted the fast growing morph (Type A) as the male and the slower growing Type B as the female. However he could also not exclude the two types representing different taxa (SANDER 2000, REMES 2004).

On the basis of the current histological study, no evidence in bone microstructure could be found to document a sexual dimorphism in the bones of *Plateosaurus engelhardti*. The qualitative and quantitative growth record indicates that growth had stopped at strongly variable final sizes, ranging from around 6.5 m to nearly 10 m (figure 18). A division into two groups that may represent the two sexes is not possible on the basis of these data. Excluding the presence of different taxa, the best explanation remains a very strong intraspecific variability.

These histologic results suggest that the morphological differences which had lead to the division into robust and gracile bones or morph before seems to represent only this high variability in final body size. On the other hand, figure 16, 17, and 18 show that there are some individuals of *Plateosaurus* which grew in shorter times than others to higher body sizes.

8.1.5 Sexual maturity

Of considerable interest for *Plateosaurus engelhardti* life history is the onset of sexual maturity. Unfortunately, this moment is difficult to determine in *Plateosaurus engelhardti* by bone histology. At least two different possible times can be considered. The first is the bone tissue change from laminar fibro-lamellar bone to lamellar-zonal bone. According to RICQLES (1976, 1980) avascular lamellar bone is deposited in extant mammals after reaching sexual maturity. Also, growth of reptiles slows clearly after sexual maturity is reached (ANDREWS 1976). While many authors prefer this bone tissue change (beside its meaning for the attainment of maximum size) also in dinosaurs as being the onset of sexual maturity

(VARRICCHIO 1993, CHINSAMY 1994, CHINSAMY & DODSON 1995, REID 1997, CURRY 1998, HORNER et al. 2001) others (SANDER 1999, 2000; HORNER et al. 2000) concluded that sexual maturity was reached well before maximum size, and thus, before the change from fibro-lamellar tissue to lamellar-zonal tissue.

But this would mean for *Plateosaurus engelhardti* that sexual maturity was reached relatively late in ontogeny. Based on the data from the long bones, this would be not before the 16th year of life. However, if this were the case, sexual maturity was either reached at the same age nor at a uniform body size. A similar pattern can be observed in extant reptiles: Size and age of adult reptiles need not to be correlated, because individual final size varies within a broad range and also size at sexual maturity varies considerably (ANDREWS 1976).

Nevertheless, the decrease in growth rate and the subsequent growth stop indicated by the change in bone tissue in all cases marks the attainment of full body size and is therefore an important landmark in the growth pattern of *P. engelhardti*.

The second possibility for the onset of sexual maturity in *P. engelhardti* is that it occurs earlier in ontogeny, and that this event is possibly only recorded in the histology of the pubis but not in the long bones. In these, the histological evidence was destroyed by the enlargement of their active and large medullary cavities. According to the growth record in pubis, sexual maturity would have been attained around the 9th year of life and at a body size of around 6 m. This seems to be a more reasonable age (and size) for the onset of sexual maturity in *Plateosaurus engelhardti*. The attainment of sexual maturity before final size is reached is also typical for most reptiles.

8.2 Quantitative growth record: Skeletochronology

This section serves to briefly summarize the quantitative aspects of *P. engelhardti* life history, keeping in mind the approximate nature of the values.

The youngest individuals have a total LAG number of 8 (left scapula SMNS F 29, 42 cm; humerus IFG 11921, unknown length), and at least the scapula belonged to an individual of around 6.2 m body size. The smallest sampled specimen had stopped growth and shows a total LAG number of 16/17. It was only around 4.8 m long (left scapula MSFM 36.5 cm). On the basis of the largest femur (left, 99.0 cm, IFG exhibition), and the tibia sample NAA A9 (53 cm), a maximum LAG number of 25, respectively 26/27 years is suggested for *Plateosaurus engelhardti*. Because these individuals, like the others at Trossingen and Frick died from an accident (miring; SANDER 1992) and not of old age, the maximum age of *Plateosaurus engelhardti* can be assumed to be higher. In contrast to the femur (IFG 99 cm),

which represents the maximum documented size for *P. engelhardti*, the tibia belongs to a medium-sized individual of only around 6.5 m body length. Most individuals grew up to their 16 year of life with laminar fibro-lamellar bone, than growth started to decrease and finally stopped. Most individuals had stopped growth completely somewhat after their 20th year of life. The most likely onset of sexual maturity, as recorded in the pubis, is after 9 years, after roughly one third of life had passed.

It is striking that the longest bones do not necessarily have the highest LAG numbers (figure 16-18). In fact, no correlation between bone length (= body size) and LAG number (= age) is apparent in *Plateosaurus engelhardti* bones (table 7-12; figure 16, 17).

A look at figure 18 shows that there is no correlation between bone length and growth cessation/growth stop, either. But again it is documented that some bones, and thus individuals grew to considerably larger size than others. The main conclusion must be again that growth stopped in *Plateosaurus engelhardti* at variable final body sizes.

There are a number of possible sources of error that could explain such a high variability: 1. An extreme methodical error in recording (but there is no evidence for this); 2. LAGs are, in spite of experiments with recent tetrapods (e.g. tetracycline, specimen sampled of known age; for references see CASTANET & SMIRINA 1990, and CASTANET et al. 1993, GROSSE 1999), not annual, but random; 3. A sexual dimorphism that is hidden in the apparent great variability . Because a sexual dimorphism cannot be worked out on the basis of the current bone histological data, and because the annual deposition of growth marks is main premise of the current study, the best explanation remains a very high intraspecific variability in *Plateosaurus engelhardti*.

9. Comparison of growth of *Plateosaurus engelhardti* with that of some other extinct and extant tetrapods

Many studies about dinosaur bone histology and some about skeletochronology were published in the last decade. In table 15, the results of a selection of these and other studies are summarized and will be compared and discussed in the following with the bone histological data for *Plateosaurus engelhardti*. The main focus is here on the similarities and differences concerning general growth pattern and life history. The tetrapods compared are discussed in order of phylogenetic proximity to *Plateosaurus*.

9.1 Other prosauropods

Only CHINSAMY (1993) did a detailed skeletochronology study of a prosauropod, using femora of *Massospondylus carinatus*. This study therefore needs to be compared in detail with the results of the current study of *Plateosaurus engelhardti* bone histology. CHINSAMY (1993) described a similar highly vascularized fibro-lamellar bone as in *Plateosaurus engelhardti*. The distribution of secondary osteons and cancellous bone is also similar in both prosauropods. Both share a stratification of the cortex through growth marks (LAGs), reflecting periods of fast and slow growth.

In small and therefore young *M. carinatus* specimens, the same bone tissue occurs as in adults, but growth rates decrease generally during ontogeny. CHINSAMY (1993) calculated that in the first 5 years, 50% of femoral growth was attained, with growth slowing down afterwards. The mathematical formula of CHINSAMY (1993), age = 0,05 (femur length)$^{1.52}$, indicates that in *M. carinatus*, in contrast to *Plateosaurus engelhardti*, size and age were much more closely correlated and that reliable age estimates on the basis of bone length are possible. Thus, CHINSAMY (1993) was able to construct a S-shaped growth curve for *M. carinatus* on the basis of her bone histological data. *M. carinatus* apparently did not have such a high variability in adult size as *P. engelhardti*, and this implies a very different growth pattern and life history of *M. carinatus*.

The life expectancy in *M. carinatus* is lower (max. 15 years documented) than in *Plateosaurus engelhardti* (max 26/27 years documented). However, this could be the result of differences in the extrapolation methods used. The method used by CHINSAMY (1993) is likely more accurate because resorbed growth marks were estimated on the basis of juvenile specimen. This was not possible in *P. engelhardti*.

As opposed to the general similarity in bone tissue, vascular system, cyclical growth, and irregular cycle distances (CHINSAMY 1993: 325: fig. 6), the two prosauropods differ in another important point. This is the lack of closely spaced LAGs in the outer cortex of *M. carinatus*, even in the largest individuals. This led CHINSAMY (1993) to conclude that *M. carinatus* had an indeterminate growth as supposedly seen in extant ectotherms. In *Plateosaurus engelhardti*, on the other hand, growth was clearly determinate and stopped in the last third of life. [The concept of indeterminate growth requires some comment: Although none of modern groups of the reptiles grow throughout their whole life, it was thought for a long time that reptiles had an indeterminate growth. Growth continues in some reptiles for quite a long time, after sexual maturity is reached, as opposed to birds and mammals.

Additionally, the variability in final size is much greater than in birds and mammals. The idea of an indeterminate growth in reptiles has its origin in these facts.]

Possible reasons for these differences are: 1. CHINSAMY did not sample adult individuals of *M. carinatus* which would have stopped growth. 2. *M. carinatus* and *P. engelhardti* are not as closely related as generally believed. 3. They are closely related and the observed differences are real.

Comparing *P. engelhardti* growth with that of *Thecodontosaurus antiquus* (CHERRY 2002) shows that they agree in bone tissue and vascular system, too but that LAGs are missing in the limb bones of *T. antiquus*. CHERRY (2002) also did not found any indication of determinate growth in *T. antiquus*. However, differences may well be due to the juvenile status of all sampled bones. CHERRY (2002) notes that there are much larger individuals of *Thecodontosaurus* than those sampled by her.

A cursory look at a fractured *Sellosaurus gracilis* pubis in the SMNS collection (SMNS 5715) shows a nearly identical bone tissue to that observed in *P. engelhardti* pubes.

9.2 Sauropods

The first who described sauropod bone tissue with LAGs was RICQLES (1983) studying the humerus of a half grown *Bothriospondylus (*now *Lapparentosaurus)*. Bone microstructure was fibro-lamellar bone with typical plexiform to reticular or, in restricted areas only, parallel longitudinal primary osteons. RICQLES (1983) counted LAGs in this sample and concluded that this individual had needed at least 16 and at most 26 years to reach slightly less than half maximum size. He suggested an age of roughly 43 years for an individual to reach 2/3 of maximum adult size, agreeing well with CASE's (1978) estimates of 40 years for the onset of sexual maturity of another sauropod, *Hypselosaurus*. This is a very great age for sauropods, and a very late onset of reproduction and seem unrealistic in comparison with modern tetrapods (DUNHAM et al. 1989). The unrealistic character also appears in the light of newer studies of sauropods (see below, table 15) which indicates substantially lower ages for reaching sexual maturity and maximum size in sauropods. Thus, e. g *Janenschia* reached sexual maturity at around 11 years (SANDER 2000). *Apatosaurus* needed around 8-10 years for reaching sub-adult size (CURRY 1998). RIMBLOT-BALY (1995) concluded that *Lapparentosaurus* needed two decades to reach "adult conditions", but they did not specify the meaning of that term.

Modern bone histological studies of sauropods document a generally uniform bone microstructure which is already observable in the earliest known sauropod, *Isanosaurus*

(SANDER et al. in press). But different interpretation of this microstructure still leads to different results, depending on the assumptions of the authors. Thus, e. g. CURRY (1998) and SANDER (1999, 2000) suggested a determinate growth on the basis of the deposition of lamellar-zonal bone in the exterior cortex, whereas RIMBLOT-BALY et al (1995) suggested an indefinite growth for *Lapparentosaurus*, although they noted a similar "lamellar, accretionary tissue at the cortical periphery in their largest samples identical to that observed in *Apatosaurus* bone" (CURRY 1998: 662). CURRY (1998) interpreted this as indication of determinate growth for *Lapparentosaurus*, too.

Cyclical growth patterns, mainly related to differences in the vascular system, are observable in many sauropod long bones. On the basis of these and other structural characteristics (SANDER 2000), ontogenetic stages are documented. True LAGs occur mainly in the exterior cortex when lamellar-zonal bone was deposited (except in *Janenschia* and some *Barosaurus* specimen in which LAGs also appear in FBL). Thus, as a general trend, it is clear that sauropods started with very rapid continuously growth, followed by a gradual decline into adulthood.

Bone tissue and vascular system are generally similar in *Plateosaurus* and sauropods (table 15), but there are major differences in bone microstructure in the amount of fibro-lamellar bone in the cortex, cyclical interruptions of growth by clear growth marks/LAGs, laminae distances, and vascular density. Laminae distances (based only on estimation, not quantified) and vascular density are in sauropods considerably greater than in prosauropods. All three differences indicate fundamentally higher growth rates in sauropods than in prosauropods.

Data from skeletochronology agree relatively well with this. Like some sauropods, *Plateosaurus* possibly shows an early onset of sexual maturity at around 9 years (table 12). A size of around 5 m may have been reached within 8 years. In that this is about half maximum size, this is also similar to data for sauropods (Of course, sauropods reached a much larger size in the same time). Growth is generally determinate in both and final size was reached in *Plateosaurus* also within similar time spans as sauropods i.e. in the 2nd and 3rd decade of life. Both seem to share the pattern of growth continuing after sexual maturity.

Thus, it can be concluded that *Plateosaurus* and sauropods show generally a similar life history, but sauropods reached in the same time interval quite a larger body sizes due to their higher growth rates and their strategy of continuously faster and uninterrupted growth. An important difference between both life history is the very high variability in adult size of

Plateosaurus, indicating a more "reptilian" growth pattern and life history, whereas most sauropods show lower or no variability in adult size range.

Table 15: *Bone histological studies in some dinosaurs, and other extant and extinct tetrapods.* *FBL = fibro-lamellar bone tissue, LZ = lamellar-zonal bone; SM = sexual maturity, MS = maximum size, bl = body length, bm= body mass.*

taxon	sampled bones	bone tissue	cyclical growth	remarks	life history data	authors
DINOSAURS						
prosauropod *Plateosaurus engelhardti*	long bones, vertebrae, ribs, phalanx, pubes, scapulae	laminar FBL, LZ	stratification of cortex by annual growth marks (zone-annulus-LAG)	only adult bones were sampled; high variation in adult body size; no correlation between age and size possible	individuals of 5 m are at least 8 years old, in most individuals growth continued with FBL up to 16 years, then growth slowed down and growth stopped around 20 years, than deposition of LZ; SM is reached at around 9-10 years, maximum documented age around 26/27, maybe higher; determinate growth.	RICQLES 1968 REID 1990 KLEIN & SANDER current study
prosauropod *Massospondylus carinatus*	growth series of femora	laminar FBL	stratification of cortex by annual growth marks (zone-annulus-LAG)	constructed a S-shaped growth curve	after 5 years half of MS was reached, growth slows down afterwards, but was indeterminate, maximum documented age was 15 years	CHINSAMY 1993a
prosauropod *Thecodontosaurus antiquus*	femora, tibiae, humeri, phalanx, rib	FBL	LAGs occur only in the rib sample	maybe only juvenile bones sampled	relatively high growth rate	CHERRY 2002
sauropod *Isanosaurus*	humerus	FBL	no growth marks	increase in growth rate must have been a considerable increase in metabolic rate, possible made by a bird-like lung	very fast growth throughout whole ontogeny	SANDER et al. 2004
sauropod *Apatosaurus*	scapulae, radii, ulnae, femur	laminar to plexiform FBL; longitudinally vascularized LZ	no LAGs documented in the FBL; cyclicity in vascularity in scapulae samples; LAGs in the LZ	radii & ulnae show consistent bone depositional rates throughout ontogeny; need 8-10 years for reaching sub-adult size	three ontogenetic phases: Growth stage A: laminar to sub-plexiform FBL up to 73% of MS, no LAGs or annuli Growth stage B: primarily parallel-fibered bone, sparse longitudinal vascularization, up to 91 % of MS, annuli, initial LAGs Growth stage C: primarily avascular and/or longitudinally vascularized lamellar bone;	CURRY 1998 SANDER & TÜCKMANTEL 2003

taxon	sampled bones	bone tissue	cyclical growth	remarks	life history data	authors
					determinate growth	
sauropod *Barosaurus* (type A & B)	humeri, femora, tibia, fibula	plexiform, reticulate, and laminar FBL	type B shows irregularly spaced LAGs throughout the cortex	ontogenetic change in histology; dense Haversian bone in Type B	SM at around 70% of MS; determinate growth; division of bones in two types (A, B), maybe related to a sexual dimorphism or to the occurrence of different taxa	SANDER 1999, 2000 REMES 2004
sauropod *Dicraeosaurus*	humeri, femora	laminar FBL; LZ	LAGs mainly in the LZ; polish lines	no ontogenetic change in histology, but only sub-adult and adult bones sampled (sample contains little size variation)	SM at around 80% of MS; determinate growth	SANDER 1999, 2000
sauropod *Brachiosaurus*	humeri, femora, ulna, tibia	laminar FBL; LZ	LAGs occurred mainly in the exterior cortex and within the LZ; polish lines	secondary osteons were scattered through the cortex; ontogenetic change in histology	SM at around 40 % of MS; determinate growth	SANDER 1999, 2000
sauropod *Lapparentosaurus madagascariensis*	growth series of humeri (30 to 155 cm)	plexiform to reticular FBL; in restricted areas parallel longitudinal primary osteons;	LAGs;	high remodeling; clear bone tissue change during ontogeny	need 43 years to reach 2/3 of MS	RICQLES 1983
sauropod *Lapparentosaurus madagascariensis*	growth series of humeri (30 to 155 cm)	laminar FBL	during later ontogeny a cyclical pattern of deposition appeared suggesting yearly cycles of growth, but no real LAGs		adult conditions in about two decades, indefinite growth	RIMBLOT-BALY et al. (1995)
sauropod *Janenschia*	humerus, femur	laminar FBL ; LZ	LAGs in the outer FBL cortex; LAGs within the LZ; polish lines		SM at around 11 years, MS was reached around 26 years, and this special specimen died at 38 years; determinate growth	SANDER 1999, 2000
taxon	**sampled bones**	**bone tissue**	**cyclical growth**	**remarks**	**life history data**	**authors**
theropod *Herrarosaurus*	femur	azonal FBL	no growth marks			STARCK & CHINSAMY 2002
theropod *Syntarsus rhodiensis*	femora	FBL	LAGs and annuli		MS reached in 7 years; determinate growth	CHINSAMY 1993B
theropod *Troodon formosus*	metatarsalia, tibiae	laminar to sub-plexiform FBL; moderate and avascular LZ	LAGs	three ontogenetic stages; after *Troodon* had reached 50 kg no more significant growth happened	adult size was possibly reached in 3-5 years, SM and MS were reached when LZ appears	VARRICCHIO 1993
ornithopod *Dryosaurus* (medium-sized; bm = 70 kg)	femora	FBL	growth without any interruptions, no LAGs		indeterminate growth	CHINSAMY 1994
ceratopsian *Psittacosaurus mongoliensis*	growth series of long bones	FBL complex	annual growth lines	ontogenetic changes documented in bone histology; *P.* had an S-shaped growth curve; max. growth was faster than in	in the first few years less increase in body mass, with 5 years body mass increase and rapid growth starts maybe up to the 8-9 years, then	ERICKSON & TUMANOVA 2000

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taxon	sampled bones	bone tissue	cyclical growth	remarks	life history data	authors
				extant reptiles and marsupials, but slower than in most avian and eutherian taxa	plateau of somatic growth is observable	
hadrosaurid *Maiasaurus peeblesorum* (MS = 7-9m)	vertebrae, ribs, limb girdles, long bones	FBL LZ in exterior cortex of some specimen	by the sub-adult stage, LAGs appeared regularly	six different ontogenetic stages were documented on the basis of relative bone size but also by histological changes	late juvenile stage (3,5 m) were reached in 1-2 years; maturity was reached at about 7 years and 7 m; adult size was reached in 6-8 years; determinate growth	HORNER et al. 2000 ; PADIAN et al 2001
taxon	**sampled bones**	**bone tissue**	**cyclical growth**	**remarks**	**life history data**	**authors**
REPTILES						
testudines *Caretta caretta*	humeri	LZ	annual deposition of zones and LAGs	captive rearing gives unnatural results, because the individuals grow faster ; secondary osteons occur	SM at 13-15 years; statistically, nesting females are of around 900 mm	ZUG et al. 1986
lizard *Megalania prisca* (bl = 4.5 m; bm = 2200 kg))	dermal bones	zonal bone	annual growth lines	gigantic size due to sustaining juvenile growth rates for a larger period of time and delaying onset of somatic adulthood		ERICKSON et al. 2003, AUFFENBERG 1980
lizard *Varanus komodiensis* (bl = 3 m, bm = 50 kg)	osteoderms, vertebrae	LZ	LAGs	high remodeling disturbs growth record, number of LAGs found in osteoderms agrees with that of LAG number found in vertebrae of the same individual;	males grew at faster rates and become larger than females; both sexes reach SM at around 150 cm and of an average of around 5 years; longevity over 26 years, some authors estimates ages of 50 years	AUFFENBERG 1980
crocodile *Deinosuchus riograndensis* (bl: 8-10, 17 m; bm: 2500-5000 kg)	dorsal osteoderms	LZ	annual growth rings	gigantism by prolonging ontogeny	needs around 35 years for adult size; maximum documented age about 50 years	ERICKSON & BROSCHU 1999
crocodile *Crocodylus niloticus* (bl = max. 5 m; bm = max. 1000 kg)	osteoderms	LZ	LAGs	SM depends strongly on age and size; males generally grow faster and get larger than females	SM between 12-15 years at a size of 2-3 m and a weight of 70-100kg; longevity at around 25, maybe up to 50 years	POOLEY & GANS 1976 CHINSAMY 1994
taxon	**sampled bones**	**bone tissue**	**cyclical growth**	**remarks**	**life history data**	**authors**
BIRDS AND MAMMALS						
extant birds		highly vascularized FBL; in the exterior cortex of adults of some species narrow layer of lamellar bone	rapid growth without zonation; in the outermost cortex, where growth slows LAGs can occur in the long bones of some extant birds	growth slowed down clearly after onset of SM; extant birds reach maturity too rapidly to lay down growth lines	grow within short periods to adult size; SM is closely followed by MS	CHINSAMY & ELZANOWSKI 2001; PADIAN et al 2001
extant mammals		FBL		fast growth up to MS, SM is closely followed by MS		

9.3 Other dinosaurs

As table 15 shows, already the earliest theropods, *Herrerasaurus* and *Syntarsus*, grew very fast with fibro-lamellar bone tissue. But while *Herrerasaurus* grew uninterrupted to adulthood, in the cortex of *Syntarsus,* LAGs and annuli appeared regularly, indicating cyclical interruptions of growth. Growth in *Syntarsus* was clearly determinate. Additionally to cyclical and determinate growth, *Troodon*, *Psittacosaurus*, and *Maiasaurus* show different growth stages, and onset of sexual maturity is in all closely followed by attainment of maximum size. Only *Dryosaurus* has had a different pattern, no growth marks appeared in its cortex, and growth seems to be indeterminate (but maybe individuals sampled were not old enough ?).

Thus, bone tissue in dinosaurs differs mainly in the occurrence or absence of growth marks within the fibro-lamellar bone and the degree of vascularization. In most dinosaurs LAGs are present within lamellar-zonal bone, deposited in the outermost cortex and clearly indicating a determinate growth. In some other dinosaurs (e. g. *Dryosaurus*) this cessation of growth is still lacking. Growth marks deposited within the fibro-lamellar bone tissue, indicating a clearly cyclical growth during main or whole ontogeny appears also regularly in dinosaurs.

Juveniles show the highest growth rates in all dinosaurs but with increasing age growth rates slowed down. Nevertheless dinosaurs grew to their adult size relatively quickly, much as large birds and mammals do today.

Thus, growth strategy and growth pattern of *Plateosaurus* fit well into the picture of dinosaurian growth strategies and patterns. It shows that *Plateosaurus* as a relatively basal dinosaur, although cyclical interrupted, had grown with fibro-lamellar bone and shows, in contrast to reptiles, relatively high growth rates. The onset of sexual maturity is assumed as relatively early in ontogeny, at somewhere between half and 2/3 of maximum size. Growth continued relatively fast up to adult size, then plateaued, and was clearly determinate, also like in most studied dinosaurs. This is the general pattern seen in all dinosaurs, only growth rates varies, following the rule the larger the dinosaur had become the faster growth was. There is only one important difference: Though the high variability in final size in *Plateosaurus* is not known from any other studied dinosaur.

9.4 Reptiles

Most reptiles grow with lamellar-zonal bone with primary longitudinal canals. Bone tissue becomes avascular in adulthood. Only monitors show an exceptionally extensive vascularization in their primary cortex. Secondary osteons are lacking, except in restricted

areas in turtles and crocodiles. Reptiles always grow cyclical interrupted, independent of living in seasonal or constant environments. This documents an endogeneous determination or rhythm of growth. Growth marks are annual in reptiles as many recent studies have shown (mark-release-recapture method; marking cycles with tetracycline; for references see CASTANET & SMIRINA 1990, and CASTANET et al. 1993, GROSSE 1999). Crocodiles and turtles under optimal captive conditions are able to grow as juveniles with fibro-lamellar tissue. They form quite periodical, fibro-lamellar bone in the zones followed by layers of lamellated bone or a LAG (CHINSAMY 1994). Beside this, crocodiles and turtles retained a rather plesiomorphic or generalized condition of their bone tissue, often close in agreement with large extinct amphibians (steogocephalians).

ANDREWS (1976) reviewed the high variability in the growth rates of reptiles depending on environmental conditions. The advantage of such a growth strategy is that low growth rates allow reptiles to persist at times or at places of low resource availability. In contrast captive reptiles, e. g. turtles of the genus *Trachemys*, can be raised under constant optimal conditions to their maximum size (around 20 cm) in less than half of the time (3 years) which they needed normally in the wild (6 years). European land tortoises (*Testudo* spp.) can be raised within 4-5 years to the size where sexual maturity usually starts, in the wild they will need around 10-12 years (ROGNER 1996). However, such fast growth is most of the time coupled with various diseases in these captive individuals and not comparable with optimal conditions in the wild.

Life history patterns of reptiles are fairly uniform. They all grow relatively fast to sexual maturity, then growth slows down but can continue for several years and usually stops. But maximum size can include in many reptiles a wide range of size (mostly in larger taxa such as crocodiles, turtles, and some of the giant snakes, not in more modern forms like lizards). Three landmarks on a growth curve of an individual reptile are significant: Size at hatching size at sexual maturity, and maximum size. The onset of sexual maturity in reptiles is coupled to a specific size and weight, and not to a specific age, because growth depends strongly on environmental conditions in reptiles. Thus, the range of age at maturity is as large as that of final size. Therefore size and age need not to be correlated (e.g. see ZUG et al 1986: figure 9). This leads to a large phenotypic diversity in many reptiles concerning the final size. In others, body size variation is limited, but maximum size is attained at a variety of possible ages, strongly depending on individual history.

Although *Plateosaurus* shows a clearly higher growth rates than modern wild reptiles it is similar in its strong variation in maximum size and growth rate. Also conspicuously

"reptilian" is the high dependency of *Plateosaurus* on environmental conditions as evidenced by irregularly deposited growth cycles.

9.5 Birds and mammals

Growth patterns and strategies of birds and mammals are also quite well known. Both show a similar, rather simple growth pattern with very fast rates, depositing highly vascularized fibro-lamellar tissue. Growth is continuous up to sexual maturity and there is little variation in adult size. When sexual maturity and maximum size is reached growth stops and lamellar-zonal tissue is deposited in some taxa in the exterior cortex. Thus, growth is clearly determinate and correlated with size. Strong remodeling and Haversian bone is common in the bones of birds and mammals. Larger mammals need longer times for growth and reaching sexual maturity and maximum size can include several years. Smaller mammals, like most rodents need only a few weeks to attain sexual maturity and maximum size. Most birds grow within their first years to maximum size and become mature, in many small songbirds it takes only a few weeks.

Thus, there is beside a similar bone tissue no more similarity between *Plateosaurus* and extant birds and mammals.

10 Summary and conclusions

The bone histological study of various cross-, polish-, and thin-sections of long and girdle bones of *Plateosaurus engelhardti* shows that the primary bone tissue in adult individuals was the laminar fibro-lamellar complex regularly interrupted by LAGs. Deposition of LAGs is a clear indication that *Plateosaurus engelhardti* individuals were not able to maintain high rates of bone deposition continuously during much of their life history. Nevertheless, the presence of laminar fibro-lamellar bone reflects a presumably high metabolic rate, and growth rate. Changes in growth during ontogeny are only observable in the exterior cortex where the fibro-lamellar complex changes in some specimen into nearly avascular lamellar-zonal tissue and clearly indicates a determinate growth pattern. Earlier changes in growth could not be documented due to the lack of juveniles.

Different rates of the bones in a single skeleton are documented. The primary cortex of the pubis consists only of lamellar-zonal bone clearly indicating a slower growth than in long bones. Therefore, the onset of sexual maturity is possibly preserved in the pubes. Large medullary cavities of the long bones makes extrapolation necessary and leads to a general overestimation of total LAG numbers (=ages) in the long bones.

Skeletochronology results in ages for different life history events similar to other studied dinosaurs. A size of around 5 m could be reached in 8 years, sexual maturity starts around 9 years. The maximum documented age was around 26/27 years, but longevity was higher than this. Most individuals approached maximum size around 16-20 years. Deposition of LAGs in largely avascular lamellar-zonal bone after growth indicates a plateauing of growth. There is a very high variability of adult size. The sample shows specimen which stopped growth around 6.5 m and others which continued growth at a body size of over 8 m. Sexual dimorphism could not be documented within this variability but remains possible. The largest sampled bone represents an individual of 10 m body size which had stopped growth at around 20 years and lived for several (5) years longer.

Bone microstructure and some aspects of life history (continued growth after onset of sexual maturity) of *Plateosaurus* were similar to other studied dinosaurs. But cyclical interrupted growth, continued growth after sexual maturity, high dependency on environmental conditions, and the high range of final body size in adults indicates a more reptilian (plesiomorphic) growth pattern than was available in most other dinosaurs. On the other hand, high growth rates, and the deposition of fibro-lamellar bone shows that *Plateosaurus* was surely "not simply reptilian". Like many other dinosaurs, *Plateosaurus engelhardti* combines features of ectothermy and endothermy, and it cannot be put easily into one of the categories used today. Therefore, physiology should be termed "dinosaurian", as REID (1990) had suggested.

Acknowledgements

References

Amprino R. 1947. La structure du tissu osseux envisagèe comme expression de diffèrences dans la vitesse de l' accroisement. *Archives de Biologie* **58:** 315-330.

Andrassy P. 2004. Gibt es Stillstandslinien bei pleistozänen Säugetieren? Paläohistologische Untersuchungen an Langknochen pleistozäner Großsäuger. Unpublished master thesis**,** University of Bonn.

Andrews RM. 1982. Patterns of growth in reptiles. In: Gans C, Pough FH., ed. *Biology of the Reptilia*. London: Academic Press, 273-320.

Auffenberg W. 1981. *The behavioral ecology of the Komodo monitor*. Gainesville: University Press Florida.

Bakker RT. 1986. *The dinosaur heresies: New theories unlocking the mystery of the dinoaurs and their extinction.* New York: William Morrow and Co. Inc.

Benton MJ, Juul L, Storrs GW, and Galton PM. 2000. Anatomy and Systematics of the Prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of Southwest England. *Journal of Vertebrate Paleontology* **20:** 77-108.

Carpenter K. 1999. *Eggs, Nests, and Baby Dinosaurs*. Bloomington and Indianapolis: Indiana University press.

Case TJ. 1978. Speculations on the growth rate and reproduction of some dinosaurs. *Paleobiology* **4:** 320-326.

Castanet J. 1994. Age existimation and longevity in reptiles. *Gerontology* **40:** 174-192.

Castanet J, Cheylan M. 1979. Les marques de croissance des os et des ecilles comme indicateur de l'age chez *Testudo hermanni* et *Testudo graeca* (Reptilia, Chelonia, Testudinidae). *Canadian Journal of Zoology* **57:** 1649-1665.

Castanet J, Francillon-Vieillot H, Meunier FJ, Ricqlès A de. 1993. Bone and individual aging. In: Hall BK, ed. *Bone. Volume 7: Bone growth - B*. Boca Raton: CRC Press, 245-283.

Castanet J, Newman DG, Saint Girons H. 1988. Skeletochronological data on the growth, age, and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand. *Herpetologica* **44:** 25-37.

Castanet J, Smirina E. 1990. Introduction to the skeletochronological method in amphibians and reptiles. *Annales des Sciences Naturelles, Zoologie, Paris, Série13.* **Vol. 11:** 191-196.

Cherry C. 2002. Bone histology of the primitive dinosaur, *Thecodontosaurus antiquus.* Unpublished master thesis**,** University of Bristol.

Chinsamy A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Palaeontologia africana* **27:** 77-82.

Chinsamy A. 1992. Ontogenetic growth of the dinosaurs *Massospondylus carinatus* and *Syntarsus rhodesiensis. Journal of Vertebrate Paleontology* **12:** 23A.

Chinsamy A. 1993a. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* (Owen). *Modern Geology* **18:** 319-329.

Chinsamy A. 1993b. Image analysis and the physiological implications of the vascularisation of femora in Archosaurs. *Modern Geology* **19:** 101-108.

Chinsamy A. 1994. Dinosaur bone histology: Implications and inferences. In: Rosenberg GD and Wolberg DL, eds. *Dino Fest.*: Paleontological Society, Special Publication No. **7:** 213-227.

Chinsamy A. 1997. Sex and old bones ? *Journal of Vertebrate Paleontology* **17:** 450.

Chinsamy A, Dodson P. 1995. Inside a dinosaur bone. *American Scientist* **83:** 174-180.

Chinsamy A, Elzanowski A. 2001. Evolution of growth pattern in birds. *Nature* **412:** 402.

Colbert EH. 1964. Relationships of saurischian dinosaurs. *American Museum Novitates* **2181:** 1-24.

Currey JD. 1962. The histology of the bone of a prosauropod dinosaur. *Palaeontology* **5:** 238-246.

Curry KA. 1998. Histological quantification of growth rates in *Apatosaurus. Journal of Vertebrate Paleontology* **18:** 36A.

Curry KA. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): New insights on growth rates and longevity. *Journal of Vertebrate Paleontology* **19:** 654-665.

Dunham AE, Overall K L, Porter W P, Forster C A. 1989. Implications of ecological energetics and biophysical and developmental constraints for life-history variation in dinosaurs. In: Farlow JOe, ed. *Paleobiology of the dinosaurs.*: The Geological Society of America, Inc., Boulder., pp. 1-21.

Enlow DH. 1969. The bone of reptiles. In: Gans Ce, ed. *Biology of the Reptilia*. London: Academic Press.

Enlow DH, Brown SO. 1956. A comparative histological study of fossil and recent bone tissues. Part I. *The Texas Journal of Science* **9:** 405-439.

Enlow DH, Brown SO. 1957. A comparative histololgical study of fossil and recent bone tissues. Part II. *The Texas Journal of Science* **9:** 186-214.

Enlow DH, Brown SO. 1958. A comparative histological study of fossil and recent bone

tissues. Part III. *The Texas Journal of Science* **10:** 187-230.

Erickson GM, Brochu CA. 1999. How the "terror crocodile" grew so big. *Nature* **398:** 205-206.

Erickson GM, Curry-Rogers K, Yerby SA. 2001. Dinosaurian growth patterns and rapid avian growth rates. *Nature* **412:** 429-432.

Erickson GM, Ricqles A de, Buffrenil V de , Molnar R, Bayless MK. 2003. Vermiform bones and the evolution of gigantism in *Megalania* - How a reptilian fox became a lion. *Journal of Vertebrate Paleontology 9* **23:** 966-970.

Erickson GM, Tumanova TA. 2000. Growth curve of *Psittacosaurus mongoloiensis* Osborn (Ceratopsia: Psittacosauridae) inferred from long bone histology. *Zoological Journal of the Linnean Society* **130:** 551-566.

Farlow JO, Brett-Surmann M.K. (eds.). 1997. *The Complete Dinosaur*. Bloomington and Indianapolis: Indiana University Press.

Farlow JO, Dodson P, Chinsamy A. 1995. Dinosaur biology. *Annual Review of Ecology and Systematics* **26:** 445-471.

Ferguson MWJ, Honig LS, Bringas P Jr., Slavkin HC. 1982. In vivo and in vitro development of first branchial arch derivates in *Alligator mississippiensis*. In: Dixon A, Sarnat B., ed. *Factors and Mechanisms influencing bone growth*. New York: Alan R. Liss., pp 275-296.

Foelix R. 1999a. Neue Saurierfunde in Frick: Internet Resource: http://www.sauriermuseum-frick.ch/grabungen.htm. 40-46.

Foelix R. 1999b. Röntgen im Museum. *Aargauische Naturforschende Gesellschaft, Mitteilungen* **35:** 147-160.

Fraas E. 1913. Die neuesten Dinosaurierfunde in der schwäbischen Trias. *Naturwissenschaften* **1913:** 1097-1100.

Francillon-Vieillot H, Buffrénil V. de, Castanet J, Géraudie J, Meunier FJ, Sire JY,
Zylberberg L, Ricqlès A de. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: Carter Je, ed. *Skeletal biomineralization: Patterns, processes and evolutionary trends.* New York: Van Nostrand Reinhold, 471-530.

Galton P, M. 2001. The prosauropod dinosaur *Plateosaurus* MEYER, 1837 (Saurischia: Sauropodomorpha; Upper Triassic). II. Notes on the referred species. *Revue de Palèobiology,* **20:** 435-502.

Galton PM. 1985. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. Part II: All the cranial

material and details of soft-part anatomy. *Geologica et Palaeontologica. Marburg* **19:** 119-159.

Galton PM. 1986. Prosauropod dinosaur *Plateosaurus* (=*Gressylosaurus*) (Saurischia: Sauropodomorpha) from the Upper Triassic of Switzerland. *Geologica et Palaeontologica* **20:** 167-183.

Galton PM. 1990. Basal Sauropodomorpha-Prosauropoda. In: Weishampel P, Dodson P, Osmòslka H., ed. *The Dinosauria*. Berkeley: University of California Press., 320-344.

Galton PM. 1997. Comments on sexual dimorphism in the prosauropod dinosaur *Plateosaurus engelhardti* (Upper Triassic, Trossingen). *Neues Jahrburch für Geologie und Paläontologie,* **Monatshefte 1997:** 674-682.

Galton PM. 2000. The prosauropod dinosaur *Plateosaurus* MEYER, 1837 (Saurischia: Sauropodomorpha). I. The syntypes of *P. engelhardti* MEYER, 1837 (Upper Triassic, Germany), with notes on other European prosauropods with "distally straight" femora. *Neues Jahrbuch Geologie und Paläontologie, Abhandlungen. Stuttgart* **216:** 233-275.

Gow C, Kitching JW, Raath MA. 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* OWEN in te collections of the Bernard PRICE Institute for Paleontological Research. *Palaeontologia africana, Johannesburg.* **27:** 45-58.

Grine F, Kitching JW. 1987. Scanning electron microscopy of early dinosaur egg shell structure: A comparsion with other rigid sauropod eggs. *Scanning Micropscope* **1:** 615-630.

Gross W. 1934. Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocepahlen und Reptilien. *Zeitschrift der Anatomie und Entwicklungsgeschichte* **203:** 731-764.

Grosse W-R. 1999. Altersbestimmung bei mitteleuropäischen Amphibien mittels Skeletochronologie am Beispiel der Kreuz-, Erd- und Wechselkröte (Anura, Bufonidae). *Elaphe* **Heft 3/1999:** 80.

Heerden J, van. 1997. Prosauropods. In: Farlow JO, Brett-Surmann MK., ed. *The complete dinosaur*. Bloomington: Indiana University Press, 242-263.

Horner J, Ricqles A de, Padian K. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: Growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* **20:** 115-129.

Horner J, Ricqlès A de, Padian K. 1999. Variation in dinosaur skeletochronology indicators: Implications for age assessment and physiology. *Paleobiology* **25:** 295-304.

Horner JR, Padian K, Ricqlès A de. 2001. Comparative osteohistology of some embryonic

and perinatal archosaurs: developmental and behavioral implications for dinosaurs. *Paleobiology* **27:** 39-58.

Hotton N. 1980. An alternative to dinosaur endothermy: The happy wanderers. In: Thomas D, Olson EC., ed. *A cold look at the warm blooded dinosaurs.*: American Association for the Advancement of Science Selected Symposium, Wetsview Press, 311-350.

Huene F, von. 1908. Die Dinosaurier der europäischen Triasformationen mit Berücksichtigung der außereuropäischen Vorkommnisse. *Geologische und Paläontologische Abhandlungen. Jena* **Supplement 1:** 1-419.

Huene F, von. 1926. Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Keuper. *Geologische und Paläontologische Abhandlungen. Jena* **Neue Folge Band 15:** 139-179.

Huene F, von. 1928. Lebensbild des Sauriervorkommens im obersten Keuper von Trossingen. *Paleobiologica* **1:** 103-116.

Huene F, von. 1929. Die Plateosaurier von Trossingen. *Umschau* **1929:** 880-882.

Huene F, von. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographie Geologie Paläontologie* **Serie 1:** 1-361.

Huene F, von. 1944. Arbeitserinnerungen. *Selbstbiographien von Naturforschern* **2:** 1-52.

Hungerbühler A. 1998. Taphonomy of the prosauropod dinosaur *Sellosaurus*, and its implications for carnivore faunas and feeding habits in the Late Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143:** 1-29.

Jaekel O. 1913-14. Über die Wirbeltierfunde in der oberen Trias von Halberstadt. *Paläontologische Zeitschrift* **1:** 155-215.

Klein N. in prep. A turtle from the Late Triassic locality of Frick (northern Switzerland).

Klevezal GA. 1996. *Recording structures of mammals: Determination of age and reconstruction of life history.* Rotterdam: Balkema.

Meyer HH, von. 1837. Mitteilung an Prof. Bronn (*Plateosaurus engelhardti*). *Neues Jahrbuch für Geologie und Paläontologie* **1837:** 316.

Moratalla JJ, Powell JE. 1994. Dinosaur nesting patterns. In: Carpenter K, Hirsch K., Horner JR., ed. *Dinosaur Eggs and Babies*. Cambridge: Cambridge University Press, 37-46.

Moser M. 2000. The influence of pedogenesis on the taxonomy of *Plateosaurus*. In: E. Frey (Ed.). *5th European Workshop on Vertebrate Paleontology.* **Program. Abstracts. Excursion Guides. Staatliches Museum für Naturkunde, Karlsruhe:** 57.

Moser M. 2003. *Plateosaurus engelhardti* Meyer, 1837 (Dinosauria: Sauropodomorpha) aus

dem Feuerletten (Mittelkeuper, Obertrias) von Bayern. *Zitteliana* **B 24:** 188.

Neill WT. 1971. *The Last of the Ruling Reptiles: Alligators, Crocodiles, and their kin.* New York and London.: Columbia University Press.

Padian K. 1997. Growth Lines. In: Currie PJ, Padian K., ed. *Encyclopedia of dinosaurs*. San Diego: Academic Press, 288-291.

Padian K, Ricqles A de, Horner JR. 2001. Dinosaurian growth rates and bird origins. *Nature* **412:** 405.

Pooley AC, Gans G. 1976. The Nile Crocodile. *Scientific American* **234:** 114-124.

Raath MA. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: Carpenter K, Currie PJ., ed. *Dinosaur Systematics. Approaches and Perspectives*. Cambridge: Cambridge University Press, 93-105.

Reid REH. 1981. Lamellar-zonal bone with zones and annuli in the pelvis of a sauropod dinosaur. *Nature* **292:** 49-51.

Reid REH. 1987. Bone and dinosaurian "endothermy". *Modern Geology* **11:** 133-154.

Reid REH. 1990. Zonal "growth rings" in dinosaurs. *Modern Geology* **15:** 19-48.

Reid REH. 1997a. How dinosaurs grew. In: Farlow JO, Brett-Surman MK., ed. *The complete dinosaurs*. Bloomington and Indianapolis: Indiana University Press, 403-413.

Reid REH. 1997b. Histology of bones and teeth. In: Currie PJ, Padian K., ed. *Encyclopedia of Dinosaurs*. London: Academic Press, 329-339.

Remes K. 2004. Revision von "*Barosaurus" africanus* (Sauropoda, Diplodocinae) aus den Tendaguru - Schichten Tansanias. unpublished master thesis**,** University of Berlin.

Ricqlès A, de. 1968. Recherches Palèohistologiques sur les os longs des tetrapodes. I.-Origine du tissu osseux plexiforme des dinosaurians sauropodes. *Annales de Palèontologie* **54:** 133-145.

Ricqlès A, de. 1976. Recherches palèohistologiques sur les os longs des tètrapodes. VII. Sur le classification, la significationfonctionelle et l' histoire des tissus osseux des tètrapodes. *Annales de Palèontologie* **62:** 71-126.

Ricqlès A, de. 1980. Tissue structures of dinosaur bone. Functional significance and possible relation to dinosaur physiology. In: Thomas RDK and Olson EC, eds. *A cold look at the warm-blooded dinosaurs. American Association for the Advancement of Science. Selected Symposium*. Boulder, Colorado: Westview Press, 103-139.

Ricqlès A, de. 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontologica Polonica* **28:** 225-232.

Ricqlès A, de, Meunier FJ, Castanet J, Francillon-Vieillot H. 1991. Comparative microstructure of bone. In: Hall BK, ed. *Bone. Volume 3: Bone matrix and bone specific products*. Boca Raton: CRC Press, 1-78.

Rieber H. 1985a. Saurier und andere Fossilien von Frick. *Frick Gestern Heute* **1:** 5-18.

Rieber H. 1985b. Der Plateosaurier von Frick. *Uni Zürich.* **1985:** 3-4.

Rimblot-Baly F, Ricqles, A de, Zylberberg L. 1995. Analyse Paléohistologique d'une série de croissance partille chez *Lapparentosaurus madagascariensis* (Jurassique Moyen): Essai sur la dynamique de croissance d'un dinosaure sauropode. *Annales de Palèontologie (Invert - Vert.)* **81:** 49-86.

Rogner M. 1996. *Schildkröten 2*. Hürtgenwald: Heidi-Rogner-Verlag.

Sander PM, Klein N, Buffetaut E, Cuny G, Suteethorn V, LeLoeuff J. 2004. Adaptive radiation in sauropod dinosaurs: Bone histology indicates rapid evolution of giant body size through acceleration. *Organisms, Diversity & Evolution* 4: 165-173.

Sander PM, Tückmantel C. 2003. Bone lamina thickness, bone apposition rates, and age estimates in sauropod humeri and femora. *Paläontologische Zeitschrift* **77:** 161-172.

Sander PM. 1990. Skeletochronology in the small Triassic reptile *Neusticosaurus*. *Annales des Sciences Naturelles, Zoologie, Paris, Série 13*, **Vol. 11:** 213-217.

Sander PM. 1992. The Norian *Plateosaurus* Bonebeds of central Europe and their taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **93 (1992):** 255-299.

Sander PM. 1998. Growth strategies of the Tendaguru sauropods: A paleohistological perspektive. *Journal of Vertebrate Paleontology* **18:** 74A (Abstract).

Sander PM. 1999a. Life history of the Tendaguru sauropods as inferred from long bone histology. *Mitteilungen aus dem Museum für Naturkunde der Humboldt-Univ. Berlin, Geowissenschaftliche Reihe* **2:** 103-112.

Sander PM. 1999b. Die Norian Plateosaurus "Friedhöfe" im Keuper: Belege für einen Massentod ? In: Hauschke N, Wild R., ed. *Trias. Eine ganz andere Welt. Mitteleuropa im frühen Erdmittelalter.* München: Pfeil, 81-104.

Sander PM. 2000. Long bone histology of the Tendaguru sauropods: Implications for growth and biology. *Paleobiology* **26**.

Sander PM, Gee CT. 1989 a. Earthwatch-Freiwillige graben Fricker Dinosaurier aus. *Uni Zürich.* **1989:** 33-34.

Sander PM, Gee CT. 1989 b. Mit Earthwatch auf Dinosaurierjagd. *Fossilien* **4:** 157-165.

Seebacher F. 2001. A new method to calculate allometric length-mass relationships of

dinosaurs. *Journal of Vertebrate Paleontology* **21:** 51-60.

Seemann R. 1932. Verlauf und Ergebnis der Trosssinger Sauriergrabung. *Jahreshefte des Vereins für vaterländische Naturkunde. Wuerttemberg* **88:** LII-LIV.

Seemann R. 1933. Das Saurischierlager in den Keupermergeln bei Trossingen. *Jahreshefte des Vereins für vaterländische Naturkunde. Wuerttemberg* **89:** 129-160.

Seitz AL. 1907. Vergleichende Studien über den makroskopischen Knochenbau fossiler und rezenter Reptilien. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* **87:** 230-370.

Sereno PC. 1989. Prosauropod monophyly and basal sauropodomorph phylogeny. *Journal of Vertebrate Paleontology* **Supplement no. 3**.

Starck JM, Chinsamy A. 2002. Bone microstructure and developmental plasticity in birds and other dinosaurs. *Journal of Morphology* **254:** 232-246.

Upchurch P. 1997. Prosauropoda. In: Currie PJ, Padian K., ed. *Encyclopedia of Dinosaurs*. London: Academic Press, 599-607.

Varricchio DJ. 1993. Bone microstructure of the Upper Cretacious theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* **13:** 99-104.

Varricchio DJ. 1997. Growth and embrylogy. In: Currie PJ and Padian K, eds. *Encyclopedia of Dinosaurs*. London: Academic Press, 282-288.

Weishampel DB. 1984. Trossingen: E. Fraas, F. v. Huene, R. Seemann and the "Schwäbische Lindwurm" *Plateosaurus*. In: Reif WE, Westphal, F., ed. *3rd Symposium of Mesozoic Terrestrail Ecosystems*. Tübingen: Attempto, 249-253.

Weishampel DB, Chapman RE. 1990. Morphometric study of *Plateosaurus* from Trossingen (Baden-Würtemberg, BRD/Germany). In: Carpenter K, Currie PJ., ed. *Dinosaur Systematics: Perspectives and Approaches*: Cambridge University Press, 43-51.

Weishampel DB, Dodson P, Osmolska H. (eds.). 1990. *The Dinosauria*. Los Angeles: University of California Press.

Weishampel DB, Westphal, F. 1986. *Die Plateosaurier von Trossingen.* Tübingen: Attempto.

Wellnhofer P. 1993. Prosauropod dinosaurs from the Feuerletten (Middle Norian) of Ellingen near Weissenburg in Bavaria. *Revue de Paèobiologie* **Vol. spec. 7:** 263-271.

Wikelski M, Thom C. 2000. Marine iguanas shrink to survive "El Nino". *Nature* **403:** 37.

Wilson JA. 2002. Sauropod dinosaur phylogeny: Critique and cladistic analysis. *Zoological Journal of the Linnean Society* **136:** 217-276.

Wink CS, Elsev RM, Hill EM. 1987. Changes in femoral robusticity and porosity during the reproductive cycle of the female alligator (*Alligator misssissippiensis*). *Journal of Morphology* **193:** 317-321.

Yates A. 2001. A new look at *Thecodontosaurus* and the origin of sauropod dinosaurs. *Journal of Vertebrate Paeontology* **21:** 116A.

Ziegler B. 1986. *Der Schwäbische Lindwurm. Funde aus der Urzeit im Museum am Löwentor*: Konrad Theiss Verlag.

Zug GR, Rand St. 1987. Estimation of age in nesting female *Iguana iguana*: Testing skeletochronology in a tropical lizard. *Amphibia-Reptilia* **8:** 237-250.

Zug GR, Wynn AH, Ruckdeschel C. 1986. Age determination of loggerhead sea turtle, *Caretta caretta*, by incremental growth marks in the skeleton. *Smithsonian contributions of zoology* **427:** 1-34.

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Erklärung

Hiermit erkläre ich an Eides statt, daß ich für meine Promotion keine anderen als die angegebenen Hilfsmittel benutzt habe, und daß die inhaltlich und wörtlich aus anderen Werken entnommenen Stellen und Zitate als solche gekennzeichnet sind.

Nicole Klein