

Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis

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Abstract

The histology of the sculptured dermal bones of skull and pectoral girdle of 19 taxa of Palaeozoic and Mesozoic basal tetrapods and of the porolepiform *Laccognathus* is investigated. The dermal bones consist generally of compact external and internal cortices that frame a cancellous or trabecular middle region. In *Laccognathus*, thin, unmineralized Sharpey's fibers that are loosely arranged penetrate the external cortex between the odontodes. After the reduction of odontodes in finned stem-tetrapods, dermal sculpture developed via preferential growth of bone without the involvement of resorptive processes. In the stem-tetrapod *Panderichthys*, the Sharpey's fibers are well-mineralized and indicate a tight connection to the overlying soft-tissue integument. The fibers are most numerous and most densely arranged in the bony ridges and tubercles, which constituted the main points of anchorage for the skin. The morphology and morphogenesis of the bony sculpture and its association with mineralized Sharpey's fibers was retained during the fish-tetrapod transition and basically conserved in the different lineages of basal tetrapods including basal amniotes.

The dermal bones of the stem-tetrapods *Panderichthys*, *Acanthostega* and *Greererpeton* are composed to a large degree of parallel-fibered bone, and a 'fish-like' character is the internal cortex that consists of isopedine. In crown-group tetrapods, the Sharpey's fibers are generally much thicker and more densely arranged than in stem-tetrapods, and metaplastic bone can be demonstrated in addition to parallel-fibered bone in many taxa. These data suggest that the first crown-group tetrapods had attained a denser integument that might have provided a better resistance against water loss and mechanical damage during locomotion on land. In contrast to extant lissamphibians, the denser integument as well as ossified dermal scales and the comparatively large body size probably precluded large-scale cutaneous respiration in most basal tetrapods.

The middle region of dermal bones shows varying degrees of resorption and secondary growth among taxa. In heavily ossified forms such as *Eryops* or *Mastodonsaurus*, the weight of the skeleton helped them to stay under water, whereas skeletal lightening by reduced cortices and a highly porous middle region may have enhanced the agility and manoeuvrability during swimming.

Key words: Bone microstructure, fish-tetrapod transition, integument, Mesozoic, metaplasia, Palaeozoic, Sharpey's fibers.

Zusammenfassung

In dieser Studie wird die Histologie der skulptierten Hautknochen des Schädels und des Schultergürtel von 19 Taxa basaler Tetrapoden aus dem Paläozoikum und Mesozoikum sowie des Porolepiformen *Laccognathus* untersucht. Die Hautknochen bestehen normalerweise aus kompakten äußeren und inneren Cortices, die eine spongiöse mittlere Region einschließen. *Laccognathus* besitzt dünne, nicht mineralisierte Sharpey'sche Fasern im externen Cortex, die locker zwischen den Odontoden angeordnet sind. Nach Reduktion der Odontoden bei fischartigen Stamm-Tetrapoden entstand die äußere Skulptur der Dermalknochen durch bevorzugtes Knochenwachstum ohne Anzeichen damit verbundener Knochenresorption. Bei dem Stamm-Tetrapoden *Panderichthys* sind die Sharpey'schen Fasern gut mineralisiert und deuten auf eine feste Verbindung zwischen der Knochenoberfläche und der überlagernden Haut hin. Die Fasern sind am zahlreichsten und dichtesten in den knöchernen Tuberkeln und Leisten angeordnet, welche die Hauptverankerungspunkte der Haut darstellten. Morphologie und Morphogenese der Knochenskulptur und ihre Assoziation mit mineralisierten Sharpey'schen Fasern wurden während des Fisch-Tetrapoden Überganges beibehalten und in den verschiedenen Linien basaler Tetrapoden einschließlich basaler Amnioten bewahrt.

Die Hautknochen der Stamm-Tetrapoden *Panderichthys*, *Acanthostega* und *Greererpeton* bestehen zu einem großen Teil aus parallelfaserigem Knochen, und ein „fischartiges“ Merkmal ist das Vorhandensein von Isopedin im internen Cortex. Bei Kronengruppen-Tetrapoden sind die Sharpey'schen Fasern im allgemeinen deutlich dicker und dichter angeordnet als bei Stamm-Tetrapoden, und neben parallelfaserigem Knochen kann oft metaplastischer Knochen nachgewiesen werden. Diese Befunde deuten darauf hin, dass die ersten Kronengruppen-Tetrapoden eine derbe Haut besessen haben, die wahrscheinlich einen besseren Schutz gegen Wasserverlust und Verletzung beim Laufen über das Land bot. Im Gegensatz zu heutigen Lissamphibien verhinderten die derbere Haut sowie die häufig vorhandenen Knochenschuppen und das ungünstige Verhältnis von Körperoberfläche zu Volumen eine weitreichende Hautatmung bei den meisten basalen Tetrapoden.

Die mittlere Region der Hautknochen war von Taxon zu Taxon in unterschiedlichem Maße von Resorption und sekundärem Wachstum betroffen. Bei schwer verknöcherten Formen wie *Eryops* und *Mastodonsaurus* wirkte das Gewicht des Skeletts dem Auftrieb im Wasser entgegen, wohingegen eine Gewichtsreduktion durch dünnere Cortices und eine stark poröse mittlere Region die Wendigkeit beim Schwimmen sicherlich erhöht hat.

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1. Introduction

Dermal bones of the skull and the pectoral girdle develop within the integument, generally in the lower layer of the dermis (CASTANET et al. 2003). These ossifications are frequently penetrated by numerous canals that carried blood vessels and nerves (including the lateral line system of fishes and non-amniote basal tetrapods) to the external bone surface and into the directly overlying integument. The histomorphology of dermal bones as well as the structure of their external surface are therefore well suited as osteological correlates of the integumentary structure in fossil vertebrates. In the different groups of fossil fishes and early vertebrates, the dermal bones of skull and pectoral girdle, the scales and armour plates have been subject to histological investigation for a long time, so that the

internal structure of these dermal ossifications are the most extensively studied among vertebrates (e. g., BYSTROW 1939, 1942, 1957; ØRVIG 1951, 1957, 1966, 1968, 1989; THOMSON 1977; GROSS 1930, 1957, 1973; BEMIS & NORTHCUTT 1992; SMITH 1977).

In fossil tetrapods, the focus of histological investigations lies most often on the long bones, including the application of skeletochronology as an important method to infer biological parameters like growth rate, individual age and mode of life, and a large amount of data has accumulated over the last decades (e. g., DE RICQLÈS 1975a, b, 1976, 1977, 1981, 1993; CHINSAMY 1993; CHINSAMY-TURAN 2005; DAMIANI 2000; STEYER et al. 2004; SANDER & ANDRÁSSY 2006; KLEIN & SANDER 2007, 2008; SANCHEZ et al. 2008). More recently, also the histology of dermal ossifications of the trunk (i. e., osteoderms) in fossil amniotes

has attracted increasing interest of palaeontologists and zoologists, e. g. in turtles (SCHEYER & SÁNCHEZ-VILLAGRA 2007; SCHEYER & ANQUETIN 2008), placodonts (SCHEYER 2007), dinosaurs (DE BUFFRÉNIL et al. 1986; DE RICQLÈS et al. 2001; SCHEYER & SANDER 2004; MAIN et al. 2005), xenarthrans (HILL 2005, 2006), and basal tetrapods (WITZMANN & SOLER-GIJÓN 2008).

The histology of the dermal ossifications of skull and pectoral girdle in temnospondyls and other basal tetrapods, in contrast, has received the attention of comparatively few workers who investigated only a very limited range of taxa. Within the work on the Early Permian 'branchiosaurs' from the Döhlen Basin in Saxony, CREDNER (1893, pl. 30, figs. 4–6; pl. 31, figs. 8–9) illustrated schematically the course of presumed blood vessels in dermal skull bones of the temnospondyl *Onchiodon* and presented a histological section of the vomer (CREDNER 1893, pl. 31, fig. 4).

SEITZ (1907) described the histology of a mandible fragment of ?*Mastodonsaurus*. He observed a compact outer region consisting of lamellar bone with simple vascular canals and primary osteons. More internally in the bone, SEITZ (1907) found secondary osteons (Haversian systems) and irregular caverns of a spongy region.

GROSS (1934) provided a short description of the dermal skull bone histology of *Mastodonsaurus*, *Metoposaurus* and *Plagiosternum*. He recognized that the dermal bones of these temnospondyls exhibit a diploë structure, i. e., a spongy middle region is framed by an external and an internal compact cortex, and designated the matrix of the cortical bone as zonal periosteal bone (zonarer Periostknochen).

AS GROSS (1934) noted, the internal cortex lacks the isopedine-like organization of many finned sarcopterygians. A detailed study of the histology of dermal skull bones in the stereospondyl *Benthosuchus* was published by BYSTROW (1935). He recognized horizontally aligned large canals in the middle, spongy region from which oblique canals branch off, traverse the external cortex and open to the external bone surface on the floor of the sculptural pits and furrows. BYSTROW (1935) described a fine network of capillaries additional to these large canals in the external region that open to the bone surface via small pores. He designated this network as 'rete vasculosum'. In a later study, BYSTROW (1947) interpreted these capillaries as serving for cutaneous respiration and compared the vascularization of the dermal bones of *Benthosuchus* with those of the stereospondylomorphs *Wetlugasaurus* and *Platyoposaurus*, and the dvinosaur *Dvinosaurus*. In his studies, BYSTROW (1935, 1947) had focused mainly on the morphology and course of blood vessels within the bone, but he neither described the bone matrix proper nor the presence of extrinsic fibers.

In the first part of their comprehensive works on bone

histology, ENLOW & BROWN (1956) concentrated on the study of long bones of tetrapods, but also commented on the arrangement and orientation of vascular canals in dermal bones of temnospondyls (*Edops*, *Trimerorhachis*, *Eryops*) and of the stem-amniote *Seymouria*. PEABODY (1961) investigated cyclical growth zones in sections of the dentaries of Early Permian 'microsaurs' and indeterminate 'labyrinthodonts' from Fort Sill, Oklahoma. On the basis of his findings, PEABODY (1961) discussed palaeoclimatic inferences like alternating wet and dry seasons for this locality.

In 1974, COLDIRON published his work on the possible function of dermal bone sculpture in temnospondyls and other basal tetrapods. He challenged BYSTROW's assumption that the 'rete vasculosum' was functionally associated with cutaneous respiration since the capillaries describe an irregular pathway and thus an inefficient route of the blood to the bone surface and the skin. Based on split-line technique in dermal skull bones of *Alligator* and the orientation of the long-axis orientation in bone cell lacunae of dermal bones of *Eryops*, COLDIRON (1974) inferred the collagen-fiber orientation within the bone. He found the collagen fibers arranged parallel to one another in the internal and middle region, but non-parallel and randomly oriented in the sculptured external region. Thus, COLDIRON (1974) concluded that dermal bone sculpture in basal tetrapods and crocodylians is a strengthening adaptation by distributing the stress that acted on the dermal skull roof.

COSGRIFF & ZAWISKIE (1979) described a capillary network that opens to the sculptured surface in the dermal bones of the rhytidosteid temnospondyl *Pneumatostega*, although they did not prepare thin sections. Following BYSTROW (1947), they interpreted this vascularization as indication of cutaneous respiration.

DE RICQLÈS (1981), in his comprehensive work on long bones of fossil tetrapods, also commented on dermal skull bones of the temnospondyl *Trematops* and the nectridean *Diplocaulus*. In *Trematops* (DE RICQLÈS 1981, pl. 1, fig. 4), he described parallel-fibered bone with simple primary canals in the external cortex, and recognized lamellar-zonal bone in the external cortex of *Diplocaulus* (DE RICQLÈS 1981, pl. 2, fig. 3).

CASTANET et al. (2003) published a useful compilation of the present knowledge on bone histology of extant and extinct amphibians including stem-amniotes and early tetrapods. They confirmed the diploë structure as described by GROSS (1934) and BYSTROW (1935, 1947) as basic pattern for most dermal bones. According to CASTANET et al. (2003), the external cortex consists of primary bone tissue with a lamellar structure and contains simple vascular canals and primary osteons. Zones and annuli (and sometimes lines of arrested growth) indicate that bone deposition was cyclic. The middle spongy or cancellous region has undergone remodeling whose degree varies between

taxa. The internal region is lamellar and usually penetrated by a small number of simple canals that run parallel to the internal bone surface. Sharpey's fibers may cross this region at a steep angle.

In his analysis of placodont osteoderm histology, SCHEYER (2007) also referred to the internal structure of temnospondyl dermal bones and illustrated histological sections of *Trimerorhachis*, *Mastodonsaurus* and *Gerrothorax*. He observed a diploë pattern with a generally high vascularization and secondary remodeling in the middle region. The external and internal cortices consist mainly of parallel-fibered bone with growth marks, and transitions to interwoven structural fibers (ISF) in *Mastodonsaurus* exist. SCHEYER (2007) observed Sharpey's fibers that penetrate the bone of the sculptural ridges in *Mastodonsaurus*.

The aim of the present paper is to close the gap in the literature about dermal bone histology in basal tetrapods, and to provide a basis for comparison with the histology of dermal bones plus the overlying integument in extant sculpture-bearing fishes and tetrapods, that will be carried out in a future paper (WITZMANN in progress). Considered in the present study are dermal bones of the skull and the pectoral girdle, whereas the histology of osteoderms in temnospondyls is dealt with in a separate publication (WITZMANN & SOLER-GUJÓN 2008). Importance is especially attached to the different types of bone tissues, the course of intrinsic bone fibers and the presence of extrinsic fibers. A further focus will be the degree of vascularization and the type and morphology of the vascular canals, and also the mode of growth of the dermal bones, especially of the external sculpture. The results will be taken to draw conclusions about the integument in which these bones were formed, and possible functional aspects of dermal bone sculpture in basal tetrapods will be discussed.

Institutional abbreviations

CMNH	Cleveland Museum of Natural History, Cleveland, Ohio (USA)
MB	Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Museum für Naturkunde (Germany)
MCZ	Museum of Comparative Zoology, Harvard, Cambridge/Mass. (USA)
SMNS	Staatliches Museum für Naturkunde Stuttgart (Germany)
UCMP	University of California, Museum of Paleontology, Berkeley (USA)
UMZC	University Museum of Zoology, Cambridge (UK)

Anatomical abbreviations

cl	bone cell lacuna
cr	crevice (artefact)
de	dentine
EC	external cortex

en	enamel
ER	erosion room
fbs	former bone surface
fl	longitudinally cut bone fibers
ft	transversely cut bone fibers
GM	growth marks
IC	internal cortex
IL	interstitial lamellae
ISF	interwoven structural fiber bundles
LB	lamellar bone
MR	middle region
ov	opening of large vessel
PB	primary bone
PFB	parallel-fibered bone
PO	primary osteon
PVC	primary vascular canal
RL	resorption line
ShF	Sharpey's fibers
SB	secondary bone
SO	secondary osteon
tr	trabeculae

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2. Material and methods

Taxa whose dermal bones were investigated histologically by thin sections and their inventory numbers are listed in Table 1. Altogether, 103 histological slides have been prepared from dermal bones of skull and pectoral girdle of 20 taxa of finned and limbed sarcopterygians. The dermal bone fragments were first embedded in synthetic resin (Paraloid B72, an ethyl-methacrylat-copolymer) and then cut vertically either parallel or transverse to the direction of the sculptural ridges. Thin-sections were prepared with a thickness of approximately 30–50 µm using the standard method of CHINSAMY & RAATH (1992). Additionally, one slide of *Plagiosuchus pustuliferus* (FRAAS, 1896) (MB.Hi.1705), one slide of *Plagiosternum granulatum* (FRAAS, 1889) (MB.Hi.1714), and six slides of dermal bones of *Metoposaurus diagnosticus* (VON MEYER, 1842) (MB.Hi.1718–1723) produced by WALTER GROSS in 1934 and stored in the Museum für Naturkunde Berlin,

Tab. 1. Taxa investigated in this study with list of specimens and their inventory numbers.

Taxon	Stratigraphy	Locality	Specimens/Remarks
Porolepiform and stem-tetrapods			
<i>Laccognathus panderi</i> GROSS, 1941	Middle Devonian	Riga, Latvia	MB.f.17666: several fragments of dermal skull or pectoral girdle. 4 slides
<i>Panderichthys rhombolepis</i> (GROSS, 1930)	Late Devonian, Gauja beds	Latvia	MB.f.17548: several fragments of dermal skull or pectoral girdle. 5 slides
<i>Acanthostega gunnari</i> JARVIK, 1952	Late Devonian, upper Famennian, Britta Dal Formation	Stensiö Bjerg, Greenland	UMZC 150b: 1 fragment of cheek. 3 slides
<i>Greererpeton burkemorani</i> ROMER, 1969	upper Viséan/lower Namurian	Greer, West Virginia, USA	CMNH 11900: several fragments of dermal skull. 6 slides
Temnospondyls			
<i>Edops craigi</i> ROMER, 1936	Early Permian	Terrapin School, Archer County, Texas, USA	MCZ 1235: 3 fragments of dermal skull roof. 6 slides
<i>Chenoprosopus milleri</i> MEHL, 1913	Early Permian, Cutler Formation	New Mexico, USA	UCMP 41104: 5 pieces of dermal skull roof. 6 slides
<i>Eryops megacephalus</i> COPE, 1877	Early Permian, Moran Formation, Wichita Group	Little Bitter Creek, Young County, Texas, USA	Dermal skull: MCZ 4325: 1 fragment, 7622: 6 fragments; UCMP 203332: 2 fragments. 16 slides
<i>Acheloma cumminsi</i> COPE, 1882	Early Permian, Putnam Formation	Archer County, Texas, USA	MCZ 1490: 3 skull roof fragments. 5 slides
<i>Sclerocephalus haeuseri</i> GOLDFUSS, 1847	Early Permian, Autunian, Jeckenbach Black Shale Horizon	Heimkirchen, Saar-Nahe Basin, Germany	SMNS 90517: cheek and circumorbital elements of a subadult specimen (c. 120 mm skull length). 1 slide
<i>Archegosaurus decheni</i> GOLDFUSS, 1847	Lower Permian, Humbert Black Shale Horizon	Lebach, Saar-Nahe Basin, Germany	MB.Am.152: prefrontal, subadult specimen (c. 200 mm skull length). 1 slide
<i>Kupferzellia wildi</i> SCHOCH, 1997	Middle Triassic, upper Ladinian, upper Lettenkeuper	Kupferzell, Württemberg, Germany	SMNS 91247: fragment of skull table (?supratemporal). 1 slide
<i>Mastodonsaurus giganteus</i> (JAEGER, 1828)	Middle Triassic, upper Ladinian, upper Lettenkeuper	Kupferzell, Württemberg, Germany	Skull roof: SMNS 91248; 91249; 91250; 80878; 91251–91254. 14 slides. Clavicle: SMNS 91255, juvenile. 2 slides
<i>Metoposaurus diagnosticus</i> (VON MEYER, 1842)	Late Triassic	Krasiejów, Poland	Dermal bone fragment: MB.Hi.1718–1723; MB.Hi.1721 was figured by GROSS (1934: fig. 3). 6 slides produced by WALTER GROSS
<i>Plagiosuchus pustuliferus</i> (FRAAS, 1896)	Middle Triassic, Ladinian, Lettenkeuper	Württemberg, Germany	SMNS 82023: fragment of skull roof. 2 slides; MB.Hi.1705: unidentified dermal bone. 1 slide produced by WALTER GROSS
<i>Plagiosternum granulosum</i> (FRAAS, 1889)	Middle Triassic, Ladinian, Grenzbonebed	Württemberg, Germany	SMNS 91256: interclavicle. 3 slides
<i>Gerrothorax</i> sp.	Middle Triassic, Ladinian, Longobardian	Württemberg, Germany	SMNS 91257, 91258: clavicles; SMNS 91259, 83033: fragments of interclavicle. 8 slides
Lepospondyls			
<i>Diplocaulus magnicornis</i> COPE, 1882	Early Permian, UCMP: Wellington Formation MCZ: Arroyo Formation, Clear Fork Group	UCMP: Orlando, Oklahoma, USA; MCZ: Texas, USA	Fragments of dermal skull roof: UCMP 203658: 5 fragments; 203505: 4 fragments; 203141: 1 fragment; 202966: 1 fragment; MCZ 2269: 4 fragments. 15 slides
<i>Pantylus cordatus</i> COPE, 1881	Early Permian, Wichita Group	Texas, USA	UCMP 20296: fragment of dermal skull roof. 1 slide
Seymouriamorpha			
<i>Seymouria baylorensis</i> BROILLI, 1904	Early Permian	Baylor County, Clear Fork, West Coffee Creek, Texas, USA	MCZ without number: 1 fragment of the lower jaw (?angular). 3 slides
Eureptilia			
<i>Labidosaurus hamatus</i> COPE, 1895	Early Permian, Clear Fork Group	Texas, USA	MCZ without number: 1 fragment of skull table. 1 slide

were studied. The thin sections were examined by using a Leica DC 300 polarising stereomicroscope with transmitted ordinary and polarised light. For the investigation of the bone structure by SEM, dermal bone fragments were first cut and polished, and the polished surface was then etched with 10 % HCL for 8–10 seconds.

All dermal bones sectioned in this study are assumed to belong to adults or, in the case of *Sclerocephalus haeuseri* GOLDFUSS, 1847, *Archegosaurus decheni* GOLDFUSS, 1847 (based on skull length) and *Acanthostega gunnari* JARVIK, 1952 (based on bone thickness of the cheek), to subadults. The only small juvenile specimen in the sample belongs to *Mastodonsaurus giganteus* (JAEGER, 1828) and is listed and described separately from the adults of this species. For each taxon investigated here, the bone microstructure and histology was consistent. Intraspecific variability was only observed in *Mastodonsaurus giganteus* and *Plagiosternum granulatum* and affects the degree of vascularization of the bone (see description).

The terminology of FRANCILLON-VIEILLOT et al. (1990) and DE RICQLÈS et al. (1991) concerning bone histology will

be used throughout the text. Furthermore, I follow SCHEYER & ANQUETIN (2008) in their work on turtle shell bone histology in the use of the term ‘external’ and ‘internal’. An appropriate alternative designation is ‘superficial’ and ‘deep’, as used by HILL (2006) instead of ‘external’ and ‘internal’, respectively. The external sculptured surface of the dermal bone faces the body surface, whereas the internal surface is oriented to the visceral surface of the body. The term ‘interior’ corresponds to the inner or middle part of the bone. In general, the dermal bones show a diploë structure, i. e., a middle region that is cancellous or trabecular is mantled by compact external and internal cortices. Three-dimensionally interwoven bundles of collagen fibers with a well ordered fiber bundle arrangement showing no general isotropy under polarized light are designated here as ‘interwoven structural fibers’ (ISF) (SCHEYER & SANDER 2004; SCHEYER & SÁNCHEZ-VILLAGRA 2007; SCHEYER 2007; SCHEYER & ANQUETIN 2008). They are distinguished from woven or fibrous bone that shows general isotropy and the collagen fibers of which are irregularly and loosely arranged (FRANCILLON-VIEILLOT et al. 1990; DE RICQLÈS et al.

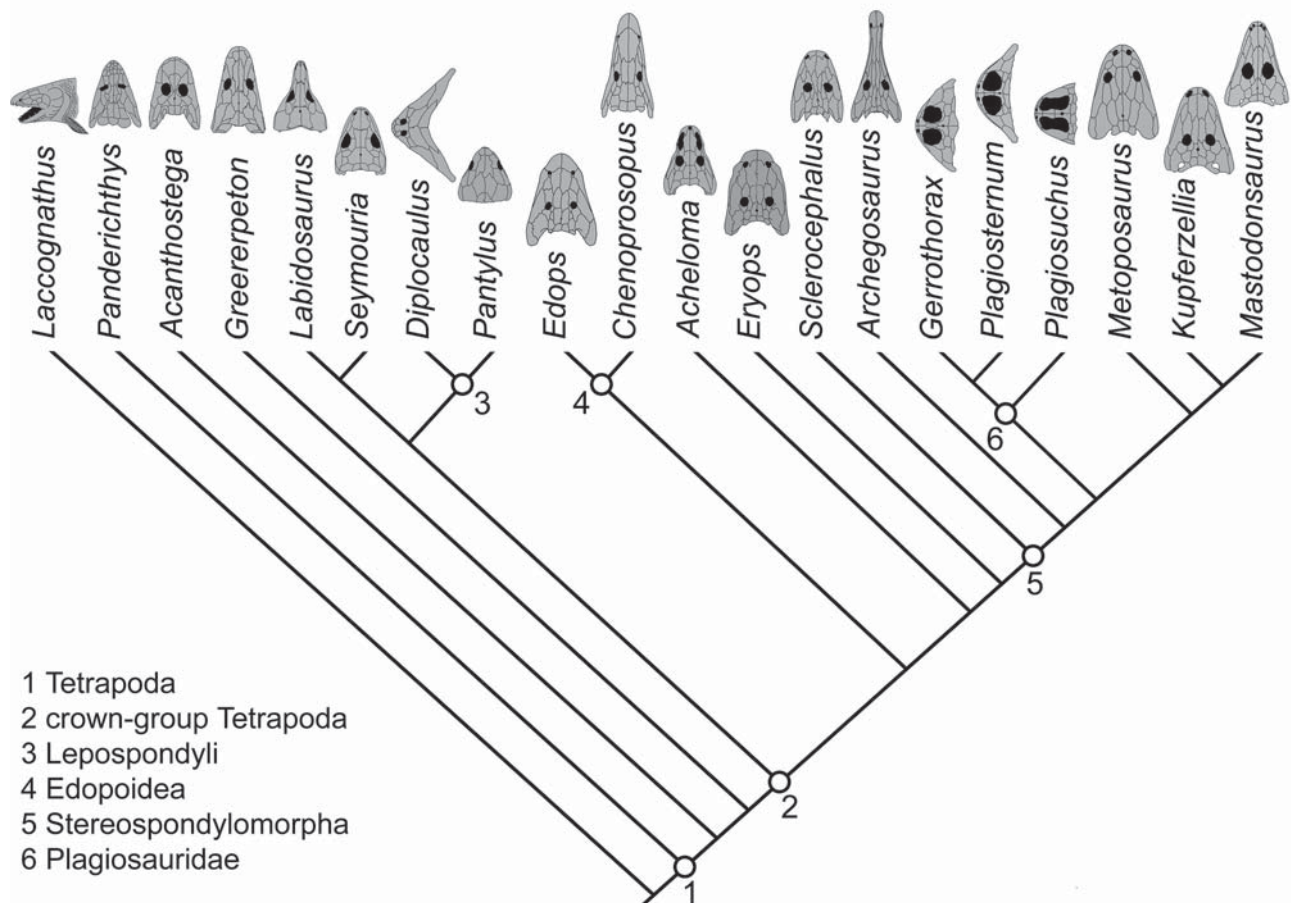


Fig. 1. Phylogenetic relationship of the taxa investigated in this study. After YATES & WARREN (2000), RUTA et al. (2003) and SCHOCH & WITZMANN (2009).

1991). The sculptural tubercles and ridges on the external surface of the dermal bones are called ‘saddles’ and the grooves between them as ‘valleys’ in the thin sections. Canaliculi that are longer than the maximum diameter of the appertaining bone cell lacuna are designated as ‘long’, those that are approximately as long as the maximum diameter are ‘moderately long’, and those whose length is shorter than maximum diameter are termed ‘short’.

The interrelationships of basal tetrapods as found in the analyses of YATES & WARREN (2000), RUTA et al. (2003) and SCHOCH & WITZMANN (2009) are taken as the phylogenetic framework of this study (Fig. 1). The term ‘crown-group tetrapod’ is used here in the sense of HENNIG (1966) as encompassing the last common ancestor of all living tetrapods and all its descendants, fossil and extant. The stem-group tetrapods define all fossil taxa that are more closely related to crown-group tetrapods than to the extant group that is most closely related to crown-group tetrapods (either actinistians [e. g., ZHU & SCHULTZE 2001] or dipnoans [e. g., CLOUTIER & AHLBERG 1996]).

3. Description of histological thin sections

3.1. Outgroup finned sarcopterygian

3.1.1. *Laccognathus panderi* (Porolepiformes)

The external surface of the dermal skull bones of *Laccognathus panderi* GROSS, 1941 bears a sculpture of small, round to oval tubercles that give the bone a pustular appearance. The sectioned bone has a thickness of approximately 4.5 mm, and the ratio external cortex : middle region : internal cortex is 1 : 1.5 : 0.6.

External cortex. As described by PANDER (1860), GROSS (1930) and ØRVIG (1957), the tubercles of the external bone surface represent odontodes (‘dermal teeth’) consisting of dentine with a cap of enamel (Fig. 2a–c), and several odontodes of earlier generations can be found ‘buried’ within the bone matrix of the external cortex and may be in the state of resorption. In some regions, the external bone surface of an earlier growth phase can readily be traced as a sharp red-brownish line, extending from odontode to odontode. Sometimes this line is scalloped out to receive a vascular canal (Fig. 2a). Short, fine Sharpey’s fibers that measure approximately 2 µm in diameter cross the former external bone surface at approximately a right angle (Fig. 2a). They are regularly but not densely arranged, are hollow inside and filled by organic substance, indicating that they were not or only poorly mineralized in the living animal. The external cortex is composed mainly of fine parallel-fibered bone (Fig. 2b). Its fibers show regional changes in orientation: fibers that course approximately parallel to the surface of the section

appear bright or dark under polarized light, depending on the orientation of the slide, and have spindle-shaped bone cell lacunae that are bipolar, i. e., they possess short canaliculi at both tapering ends. Fibers that are cut approximately perpendicularly remain dark under polarized light and the bone cell lacunae appear round. Vascularization is high and consists of anastomosing primary vascular canals and primary osteons, that are often aligned in layers.

Middle region. The external cortex grades into the coarse cancellous and well vascularized middle region that possesses several primary and secondary osteons (Fig. 2c). In some areas, the bone is trabecular with large, irregularly shaped erosion rooms. The trabeculae are irregular in outline and lack lining of secondary bone. The primary bone matrix consists of parallel-fibered bone whose fibers show regionally different orientations, similar to the external region. Near the transition to the internal cortex, the bone matrix of the middle region contains several primary osteons aligned in rows.

Internal cortex. The internal cortex is separated from the middle region by a distinct transition. As outlined by PANDER (1860) and GROSS (1930), the internal cortex of *Laccognathus* exhibits a plywood-structure that can be designated as isopedine (Fig. 2d). In polarized light, a regular pattern of horizontal bands is visible. Those bands in which the fibers are cut longitudinally appear bright or dark under polarized light (with elongate cell lacunae), depending on the orientation of the slide, whereas those in which the fibers and bone cell lacunae are obliquely cut brighten up to a lesser extent. Bands with transversely cut fibers remain dark in polarized light (with round cell-lacunae) and exhibit a fine bright meshwork that delineates the single fiber bundles. Fine fibers, which are oriented approximately perpendicular to the internal bone surface, are discernable also in normal transmitted light. The internal cortex is avascular.

3.2. Stem-group tetrapods

3.2.1. *Panderichthys rhombolepis* (“Elpistostegalia”)

The dermal skull bones of *Panderichthys rhombolepis* (GROSS, 1930) bear basically a tubercular sculpture, and low sculptural ridges may connect the tubercles. The thickness of the sectioned bones amounts approximately 4 mm. The ratio external cortex : middle region : internal cortex is 1 : 0.8 : 0.4.

External cortex. The dermal bones of *Panderichthys* lack any dentine and enamel components, so that the sculptural tubercles and ridges are composed solely of bone tissue (Fig. 2e). Similar to odontodes, ‘buried’ tubercles of earlier generations are visible in the external region. As in *Laccognathus*, the bone matrix consists of

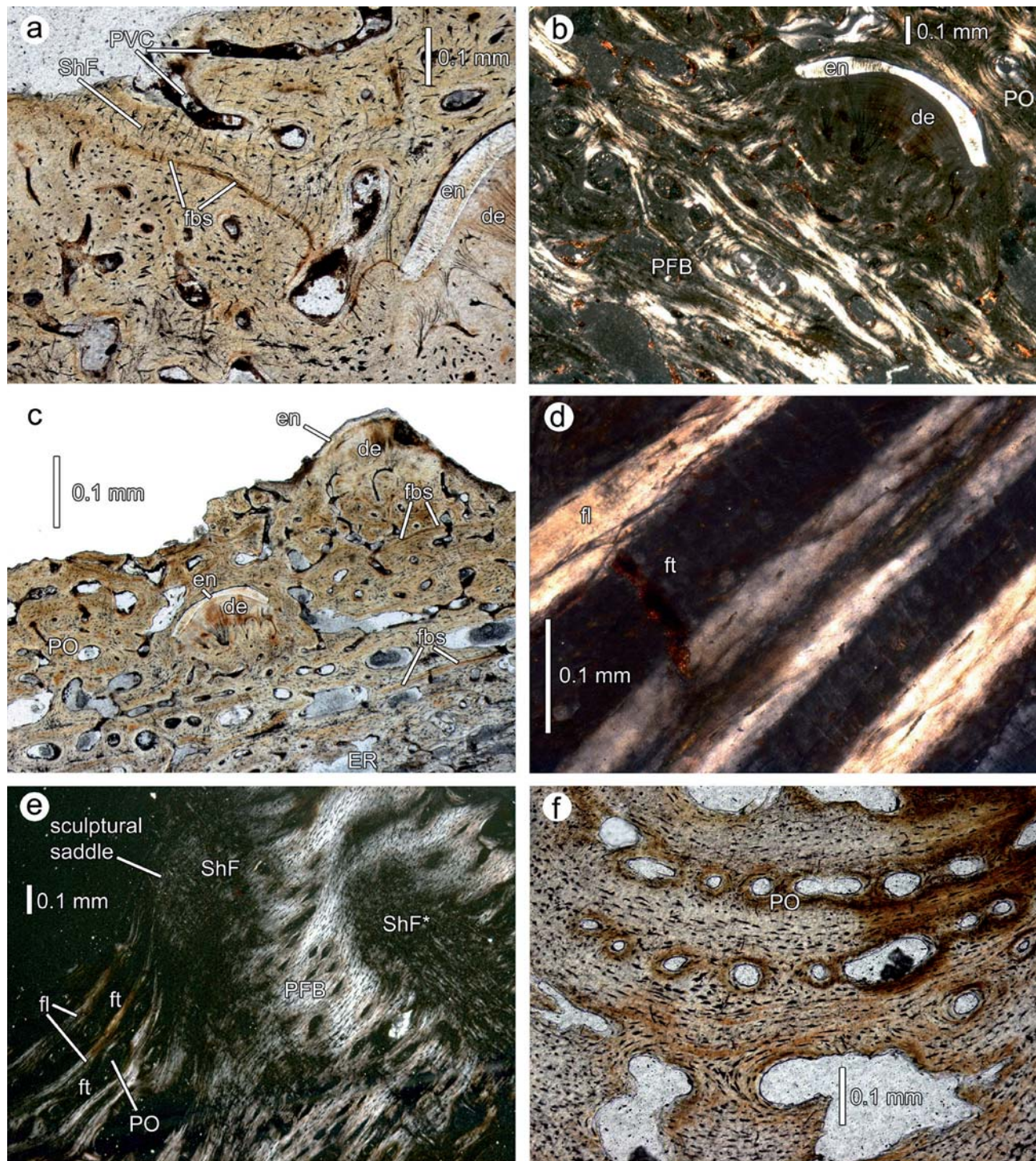


Fig. 2. a–d. *Laccognathus panderi* GROSS, 1941, MB.f.17666. Vertical sections of dermal bones of skull or pectoral girdle. **a.** External cortex in normal transmitted light; next to the odontode, the bone surface of an earlier growth stage with perpendicular, unmineralized Sharpey's fibers is visible. **b.** External cortex with odontode in polarized light. **c.** External cortex with two odontodes and external part of middle region in normal transmitted light; primary and secondary osteons are arranged in rows. **d.** Internal cortex consisting of isopedine, polarized light. – **e–f.** *Panderichthys rhombolepis* (Gross, 1930), MB.f.17548. Vertical sections of dermal bones of skull or pectoral girdle. **e.** External cortex in polarized light with sculptural valley and saddle, which consists solely of bone, the asterisk (*) indicates a 'buried' sculptural saddle of an earlier generation. **f.** Rows of primary osteons in a sculptural valley, normal transmitted light. – For abbreviations, see text.

fine parallel-fibered bone whose fibers show locally different orientations. Growth marks cannot be detected. Vascularization is moderate and consists of a succession of layers of primary osteons interior to the sculptural valleys, and more interiorly, larger erosion cavities are visible (Fig. 2f). These layers of primary osteons are located in a parallel-fibered bone matrix with mostly transversely cut fibers (remain dark under polarized light) and round cell lacunae (Fig. 2e, f). Between these layers, layers of parallel-fibered bone whose fibers are cut longitudinally with spindular, bipolar bone cell lacunae are intercalated. This gives the bone the appearance of alternating dark and bright bands that wedge out at the lateral bases of the sculptural saddles under polarized light (Fig. 2e, on the left). In contrast to the valleys, the saddles are poorly vascularized by primary vascular canals, whereas more interiorly, several anastomosing primary vascular canals are present. Fine Sharpey's fibers that extend far interiorly until to the middle region penetrate the sculptural saddles, both in the superficial saddles and in the 'buried' ones of earlier generations, but are absent in the valleys (Fig. 2e). The Sharpey's fibers have a diameter of 5 to 6 μm . In polarized light, the Sharpey's fibers appear bright and dark, respectively, depending on the orientation of the slide. This indicates that they were well mineralized in the living animal.

Middle region. This region is coarse cancellous. In the more interior part, the region is trabecular with irregular, thin to moderately thick trabeculae that enclose large erosion cavities that are lined by secondary bone lamellae (Fig. 3a). The primary matrix consists mostly of fine parallel-fibered bone. Several smaller secondary osteons are present and some of them cut each other, but do not form Haversian tissue. The middle region is separated from the internal cortex by a distinct transition.

Internal cortex. The internal cortex consists of isopedine, similar to the internal cortex of *Laccognathus*, but appears less regular, since the bands are of different thickness and may fray out at their lateral ends (Fig. 3b). Fine fibers that are approximately perpendicular to the internal bone surface are visible in the dark bands. Scattered primary vascular canals run parallel or oblique to the internal bone surface.

3.2.2. *Acanthostega gunnari*

The investigated sections of *Acanthostega gunnari* JARVIK, 1952 were prepared through the cheek region (probably the squamosal, whose bone thickness varies between 1 mm and 3 mm) with polygonal sculpture. The ratio external cortex : middle region : internal cortex is 1 : 1.8 : 0.9.

External cortex. The bone matrix consists of

parallel-fibered bone that is mostly homogeneous, whereas in some regions, it appears coarse and less regular (Fig. 3c, d). As in the finned sarcopterygians described above, the bone fibers may change their orientation in different regions, and this is reflected by the shape of the bone cell lacunae. The bone is moderately to highly vascularized by primary vascular canals and primary osteons. Loosely arranged Sharpey's fibers with a diameter of 3 to 5 μm penetrate the sculptural saddles until to the middle region (Fig. 3c), but they can also be found in the valleys where they are less abundant. Growth marks are not visible in the external cortex.

Middle region. This region is coarse cancellous with primary osteons and several, partially large secondary osteons (Fig. 3d). The bone matrix consists of fine parallel-fibered bone and of the lamellar bone of the secondary osteons.

Internal cortex. Isolated primary vascular canals may locally be present and run parallel to the internal bone surface. The bone matrix is composed of parallel-fibered bone that appears fine in most regions, but may also change its fiber orientation in irregular layers, so that the internal cortex resembles irregular isopedine in some regions (Fig. 3e). Fine fibers are visible that cross the internal cortex approximately at a right angle.

3.2.3. *Greererpeton burkemorani* (Colosteidae)

Greererpeton burkemorani ROMER, 1969 has strongly sculptured dermal bones with high sculptural ridges. The skull fragment used for sectioning (?quadratojugal) has a sculpture of polygons and furrows of irregular outline, and its thickness ranges from 3.5 mm to more than 5 mm. The ratio external cortex : middle region : internal cortex is 1 : 1.4 : 1.3.

External cortex. As in the taxa described above, the bone matrix of the external cortex consists mainly of parallel-fibered bone the fibers of which show varying orientation in some regions (Fig. 3f), what is reflected in the shape of the bone cell lacunae (Fig. 4a). The intrinsic fibers of the parallel-fibered bone are mostly coarse and vary in extent and direction what gives the bone tissue often a less ordered appearance. Fine Sharpey's fibers (Fig. 3f) that are well mineralized penetrate the external region at approximately a right angle to the surface and are more abundant in the sculptural saddles than in the valleys. The Sharpey's fibers have a diameter of 3 to 7 μm . The external region is well vascularized by partially anastomosing primary vascular canals (Fig. 4a) and scattered primary osteons. Growth marks cannot be observed.

Middle region. The external cortex grades into a fine to coarse cancellous region that is very well vascularized by numerous primary and secondary osteons whose

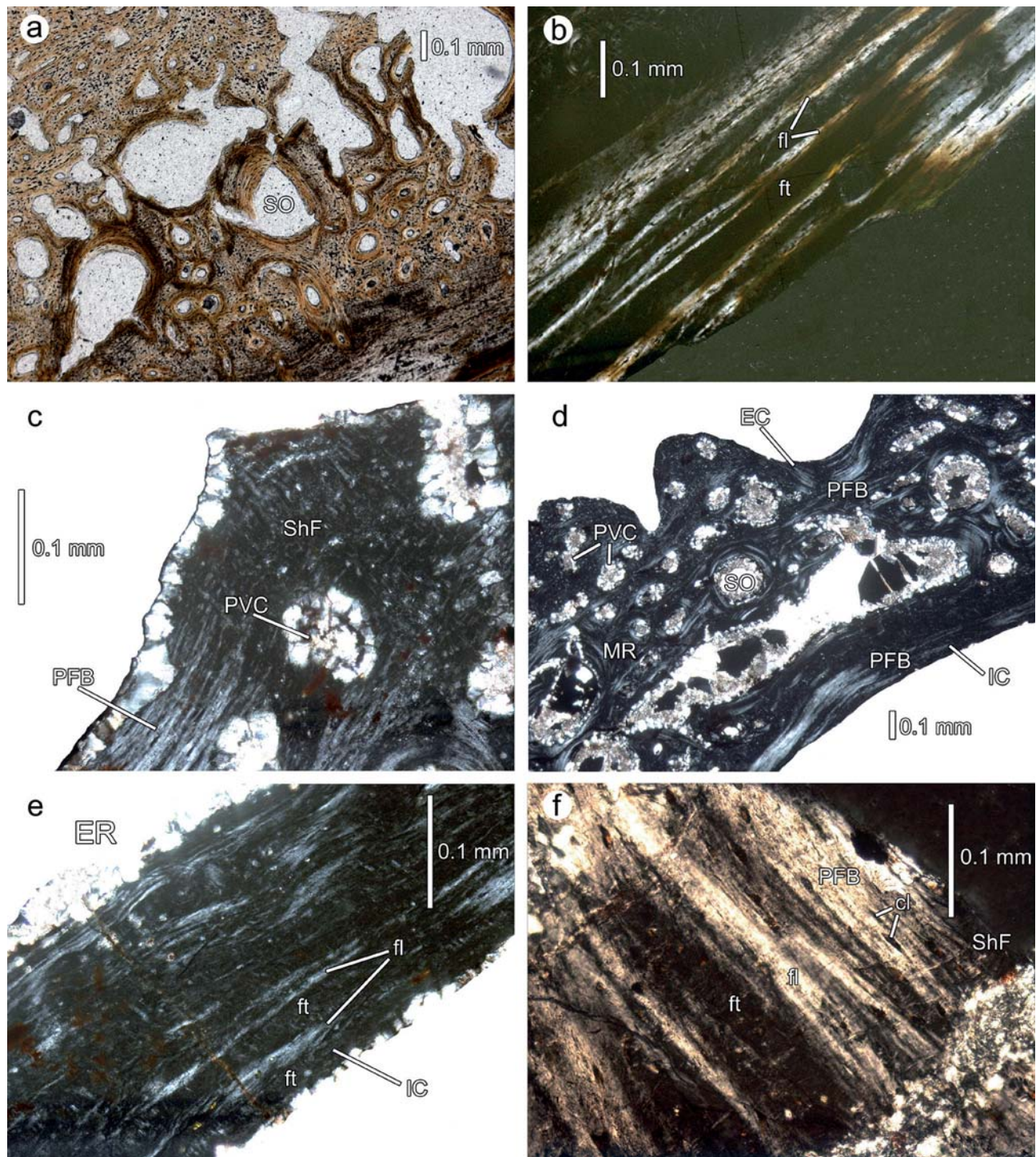


Fig. 3. a–b. *Panderichthys rhombolepis* (GROSS, 1930), MB.f.17548. Vertical sections of dermal bones of skull or pectoral girdle. **a.** Middle region in normal transmitted light with secondary osteons. **b.** Internal cortex consisting of isopedine, polarized light. – **c–e.** *Acanthostega gunnari* JARVIK, 1952, UMZC T 150b. Vertical section of the cheek, probably squamosal. **c.** Sculptural saddle of external cortex with Sharpey's fibers and primary vascular canals, polarized light. **d.** Histological overview in polarized light, the external cortex is well vascularized, and secondary remodeling took place in the middle region. **e.** Internal region in polarized light, the bone fibers may show changing orientation in different layers, so that it has locally an isopedine-like appearance. – **f.** *Greererpeton burkemorani* ROMER, 1969, CMNH 11900. Vertical sections of dermal skull bone (?quadratojugal). Low sculptural saddle of external cortex in polarized light; the parallel-fibered bone shows regional changes of its bone fiber orientation, and thin Sharpey's fibers are present. – For abbreviations, see text.

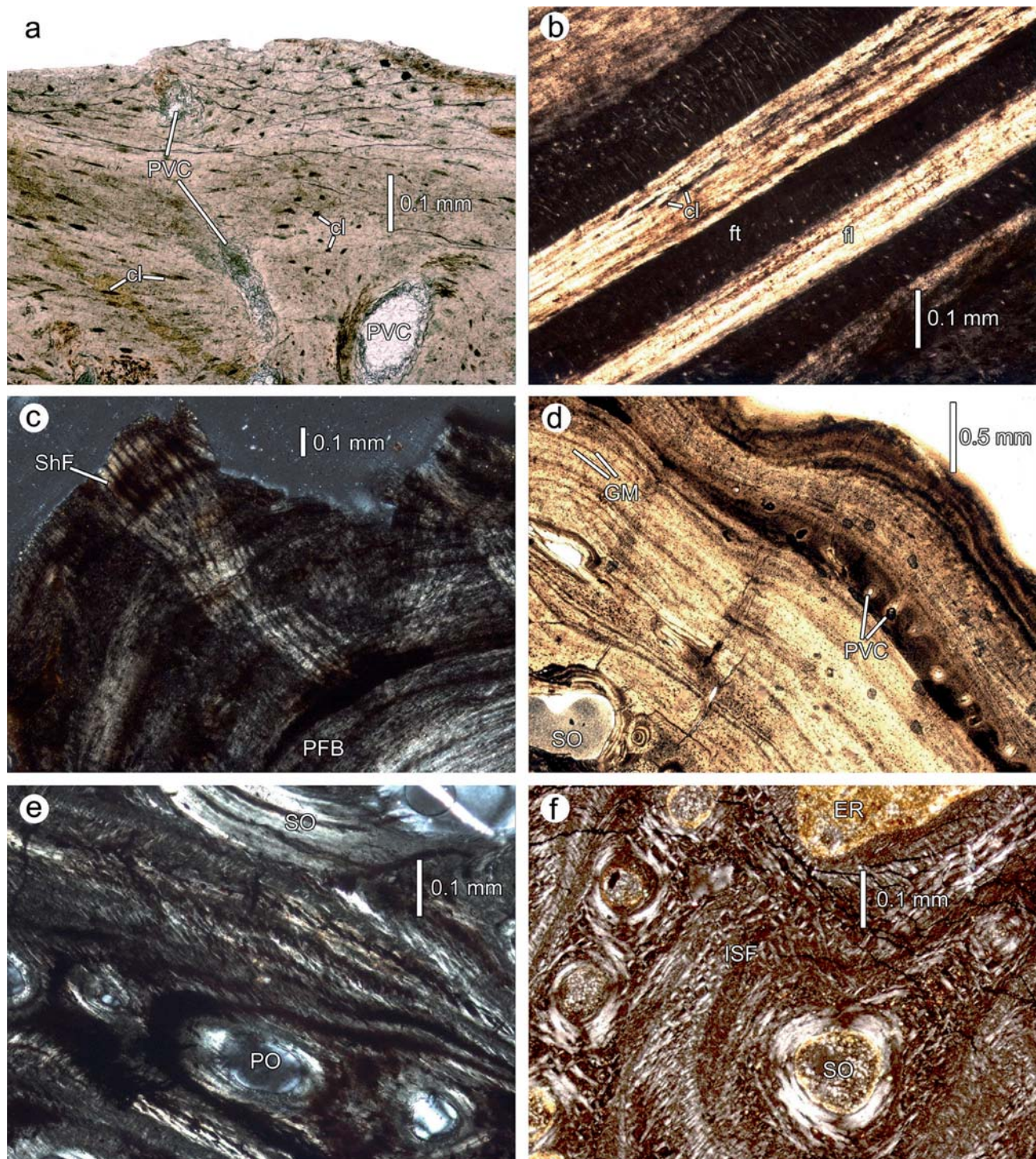


Fig. 4. a–b. *Greererpeton burkemorani* ROMER, 1969, CMNH 11900. Vertical sections of dermal skull bone (?quadratojugal). **a.** Low sculptural saddle of external cortex in normal transmitted light, the shape of the bone cell lacunae represents the direction of the bone fibers: on the left, the lacunae are spindular and indicate that the fibers are oriented parallel to the image plane, and on the right, the lacunae are round and indicate transverse section of the fibers. **b.** Internal cortex consisting of isopedine in polarized light. – **c–f.** *Edops craigi* ROMER, 1936, MCZ 1235. Vertical section of skull table bone. **c.** External cortex, sculptural saddle with Sharpey's fibers, polarized light. **d.** External cortex showing growth marks and sparse vascularization, normal transmitted light. **e.** Middle region with primary matrix of fine, subparallel fibers and primary and secondary osteons, polarized light. **f.** Middle region with interwoven structural fibers as primary tissue, polarized light. – For abbreviations, see text.

Haversian canals may constitute large cavities, but true Haversian tissue cannot be observed. The interstitial, primary bone matrix consists of fine parallel-fibered bone.

I n t e r n a l c o r t e x . The compact internal cortex consists of isopedine, and the shape of the bone cell lacunae reflects the orientation of the fibers. However, the discrete bands exhibit a broad variation in their thickness (Fig. 4b). Most parts of the internal cortex are avascular, but in the most interior part, isolated primary vascular canals and few secondary osteons are visible that are parallel to the internal bone surface. Fine fibers that are arranged perpendicular to the internal bone surface are visible in the 'dark layers'.

3.3. Crown-group tetrapods

3.3.1. *Edops craigi* (Temnospondyli, Edopoidea)

The bone fragments of *Edops craigi* ROMER, 1936 used for sectioning stem from the skull table and bear a rather irregular, polygonal sculpture of ridges and pits. Histologically, the middle region of the bone is much thickened with respect to the cortices. The sectioned bone fragments attain a thickness of more than 12 mm. The ratio external cortex : middle region : internal cortex is 1 : 3.6 : 0.6.

E x t e r n a l c o r t e x . In large areas, the external cortex consists of coarse parallel-fibered bone with spinular bone cell lacunae that have long, branching canaliculi. Distinct growth marks are present, and the bone can thus be designated as lamellar-zonal (Fig. 4c, d). Vascularization is in most parts low and consists of isolated primary vascular canals and few primary osteons that may be aligned in single rows (Fig. 4d). Sculptural saddles of earlier generations are embedded within the cortex. Fan-shaped clusters of densely arranged Sharpey's fibers appear irregularly in the sculptural saddles, where they penetrate the bone tissue (Fig. 4c). In the sculptural valleys, the fibers are less numerous. The sometimes bifurcating Sharpey's fibers measure around 21 μm in diameter and may extend to the middle region. In some areas more interior within the cortex, primary interwoven structural fiber bundles (ISF) sensu SCHEYER & SÁNCHEZ-VILLAGRA (2007) are present and show a non-homogeneous distribution. Such interwoven structural fibers are more abundant in the middle region and are therefore described below. The outer parts of the external layer are in few places disturbed by areas of secondary bone remodeling with a distinct resorption line. These resorption structures at the bone surface are described in more detail for *Eryops* (see below). The external cortex is separated from the middle region by a distinct transition, with the occurrence of several small secondary osteons.

M i d d l e r e g i o n . This fine to coarse cancellous

region underwent extensive remodeling with numerous secondary osteons that constitute Haversian tissue in many areas. The interstitial primary bone consists in many areas of parallel-fibered bone. Rather fine primary fibers that are oriented subparallel, but may change their direction in succeeding layers, can frequently be observed (Fig. 4e). These layers can be arranged irregularly in a 'flowmark'-like fashion. In some areas or layers, primary fibers cross each other at an angle of approximately 90° and constitute a three-dimensional network of interwoven structural fibers (Fig. 4f). Under polarized light, the birefringence patterns of the collagen fibers are well visible. Approximately transversely cut fiber bundles have a globular appearance. Focusing on different planes of the slide under the microscope shows that these structures do not represent real globules like cell spaces, for instance, but fibers that extend perpendicularly or obliquely to the image plane. Between the fibers, bone cell lacunae of irregular outline with no or only stumpy canaliculi are present. These areas of fibers are remains of primary bone, which was remodelled and partially bounded by secondary bone. Near the internal cortex, primary osteons may be aligned regularly in layers.

I n t e r n a l c o r t e x . Only parts of the compact internal cortex are preserved. As far as it can be discerned, it consists of coarse, less organized parallel-fibered bone that is avascular.

3.3.2. *Chenoprosopus milleri* (Temnospondyli, Edopoidea)

Bone fragments of the skull table of *Chenoprosopus milleri* MEHL, 1913 were sectioned that bear a sculpture of rounded polygons. The internal part of the middle region, and the complete internal cortex are eroded. The thickness of the sectioned bone fragments ranges from 3 mm to 6 mm.

E x t e r n a l c o r t e x . The external cortex is mainly composed of coarse parallel-fibered bone that shows cyclic growth marks (lamellar-zonal bone). The bone cells are variable in outline with varying length of their canaliculi, and are randomly distributed. In the external part of the sculptural saddles, densely arranged Sharpey's fibers with a diameter of 8 to 17 μm are present (Fig. 5a). Some of the fibers may extend until to the external part of the middle region. The fibers may ramify into two or three branches. In the sculptural valleys, the Sharpey's fibers are less numerous than in the saddles and may also be absent in places. In the more interior part of the external cortex, the parallel-fibered bone shows transitions to a network of interwoven structural fibers that extend obliquely to the bone surface (Fig. 5b). The bone cell lacunae in this bone tissue are irregularly arranged and pos-

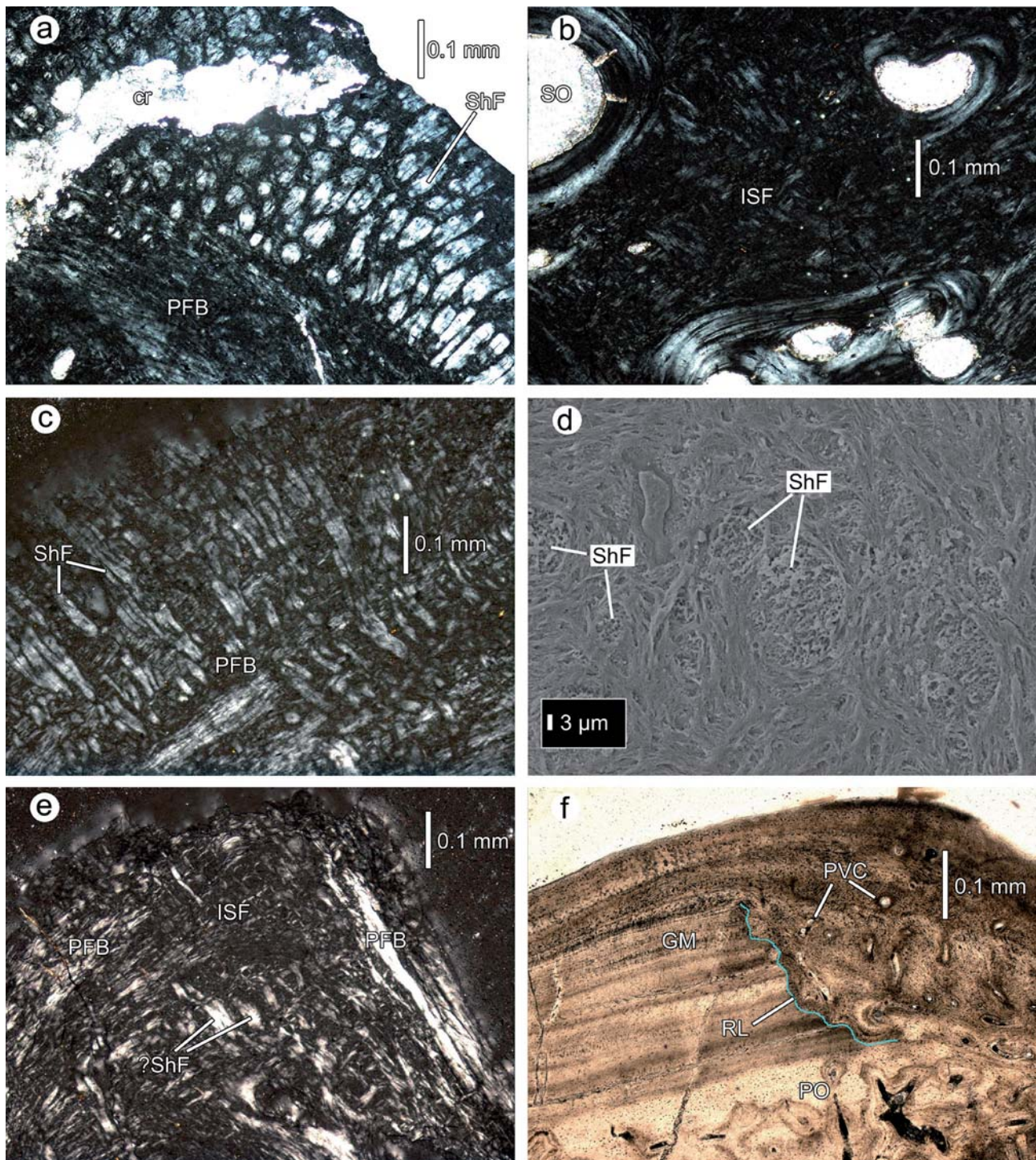


Fig. 5. a–b. *Chenoprosopus milleri* MEHL, 1913, UCMP 41104. Vertical section of skull table bone. **a.** Sculptural saddle of external cortex consisting of parallel-fibered bone with strong bundles of Sharpey's fibers that are obliquely cut, polarized light. **b.** More interior part of external cortex with interwoven structural fibers, polarized light. – **c–f.** *Eryops megacephalus* COPE, 1877. Vertical section of dermal skull bones. **c.** MCZ 7622, external cortex with parallel-fibered bone and bundles of Sharpey's fibers, polarized light. **d.** UCMP 203332, SEM of horizontally cut external cortex with Sharpey's fibers in cross-section. **e.** MCZ 7622, sculptural saddle in polarized light showing parallel-fibered bone and interwoven structural fibers. **f.** MCZ 7622, vertical section of external cortex with secondary remodeling in the externalmost part; the boundary between primary bone and remodelled bone is indicated as a blue line. – For abbreviations, see text.

sess no canaliculi. The external cortex is poorly vascularized with scattered primary vascular canals and isolated primary osteons. In one slide, a layer of primary osteons is visible interior to a sculptural valley. The external cortex grades into the middle region with the occurrence of scattered secondary osteons that increase in number and density in a small transitional zone.

Middle region. This fine to coarse cancellous region is characterized by extensive remodeling of the bone. Numerous secondary osteons that may course in different directions are present that in parts build Haversian tissue. The interstitial primary bone consists of parallel-fibered bone that shows transitions to fine interwoven structural fibers in some regions.

3.3.3. *Eryops megacephalus* (Temnospondyli, Eryopidae)

The bone fragments of the dermal skull roof of *Eryops megacephalus* COPE, 1877 sectioned for this study bear pits of variable outline, and thus the sculpture appears rather irregular. The ratio external cortex : middle region : internal cortex is 1 : 3.3 : 0.6. The bone fragments used for sectioning attain a thickness of more than 14 mm.

External cortex. Densely arranged Sharpey's fibers with a diameter of mostly 21 to 29 μm penetrate the external cortex until to the middle region (Fig. 5c, d). The Sharpey's fibers may be numerous also in the valleys. Coarse, often less ordered parallel-fibered bone predominates the bone matrix of the external cortex and has bone cell lacunae of variable shape that are arranged in rows and have branching, moderately long to long canaliculi. The bone matrix shows local islets of interwoven structural fibers especially in the more interior parts of the cortex, but they may also be present individually in the more external parts (Fig. 5e). Conspicuous growth marks are present in the external cortex (Fig. 5f). Similar to *Edops*, the more superficial parts of the external cortex may be disturbed by areas of secondary bone remodeling (Fig. 5f). The remodelled bone lies discordantly on the primary bone, separated by a distinct resorption line. Whereas the adjacent primary bone is only sporadically pervaded by primary vascular canals and primary osteons, the secondary bone is well vascularized. It consists of parallel-fibered bone and interwoven structural fibers and lacks the clear zonal pattern. In specimen MCZ 7622-2, the remodelled area was subsequently overgrown by 'normal' parallel-fibered bone.

Middle region. The external cortex is separated from the middle region by a short transition zone that contains scattered secondary osteons. The middle region is mostly fine to coarse cancellous and shows extensive remodeling with Haversian tissue (Fig. 6a, b). Also subordinate areas are present in which large vascular spaces are

separated by irregularly arranged trabeculae that are rather thick and short. The interstitial primary bone consists of parallel-fibered bone and of the three-dimensional network of interwoven structural fibers (Fig. 6b–d), as described for *Edops*. The transversely cut fibers are visible as 'globules', and between the fibers, bone cell lacunae of irregular outline with no or short canaliculi are visible (Fig. 6c).

Internal cortex. This only fragmentarily preserved region consists mostly of coarse parallel-fibered bone with a less ordered appearance. Transitions to islets of interwoven structural fibers may occur in some areas. Fine, oblique extrinsic fibers that are densely arranged and probably represent Sharpey's fibers cross the internal cortex in MCZ 7622-2. The cortex is poorly vascularized by scattered primary osteons and primary vascular canals.

3.3.4. *Acheloma cumminsi* (Temnospondyli, Dissorophoidea, Trematopidae)

The bone fragments of the dermal skull roof of *Acheloma cumminsi* COPE, 1882 used for sectioning possess rather regular, rounded sculptural pits on their external surface. The bone fragment investigated has a thickness of almost 9 mm, and the ratio external cortex : middle region : internal cortex is 1 : 6.1 : 1.2.

External cortex. The bone matrix is constituted by mostly homogeneous, fine parallel-fibered bone. Vascularization is poorly developed and consists of few primary vascular canals and primary osteons. The sometimes bifurcating Sharpey's fibers with a diameter of 15 to 31 μm are conspicuous. They are restricted to the sculptural saddles where they are moderately to densely arranged (Fig. 6e). Growth marks are present, but are indistinct and difficult to follow. Bone cell lacunae are often oval in shape and possess branching canaliculi. They are more orderly arranged in the valleys than in the saddles, where they have frequently a rather round shape.

Middle region. The transition from the external and internal cortex to the trabecular middle region is abrupt. The middle region underwent strong resorption and remodeling and possesses numerous bone cavities of irregular shape and size, most of which are lined by secondary lamellar bone. The rather short trabeculae are irregularly arranged. The primary bone matrix in the trabeculae consists of homogeneous parallel-fibered bone.

Internal cortex. This region is made of avascular, fine parallel-fibered bone, which is penetrated in some areas by thin fibers at an angle of approximately 60°. Bone cell lacunae are spindular, have long, branching canaliculi and are arranged in rows (Fig. 6f). They may form dark layers of densely arranged lacunae within the internal cortex.

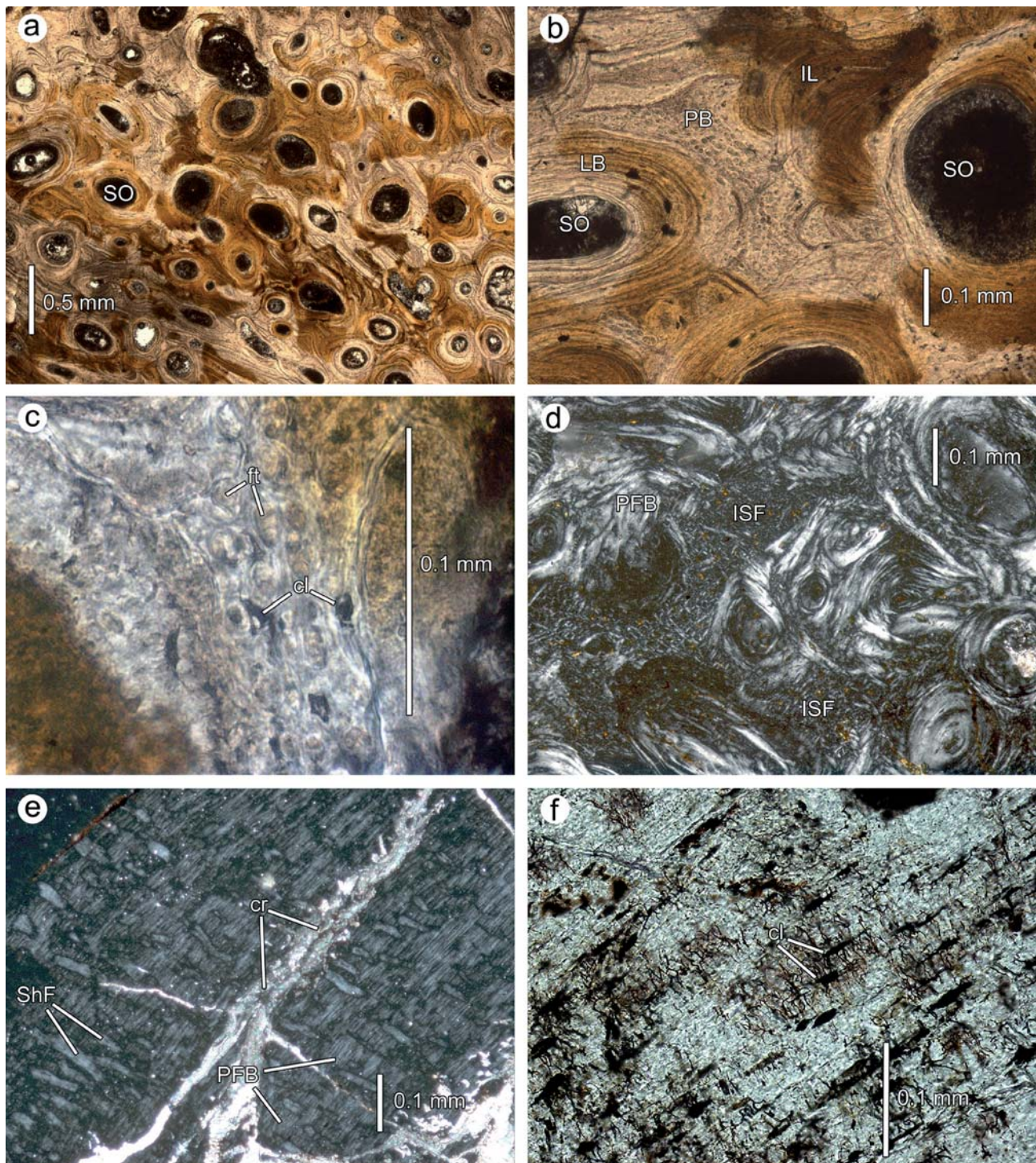


Fig. 6. a–d. *Eryops megacephalus* COPE, 1877, MCZ 7622. Vertical sections of dermal skull bones. **a.** Overview of middle region with Haversian tissue, normal transmitted light. **b.** Middle region with secondary osteons and interstitial primary bone tissue, normal transmitted light. **c.** Close up of interstitial primary bone tissue of middle region, showing ‘globular’ fibers in cross section, normal transmitted light. **d.** Middle region in polarized light, showing primary interwoven structural fibers. – **e–f.** *Acheloma cummingsi* COPE, 1882, MCZ 1490. Vertical section of skull roof fragment. **e.** Sculptural saddle of parallel-fibered bone with Sharpey’s fibers in polarized light. **f.** Internal cortex with bone cell lacunae, normal transmitted light. – For abbreviations, see text.

3.3.5. *Sclerocephalus haeuseri* (Temnospondyli, Stereospondylomorpha)

The postfrontal of a subadult specimen of *Sclerocephalus haeuseri* GOLDFUSS, 1847 was sectioned. The bone has a maximum thickness of 4.2 mm, and the ratio external cortex : middle region : internal cortex amounts 1 : 4.2 : 1.1. Unfortunately, the bone was heavily altered by recrystallization, so that nothing can be said about the bone tissue itself or the intrinsic and extrinsic fibers. However, the slide shows the vascularization of the cortices, the bone's microstructure and growth marks. The bone structure is best visible in reflected light (Fig. 7a, b). The external cortex is moderately to low vascularized by primary vascular canals (Fig. 7a). Bone cell lacunae are abundant, but their exact shape cannot be determined. Cyclical growth marks are conspicuous and follow the relief of the external bone sculpture. The middle region can be designated as trabecular with large erosion rooms that are lined by secondary lamellar bone (Fig. 7a, b). The internal cortex is poorly vascularized by scattered primary vascular canals.

3.3.6. *Archegosaurus decheni* (Temnospondyli, Stereospondylomorpha)

A prefrontal of a subadult specimen of *Archegosaurus decheni* GOLDFUSS, 1847 was sectioned. The external bone surface possesses a polygonal sculpture in the ossification centre and radiating ridges in the periphery. Unfortunately, the external portion of the external cortex is eroded. This is rather common in *Archegosaurus*, since the specimens are preserved in siderite concretions (geodes) and divide into part and counterpart when the concretions are split. Because of this surface erosion, the ratio between the thickness of the cortices and the middle region cannot be calculated. The maximum thickness of the bone is approximately 2.5 mm.

External cortex. The preserved parts of the external cortex consist homogeneously of parallel-fibered bone that is moderately to highly vascularized by primary canals, primary osteons (partially anastomosing) and, more interiorly, by secondary osteons (Fig. 7c). The latter mark the transition zone to the middle region. Bone cell lacunae are numerous, randomly arranged in the primary bone matrix and are of varying shape. The canaliculi are moderately long to long and branching. Sharpey's fibers that penetrate the external bone surface are not visible (probably due to erosion of the external portion of the cortex). However, the prefrontal forms a rather thin, underplating shelf for articulation with the lacrimal; in this region, densely arranged, almost horizontally oriented Sharpey's fibers are visible that connected the two adjacent bones (Fig. 7d).

Middle region. The trabecular middle region experienced extensive erosion and remodeling. Large erosion rooms, some of them lined by secondary lamellar bone, are separated from each other by trabeculae of irregular outline and direction (Fig. 7c). Many of the trabeculae are stout, others are slender and long. The interstitial bone matrix of the trabeculae may contain small primary or secondary osteons, which are sometimes cut. The primary matrix of the middle region consists of parallel-fibered bone, and morphology and alignment of the bone cells corresponds to those of the external cortex.

Internal cortex. The internal cortex is separated from the trabecular middle region by a thin transition zone with small secondary osteons (Fig. 7c) and consists of rather coarse parallel-fibered bone. The matrix is penetrated by scattered primary vascular canals that course in different directions. Bone cell lacunae are aligned in rows and have an elongate, flattened shape with long, branching canaliculi.

3.3.7. *Kupferzellia wildi* (Temnospondyli, Stereospondylomorpha, Capitosauroida)

The bone fragment of *Kupferzellia wildi* SCHOCH, 1997 under study is derived from the skull table and probably represents a part of the supratemporal. Its dermal sculpture consists of rather regular, wide polygons. The thickness of the investigated bone amounts slightly more than 5 mm, and the ratio external cortex : middle region : internal cortex is 1 : 1.7 : 0.5.

External cortex. The bone matrix consists mainly of coarse parallel-fibered bone with a rather irregular fibrous arrangement (Fig. 7e). In the sculptural saddles, the parallel-fibered bone is even less organized than in the valleys. The external cortex is moderately vascularized: more externally, only isolated, small primary vascular canals and primary osteons are visible, whereas more interiorly, a larger number of small primary canals and primary osteons (as well as few secondary osteons) are present and may anastomose. Sharpey's fibers are restricted to the sculptural saddles and measure 5 to 16 μm in diameter. In the parallel-fibered bone of the sculptural valleys, the bone cell lacunae are mostly spindular with long canaliculi and are arranged in layers. In contrast, their shape is variable in the more coarse parallel-fibered bone of the saddles. Growth marks are present but difficult to follow.

Middle region. This region is coarse cancellous with several secondary osteons of varying size, but Haversian tissue is not present (Fig. 7f). In the interior part, the Haversian canals may be quite large. The primary matrix consists of fine parallel-fibered bone with generally spindular cell lacunae. Local transitions to interwoven struc-

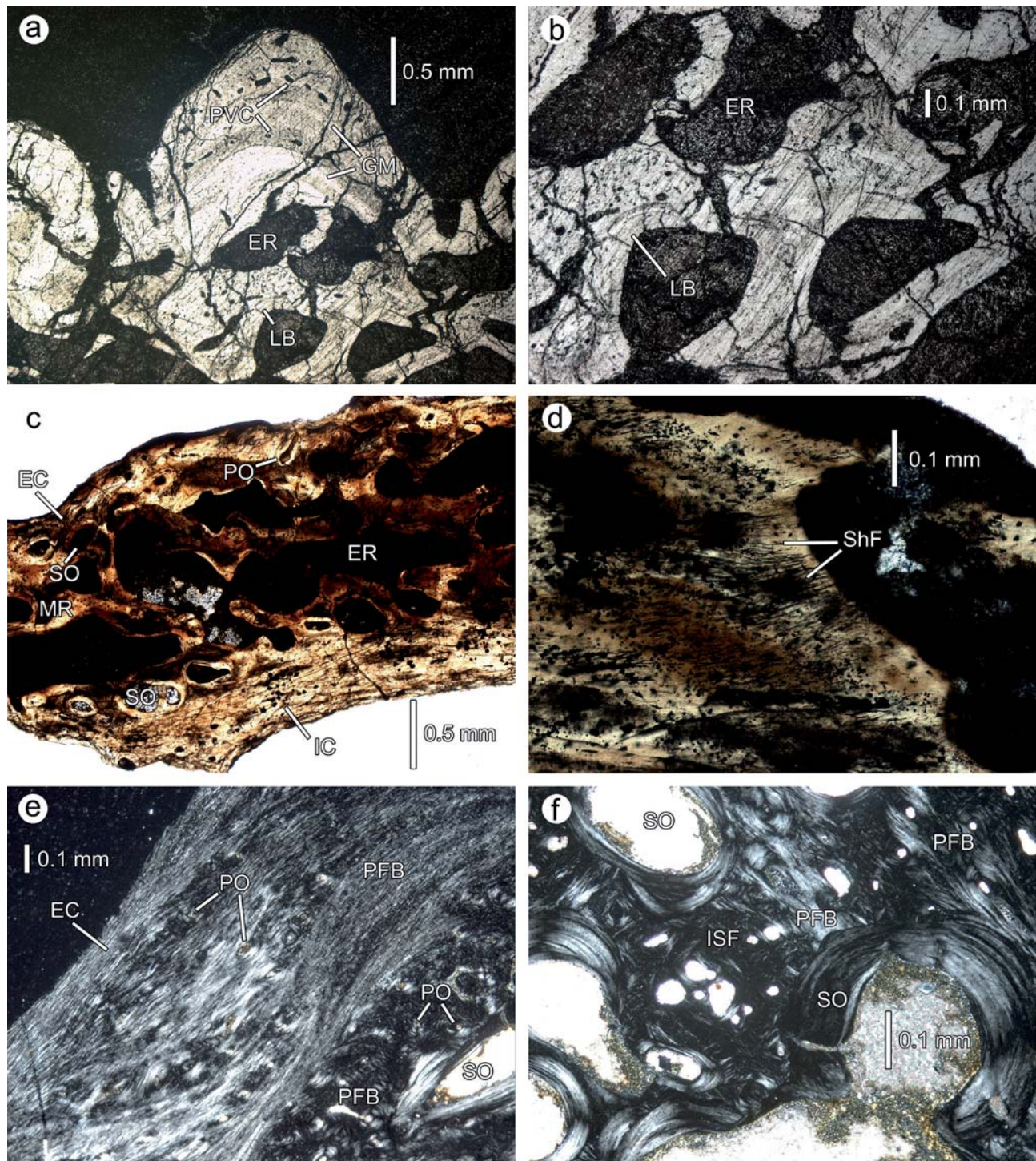


Fig. 7. a–b. *Sclerocephalus haeuseri* GOLDFUSS, 1847, SMNS 90517. Vertical section of postfrontal, reflected light. a. External cortex with external portion of middle region. b. Close up of middle region with large erosion rooms lined by secondary bone. c–d. *Archegosaurus decheni* GOLDFUSS, 1847, MB.Am.152. Vertical section of prefrontal. c. Histological overview in normal transmitted light. d. Close up of shelf for articulation with the lacrimal with horizontally oriented Sharpey's fibers in normal transmitted light. – e–f. *Kupferzellia wildi*, SCHOCH, 1997, SMNS 91247. Vertical section of ?supratemporal. e. External cortex with lateral part of sculptural saddle, polarized light. f. Middle region with secondary osteons, polarized light. – For abbreviations, see text.

tural fibers are present, in which most of the lacunae are round. Canaliculi are mostly short. More internally, the secondary osteons are smaller and aligned in two to four rows that are separated by avascular layers of parallel-fibered bone.

I n t e r n a l c o r t e x . Coarse parallel-fibered bone constitutes the bone matrix of the internal cortex, with locally changing directions of its fibers. Most of the bone cell lacunae are spindle-shaped and have few canaliculi. Extrinsic fibers are not visible. Vascularization is poor and consists of scattered primary vascular canals.

3.3.8. *Mastodonsaurus giganteus* (Temnospondyli, Steirospondylomorpha, Capitosauroida)

The dermal sculpture of *Mastodonsaurus giganteus* (JAEGER, 1828) is composed of regular, rather square pits on the skull table. The peripheral parts of the bones of the postorbital skull table consist of radiating ridges and furrows. Some sections for this study were cut through bones with polygonal sculpture, and others were made perpendicular or parallel to the radiating ridges. The ratio external cortex : middle region : internal cortex is 1 : 3 : 0.4. The bone thickness of the investigated specimens ranges from 8 mm to 17 mm. Additionally, the clavicular blade of a small juvenile specimen has been sectioned and is described separately below.

E x t e r n a l c o r t e x . The bone matrix consists of both rather coarse parallel-fibered bone and fine interwoven structural fibers. In some saddles, more parallel-fibered bone is present than interwoven structural fibers, whereas in others, a matrix of interwoven structural fibers predominates (Fig. 8a). In the sculptural valleys, coarse parallel-fibered bone is generally (but not always) more common, and layers of interwoven structural fibers may be intercalated within the parallel-fibered bone. The bone cell lacunae in interwoven structural fibers are often irregular in outline and arrangement, and possess short or no canaliculi (Fig. 8b). Rather short, but thick Sharpey's fibers with a diameter of 25 to 28 μm are present in the sculptural saddles and are loosely arranged. Sharpey's fibers are less abundant in the sculptural valleys, and may also be absent. In some specimens, the external parts of the external cortex are poorly vascularized by isolated primary vascular canals and primary osteons, but more interiorly in the cortex, primary osteons are abundant and are aligned in rows or form an anastomosing network. In other specimens (SMNS 91252), almost the complete external cortex is well vascularized by primary vascular canals and especially primary osteons, which are arranged in a regular succession parallel to the external surface (Fig. 8c). In the more external part of the cortex, the canals are distinctly

smaller than the canals in the more interior portion, and in the most external part, some of the canals have become larger again. These differences in vascularization between specimens might be explained as ontogenetic variation (see discussion). Isolated secondary osteons are present in the interlaced intermediate zone between external cortex and middle region. Growth marks are often conspicuous and follow the pattern of the external sculpture (Fig. 8d). In the external cortex of SMNS 91249, an almost horizontal line represents the former external bone surface in an earlier ontogenetic stage. More externally, three succeeding generations of sculptural saddles are visible that became increasingly steeper in ontogeny (Fig. 8e). External surface resorption and remodeling as described above for *Edops* and *Eryops* are present in some specimens (Fig. 9a). In SMNS 80878, the external cortex is in some areas extensively remodelled by secondary osteons that sometimes occur in clusters and may form Haversian tissue.

M i d d l e r e g i o n . This mostly coarse cancellous region is extensively vascularized by primary and secondary osteons (Fig. 9b), and large vascular spaces may occur in the more interior portion. These areas can be designated as trabecular with thick, short trabeculae, which are irregularly arranged. More externally and internally, in direction to the cortices, primary osteons are frequently arranged in rows, with less vascularized layers of bone intercalated between them. The secondary osteons form Haversian tissue in many areas (Fig. 9b, bottom). More externally, erosion rooms with Howship's lacunae are detectable (Fig. 8d, e).

The primary and secondary osteons course frequently approximately parallel to the radiating sculptural saddles. The interstitial primary bone consists mainly of parallel-fibered bone. Rather fine primary fibers are present that are oriented subparallel, but change their direction in succeeding, often irregular layers, similar to *Edops* and *Eryops* as described above. These fiber areas are remains of primary bone, which was remodelled and separated from secondary bone by resorption lines. In some areas or layers, primary fibers cross each other at approximately a right angle and form interwoven structural fibers. Bone cell lacunae in the fibrous areas are most often irregular in outline, whereas they are mostly spindle-shaped and possess branching canaliculi in the parallel-fibered bone.

I n t e r n a l c o r t e x . The internal cortex consists of less organized parallel-fibered bone whose fibers show an often irregular arrangement, and transitions to interwoven structural fibers exist. In the interior portion, primary vascular canals and primary osteons are arranged in rows and course mainly in the direction of radial sculpture (Fig. 9c). The more internal region is poorly vascularized. Thin extrinsic fibers (Sharpey's fibers) may extend obliquely into the bone.

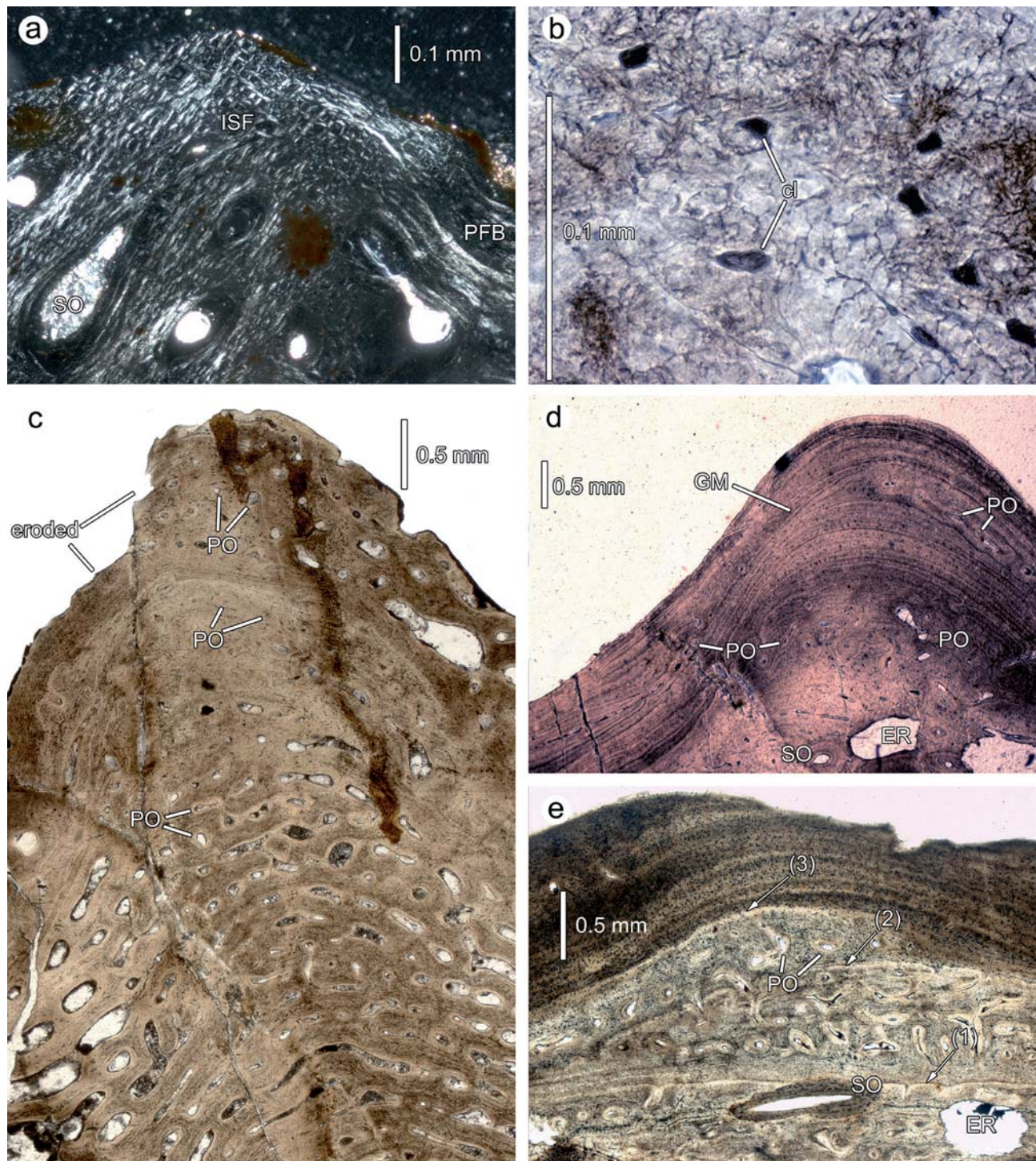


Fig. 8. *Mastodonsaurus giganteus* (JAEGER, 1828). Vertical sections of external cortex. – **a.** SMNS 91251. Slightly eroded sculptural saddle showing interwoven structural fibers. Polarized light. **b.** SMNS 91248. Bone cell lacunae in a matrix of interwoven structural fibers. **c.** SMNS 91252. Sculptural saddle with numerous primary osteons that are often arranged in a regular succession parallel to the external surface. **d.** SMNS 91248. Sculptural saddle showing growth marks; the more interior portion is well vascularized. **e.** SMNS 91248. The former bone surfaces of three succeeding generations of a sculptural saddle are visible; the first is almost horizontally aligned. – For abbreviations, see text.

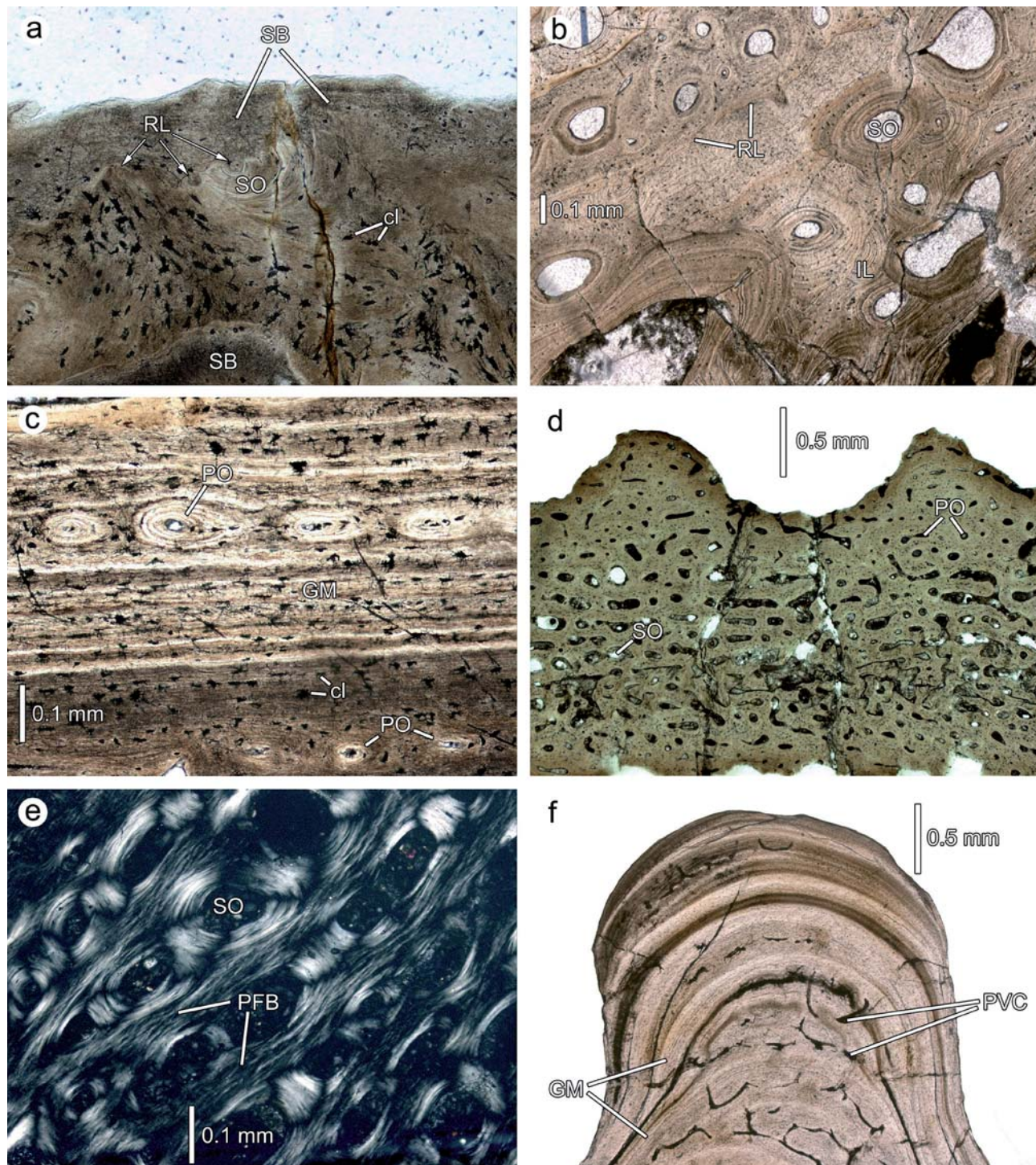


Fig. 9. a–e. *Mastodonsaurus giganteus* (JAEGER, 1828). a. SMNS 80878. Vertical section parallel to a sculptural ridge showing structures of surface resorption. b. SMNS 91248. Middle region in normal transmitted light, vertical section. Zone of extensive remodeling and Haversian tissue. c. SMNS 91248. More interior part of internal region with primary osteons in rows. d–e. Juvenile specimen, SMNS 91255. Interclavicle, vertical section transverse to the sculptural ridges. – d. Histological overview, normal transmitted light. e. The fine to coarse cancellous middle region with a matrix of coarse parallel-fibered bone, polarized light. f. *Metoposaurus diagnosticus* (VON MEYER, 1842), MB.Hi.1719. Sculptural saddle of an unidentified dermal bone in normal transmitted light. – For abbreviations, see text.

3.3.9. Clavicular blade of a small juvenile specimen of *Mastodonsaurus giganteus*

The section is aligned transversely to the radiating sculptural ridges of this approximately 2.1 mm thick bone. The cortices are so extensively vascularised that they resemble closely the middle region. Therefore, it is no more appropriate to speak of a clear diploë structure, in contrast to the ontogenetically more advanced specimens. The determination of boundaries between the cortices and the middle region is thus rather arbitrary.

External cortex. The external cortex is highly vascularized by numerous, anastomosing primary vascular canals and primary osteons (Fig. 9d). Also few secondary osteons can be observed. There is no difference in the degree of vascularization and nature of the bone tissue between saddles and valleys. Growth marks are not visible. The primary bone tissue consists of coarse, poorly organized parallel-fibered bone that may fray out in fibers with changing direction. Interwoven structural fibers and Sharpey's fibers are not visible in the material under study. Most bone cell lacunae are randomly arranged, irregular in shape and possess few or no canaliculi.

Middle region. This fine to coarse cancellous region is distinguished from the cortices by the slightly larger diameter of many of its vascular canals, and the presence of several secondary osteons that may anastomose. Haversian tissue is not present. The rather small osteons are frequently arranged in layers (Fig. 9e). Few slightly larger erosion rooms without lining of lamellar bone are present. The interstitial primary tissue consists mainly of coarse, less organized parallel-fibered bone (Fig. 9e). In the primary bone matrix, the longitudinal axes of the spindle bone cell lacunae are directed parallel to the bone fibers. Canaliculi are hardly visible.

Internal cortex. The internal cortex is composed of coarse parallel-fibered bone. It is well vascularized by primary vascular canals and primary osteons that may anastomose (Fig. 9d). The bone cell lacunae are ordered and spindle-shaped with few canaliculi.

3.3.10. *Metoposaurus diagnosticus* (Temnospondyli, Steurospondylomorpha, Trematosauroidea)

It is not clear if the slides investigated here from *Metoposaurus diagnosticus* (VON MEYER, 1842) are derived from the skull roof or the dermal pectoral girdle. The ratio external cortex : middle region : internal cortex is 1 : 1.5 : 0.3. However, the middle region has collapsed by the superimposed load of sediment in the specimens under study and was therefore originally probably somewhat thicker. The bone investigated attains a thickness of 9 mm.

External cortex. The more interior part of the cortex is well vascularized by numerous, partially anastomosing primary vascular canals of mostly a small diameter, whereas the number of canals decreases in direction to the external bone surface and the top of the saddles (Fig. 9f). The bone matrix is composed of homogeneous parallel-fibered bone and shows several distinct growth marks that allow to trace the growth of the rather steep sculptural saddles. Numerous bone cell lacunae are visible that appear mostly irregular-elongate in shape. Poor preservation precludes recognition of canaliculi. In the sculptural saddles, the Sharpey's fibers are arranged in clusters that are mostly present in the lateral parts of the saddles (Fig. 10a), where they are oriented anteriorly and medially. In the sculptural valleys, the clusters are more densely arranged and extend deep into the cortex (Fig. 10a). The diameter of the fibers amounts 17 to 25 μm .

Middle region. The external cortex grades into the coarse cancellous middle region with numerous secondary osteons that may form Haversian tissue. The primary bone matrix is represented by fine, homogeneous parallel-fibered bone.

Internal cortex. The internal cortex is thin compared to the middle and external region and consists of homogeneous parallel-fibered bone that is largely avascular (Fig. 10b). It can be distinguished from the middle region by a distinct transition zone.

3.3.11. *Plagiosuchus pustuliferus* (Temnospondyli, Steurospondylomorpha, Plagiosauridae)

For the present study, a dermal bone fragment of *Plagiosuchus pustuliferus* (FRAAS, 1896) (SMNS 82023), which derives probably from the skull roof and bears a sculpture of tubercles and low ridges between them, was sectioned. The bone thickness amounts 11 mm. In this fragment, the cortices are highly vascularized similar to the middle region, and thus a diploë structure is not visible. The determination of external cortex, middle region, and internal cortex in the following is somewhat arbitrarily and based on the higher density of vascular canals in the middle region and the presence of extrinsic fibers (Sharpey's fibers) in the cortices. The vascularization is slightly less well developed in the external cortex of MB.Hi.1705 (maximum bone thickness 4 mm), a slide of an unidentified dermal bone of *Plagiosuchus*, than in that of SMNS 82023. Nevertheless, a clear diploë structure is not developed also in MB.Hi.1705.

External cortex. The complete external cortex is well vascularized by numerous, partially anastomosing primary vascular canals and primary osteons in SMNS 82023, whereas in MB.Hi.1705, the external portion of the cortex is nearly avascular. Densely arranged Sharpey's

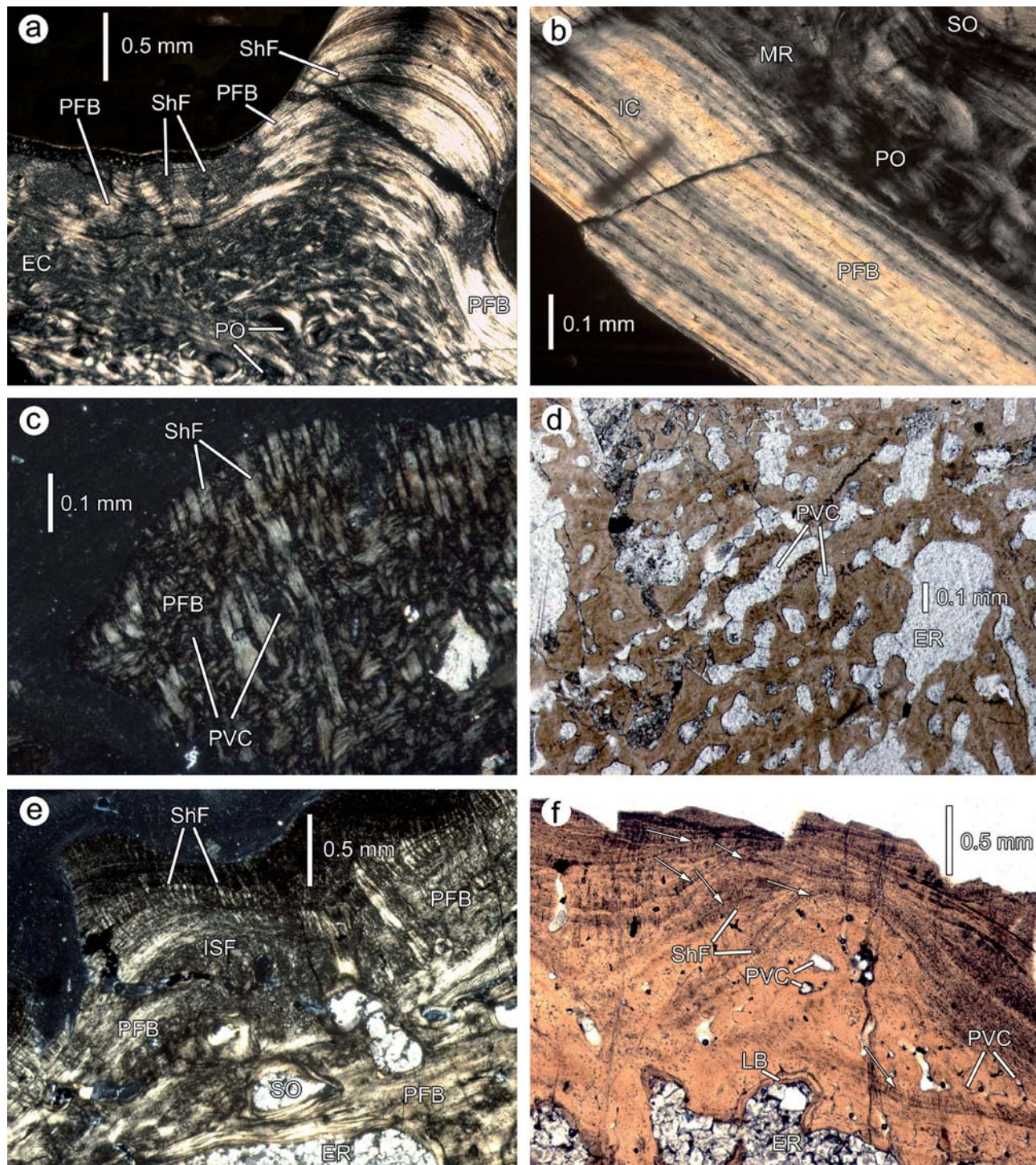


Fig. 10. a–b. *Metoposaurus diagnosticus* (VON MEYER, 1842), vertical sections through unidentified dermal bone. **a.** MB.Hi.1720. Sculptural saddle and external cortex in polarized light. **b.** MB.Hi.1721. Internal cortex in polarized light. – **c–d.** *Plagiosuchus pustuliferus* (FRAAS, 1896), SMNS 82023. Vertical section through fragment of dermal skull roof. **c.** Sculptural saddle with Sharpey's fibers in polarized light. **d.** Middle region with primary vascular canals and erosion rooms, normal transmitted light. – **e–f.** *Plagiosternum granulosum* (FRAAS, 1889), SMNS 91256. Vertical section of interclavicle. **e.** Sculptural saddle and valley with Sharpey's fibers and external part of middle region, polarized light. **f.** External cortex with eroded surface, showing sculptural saddles of different generations (indicated by arrows) and Sharpey's fibers both in saddles and valleys, normal transmitted light. – For abbreviations, see text.

fibers penetrate the external region both in the sculptural saddles and valleys (Fig. 10c) and extend far interiorly within the cortex. The fibers have a diameter of mostly 22 to 26 μm and may ramify in two or three branches. The largest part of the bone tissue consists of coarse parallel-fibered bone with a more irregular fibrous arrangement. Spindle-shaped bone cell lacunae are present that possess branching canaliculi. In some areas, especially the sculptural saddles, also islets of interwoven structural fibers are discernable. Cyclic growth marks are not continuous and have an indistinct appearance in SMNS 82023, whereas they are more distinct in the external part of the external cortex in MB.Hi.1705.

Middle region. This coarse cancellous region is extensively vascularized by primary vascular canals and primary osteons, and isolated, medium-sized erosion cavities are present (Fig. 10d). Some of them show Howship's lacunae, and secondary lamellar bone lining is absent in the SMNS specimen under study, whereas in MB.Hi.1705, scattered, small secondary osteons are discernable. The bone matrix consists in large parts of interwoven structural fibers, and also parallel-fibered bone is present.

Internal cortex. The bone matrix consists mostly of poorly organized parallel-fibered bone. Sharpey's fibers are present that are shorter and distinctly thinner than those of the external cortex. Vascularization is well developed and consists of numerous primary vascular canals that are often aligned in rows or may anastomose.

3.3.12. *Plagiosternum granulosum* (Temnospondyli, Stereospondylomorpha, Plagiosauridae)

A fragment of an interclavicle of *Plagiosternum granulosum* (FRAAS, 1889) (SMNS 91256) with polygonal sculpture was sectioned that has a maximum thickness of 11 mm. Additionally, the vertical section of an unidentified, 7 mm thick dermal bone of *Plagiosternum* (MB.Hi.1714) was investigated. The ratio external cortex : middle region : internal cortex is 1 : 2.9 : 0.8.

External cortex. The external cortex is composed of coarse, poorly ordered parallel-fibered bone, and islets of interwoven structural fibers can be found especially in the more internal regions of the sculptural saddles and in the interior parts of the cortex (Fig. 10e). The bone cell lacunae in the parallel-fibered bone are of irregular shape with moderately long canaliculi. In the SMNS specimen, Sharpey's fibers are densely arranged in both the sculptural saddles and in the valleys, comparable to the situation in *Plagiosuchus*. The diameter of the Sharpey's fibers varies between 17 to 26 μm , and most of them terminate in approximately the external half of the external region. Zones and annuli are well visible and delineate sculptural saddles of earlier generations, in which Sharp-

pey's fibers are visible (Fig. 10f). The external cortex of the SMNS specimen is moderately vascularized in its interior portion by primary vascular canals, whereas the external portion is largely avascular (Fig. 10f). In MB.Hi.1714, the complete cortex is well vascularized by anastomosing primary canals whose diameters decrease in size in the more external portion of the cortex (Fig. 11a). The difference in the degree of vascularization between the Berlin and the Stuttgart specimen might be explained as ontogenetic variation (see discussion).

Middle region. A rather small transition zone between the external cortex and the middle region is characterised by scattered secondary osteons. The middle region was extensively affected by remodeling. It is characterised by large erosion rooms that are separated by long, irregularly arranged trabeculae of varying thickness (Fig. 11b). Some erosion rooms are lined by secondary lamellar bone. The primary bone matrix within the trabeculae consists of well-ordered parallel-fibered bone with spindular bone cell lacunae.

Internal cortex. The bone tissue is composed of parallel-fibered bone with often irregularly arranged fibers, and transitions to interwoven structural fibers are locally present. Sharpey's fibers that are distinctly thinner than those of the external region penetrate the internal cortex obliquely at an angle of about 60° and are densely arranged. Primary vascular canals that may anastomose are more numerous in the interior than in the internal part of the cortex. Cyclic growth marks are well visible (Fig. 11c).

3.3.13. *Gerrothorax* sp. (Temnospondyli, Stereospondylomorpha, Plagiosauridae)

The thin sections were prepared from bone fragments of the interclavicle and clavicle, ranging from 3.3 mm to 9 mm in thickness. The dermal sculpture is tubercular, and low sculptural ridges may connect the tubercles. The ratio external cortex : middle region : internal cortex is 1 : 1.9 : 0.9.

External cortex. The interior portion of the external cortex is moderately to highly vascularized by primary vascular canals and primary osteons that often branch and anastomose, whereas vascularization is low in the external portion of the cortex (Fig. 11d). The sculptural valleys and the lateral parts of the saddles consist mainly of fine to coarse parallel-fibered bone in which the bone cell lacunae are often spindular with moderately long to long canaliculi. The interior parts of the sculptural saddles, in contrast, show general isotropy under polarized light, and the bone cell lacunae are rather round and haven often long, branching canaliculi. The isotropy can probably be attributed to the superposition of the Sharp-

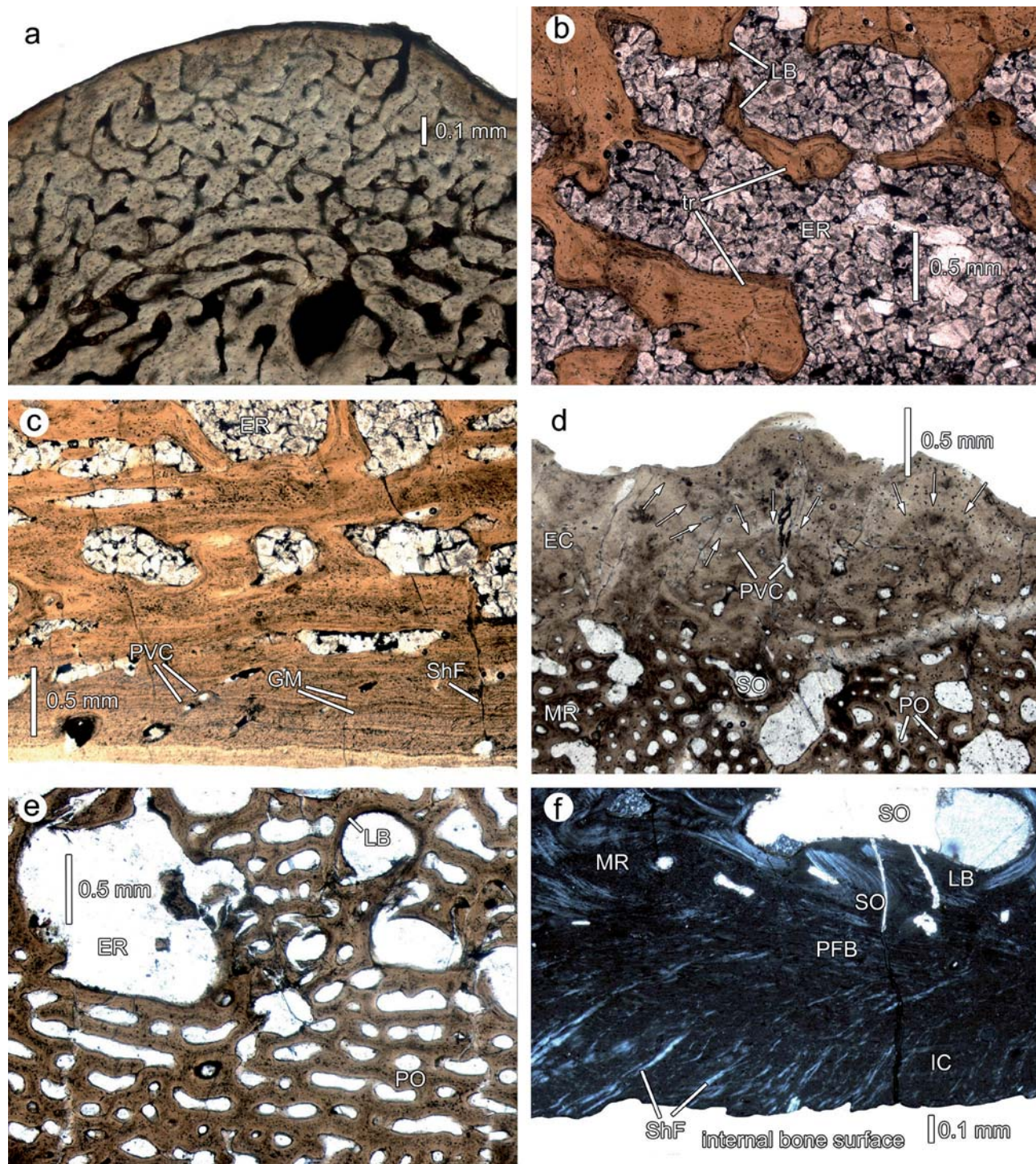


Fig. 11. a–c. *Plagiosternum granulosum* (FRAAS, 1889). a. MB.Hi.1714. Vertical section of unidentified dermal bone, sculptural saddle, normal transmitted light. b–c. SMNS 91256. Vertical section of interclavicle. b. Middle region showing trabecular structure with large erosion rooms. c. Internal cortex in normal transmitted light. – d–f. *Gerrothorax* sp. d. SMNS 91258. Vertical section of clavicle, histological overview of external cortex and middle region in normal transmitted light; the arrows indicate the bone surface of a former generation. e. SMNS 91257. Vertical section of clavicle in polarized light, showing the middle region with numerous primary osteons and larger erosion rooms. f. SMNS 83033. Vertical section of interclavicle, internal cortex in polarized light; note the oblique Sharpey's fibers penetrating the bone. – For abbreviations, see text.

ey's fibers in the cores of the saddles. In some regions more interior in the cortex, the bone tissue may show transitions to diagonally arranged interwoven structural fibers of irregular size. Rather thin Sharpey's fibers with a diameter of 8 to 11 μm , that are not as densely arranged as in *Plagiosuchus* and *Plagiosternum*, are visible in the sculptural tubercles and are fewer in number in the valleys. Cyclic growth marks are present in the external cortex. In one interclavicle (SMNS 83033), a former generation of sculptural saddles is visible in the interior part of the external cortex (Fig. 11d). These old sculptural saddles are distinctly smaller and the valleys narrower than those of the actual external surface.

Middle region. The transition zone from the external cortex to the middle region is rather thin and bears scattered secondary osteons. In most specimens, the middle region varies from coarse cancellous to trabecular (Fig. 11e). In some areas, numerous primary osteons predominate and may be arranged in rows, whereas in other areas, scattered, large erosion rooms prevail, that are separated by irregularly arranged trabeculae. In some parts, remodeling was so extensive that Haversian tissue was formed (Fig. 11f, on top). The primary tissue is parallel-fibered bone, but also a matrix of interwoven structural fibers that are diagonally arranged with respect to the bone surface occurs, whose sparse bone cell lacunae are mostly round and bear no or only short canaliculi.

Internal cortex. The internal cortex is composed of coarse, less ordered parallel-fibered bone. Rather loosely arranged Sharpey's fibers of varying size extend into the internal region at an oblique angle (30–50°), some of them extending until to the middle region (Fig. 11f). Only very few primary vascular canals are visible. These are mostly situated more interiorly in the internal cortex and course parallel to the internal bone surface.

3.3.14. *Diplocaulus magnicornis* (Lepospondyli, Nectridea)

The sectioned bone fragments of *Diplocaulus magnicornis* COPE, 1882, ranging from 7 mm to 14 mm in thickness, represent lateral parts of the conspicuous 'horns' of this nectridean, so that a sculptured compact cortex encloses the middle region dorsally, laterally, and ventrally. Therefore, in the following, the cortex will be referred to as 'external cortex' only. The external cortex is much reduced with respect to the extensive middle region, the ratio external cortex : middle region : external cortex is 1 : 11.1 : 1. The dermal sculpture is composed of rounded polygons.

External cortex. The externalmost portion of the rather thin cortex is for the largest part avascular with very few, small primary canals, whereas its more interior

part is well vascularized by primary canals and primary osteons. In a transitional region between cortex and middle region, several small erosion rooms and primary and secondary osteons are present (Fig. 12a). The bone matrix of the cortex consists largely of coarse parallel-fibered bone (Fig. 12b), and Sharpey's fibers are restricted to the sculptural saddles, where their arrangement is moderately dense. The fibers have a comparatively small diameter of 11 to 13 μm . The cores of many sculptural saddles show isotropy under polarized light; as outlined for *Gerrothorax* (see above), this might be attributed to superposition of the Sharpey's fibers. In most specimens, interwoven structural fibers constitute the predominant matrix in the more interior part of the external cortex (Fig. 12c). In the parallel-fibered bone, the cell lacunae have often long, branching canaliculi and are most often spindle-shaped (in the valleys) and rounded (in the saddles). The cell lacunae within the interwoven structural fibers, in contrast, are irregular in shape and have often no or only stumpy canaliculi. Throughout the external cortex, growth marks are present that are continuous in saddles and valleys and follow their relief.

Middle region. The middle region of *Diplocaulus* is highly porous and strongly affected by successive resorption and reconstruction of bone. Thin, long trabeculae that are mostly orientated in a dorsoventral and horizontal direction enclose rectangular shaped bone cavities of similar size (Fig. 12d). The ordered appearance of trabeculae and cavities is unique among the basal tetrapods studied here. Most of the cavities have a thin covering of secondary lamellar bone (Fig. 12e). In the more external cavities, the lining of lamellar bone is frequently absent. The primary bone tissue consists in large parts of coarse parallel-fibered bone, but also areas with interwoven structural fibers do exist. Partially cut primary osteons can be discerned in the primary tissue of the trabeculae.

Specimen MCZ 2269-3 provides interesting data concerning the extensive resorption and remodeling of the middle region. Structures of resorption are visible both in the primary matrix and the secondary lamellae (Fig. 12f). The primary bone matrix exhibits cyclical growth marks, with the different zones being delimited by distinct growth lines. The secondary lamellae surround the zones of primary bone matrix continuously, indicating their deposition after the formation of the zones.

3.3.15. *Pantylus cordatus* (Lepospondyli, 'Microsauria')

A small, 3 mm thick fragment of the dermal skull roof of *Pantylus cordatus* COPE, 1881 consisting of one sculptural saddle and one valley plus parts of the middle region was sectioned. *Pantylus* has a pronounced polygonal sculpture on its dermal skull roof. The internal cortex and

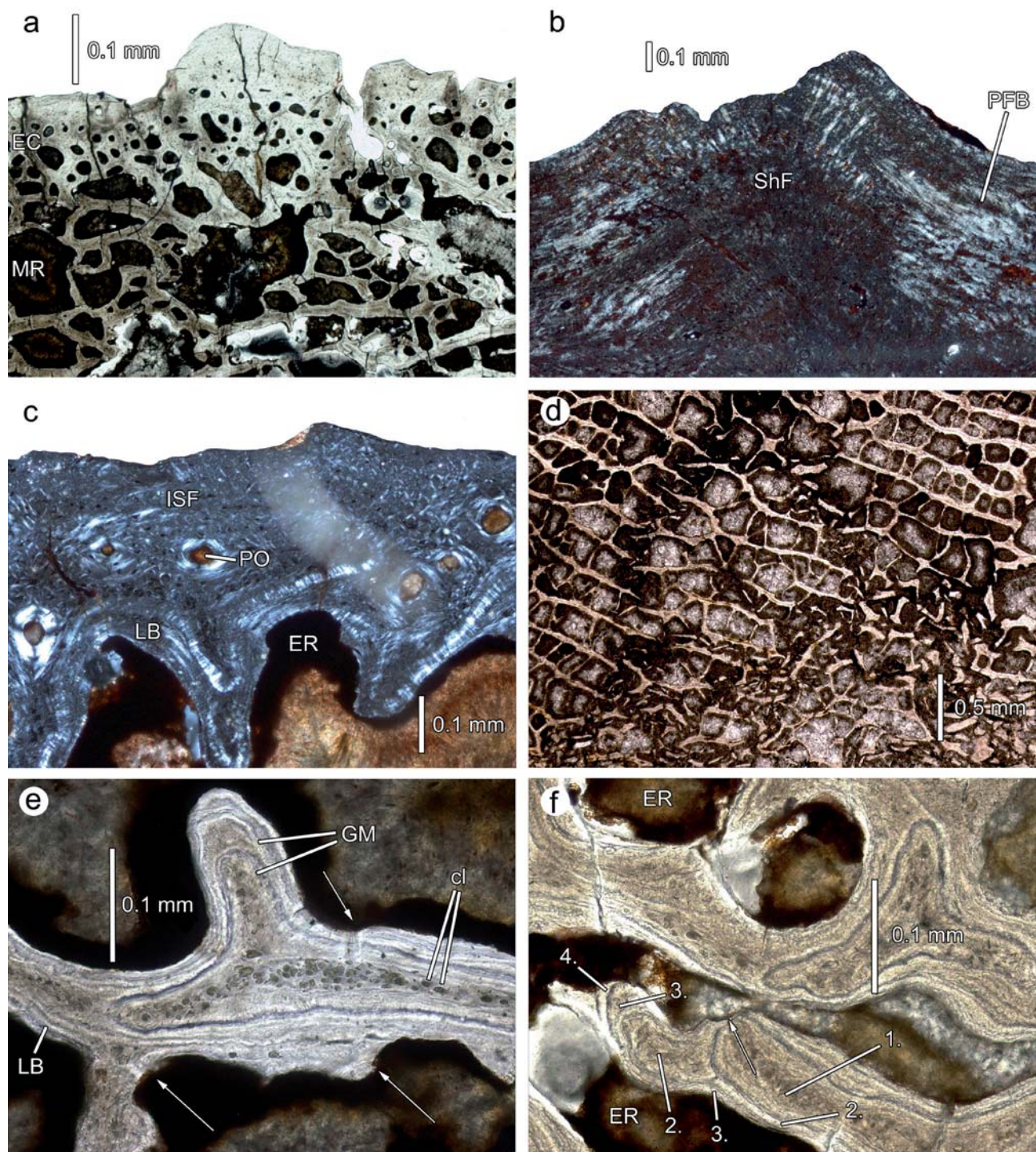


Fig. 12. *Diplocaulus magnicornis* COPE, 1882. Vertical sections of the 'cheek'-region. – a. UCMP 203658. Histological overview of external cortex with middle region in normal transmitted light. b. UCMP 203505. Sculptural saddle (partially eroded) in polarized light showing fan-shaped Sharpey's fibers and matrix of parallel-fibered bone. c. UCMP 203658. Interior part of external cortex (the more external part is eroded) with erosion rooms of the middle region. d. MCZ 2269. Overview of the trabecular middle region in normal transmitted light. e. UCMP 203658. Trabeculae of the middle region in normal transmitted light, resorptive structures are indicated by arrows. f. MCZ 2269. Trabeculae of middle region in normal transmitted light, the numbers 1–4 indicate the order of bone deposition, the arrow marks a resorptive structure. – For abbreviations, see text.

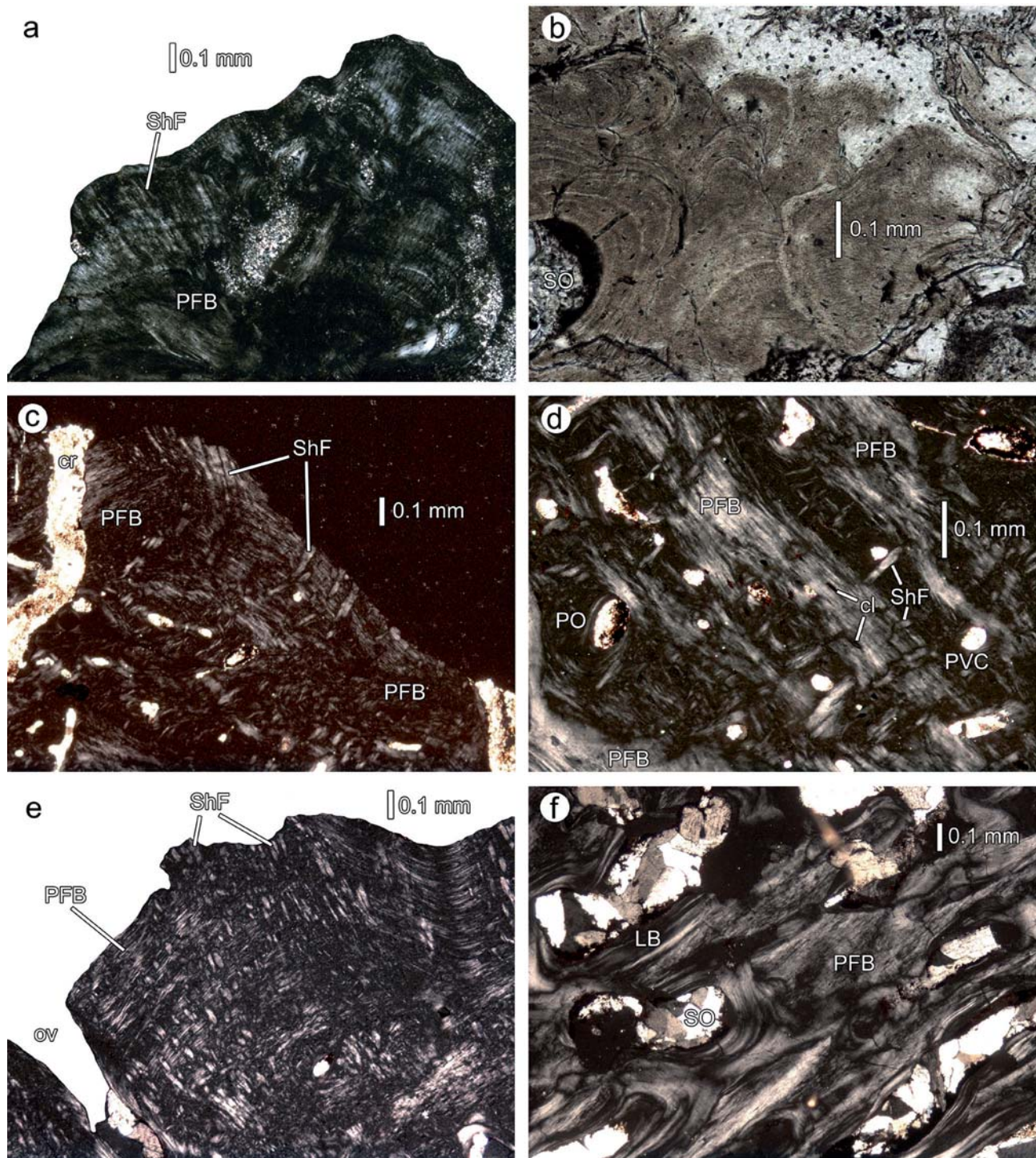


Fig. 13. a–b. *Pantylus cordatus* COPE, 1881, UCMP 20296. Vertical section of dermal skull fragment. a. Sculptural saddles in polarized light. b. Transitional zone between external cortex and middle region in normal transmitted light, showing extensive bone remodeling. – c–d. *Seymouria baylorensis* BROILI, 1904. MCZ without number. Vertical section of ?angular. c. Sculptural saddle in polarized light. d. More interior portion of external cortex. – e–f. *Labidosaurus hamatus* COPE, 1895, MCZ without number. Vertical section of skull table bone. e. Sculptural saddle with adjacent sculptural valleys in polarized light, a vascular canal opens in the valley on the left. f. Middle region with secondary osteons in polarized light. – For abbreviations, see text.

the more internal part of the middle region of this specimen are eroded.

External cortex. Densely arranged Sharpey's fibers penetrate the high, steep sculptural saddles (Fig. 13a). The diameter of the fibers varies between 13 and 21 μm . The primary bone matrix consists of parallel-fibered bone. The sculptural valley is diagenetically altered so that the original bone matrix cannot be discerned, and it cannot be stated if Sharpey's fibers were present. The vascularization of the external cortex is low with scattered primary vascular canals and primary osteons. On the left side of the sculptural saddle, a conspicuous resorption line is visible, similar to the situation described for *Edops*, *Eryops* and *Mastodonsaurus* (see above). Here, surface erosion with formation of secondary bone including a secondary osteon has taken place. The bone cell lacunae in the primary bone tissue are round throughout with no or short canaliculi. In the secondary bone tissue, the lacunae are larger, more numerous, and have longer canaliculi. Cyclic growth marks that follow the external sculpture are visible, but are absent in the remodelled area.

Middle region. The transitional zone between the external cortex and the middle region is still rather compact with scattered secondary osteons and several, 'chaotic' resorption lines, indicating that this region underwent extensive remodeling (Fig. 13b). In the middle region, the erosion cavities become larger and constitute extensive spaces, so that this region can be designated as trabecular. The cavities are bounded by thick, irregularly arranged trabeculae that may be covered by secondary lamellar bone. The primary bone matrix consists mostly of coarse, less ordered parallel-fibered bone.

3.3.16. *Seymouria baylorensis* (Seymouriamorpha)

From *Seymouria baylorensis* BROILI, 1904, a small dermal bone fragment of the lower jaw, probably the angular, was studied. The 5.5 mm thick bone was sectioned perpendicular to the sculptural ridges. The ratio external cortex : middle region : internal cortex is 1 : 2.7 : 0.9.

External cortex. The bone tissue comprises mostly poorly organized parallel-fibered bone (Fig. 13c). Bone cell lacunae appear spindular or round, depending on their orientation (see below), and have moderately long to long, branching canaliculi. In the interior portion of the cortex, layers of fine parallel-fibered bone are present, whose fibers are cut roughly longitudinally (with spindular cell lacunae) and brighten up in polarized light. They alternate with those whose fibers are cut transversely (with round bone cell lacunae) and remain dark in polarized

light, so that the bone is reminiscent of an isopedine-like tissue (Fig. 13d). Scattered Sharpey's fibers that may bifurcate penetrate the sculptural saddles. They are of different length and measure 21 to 32 μm in diameter. Compared e. g. to *Eryops* or *Plagiosuchus* (see above), they are rather loosely arranged. The Sharpey's fibers are only sporadically present in the sculptural valleys. The interior portion of the cortex is moderately to highly vascularized by primary canals and primary osteons. In the external portion of the external cortex, however, vascularization is low and consists of isolated primary canals.

Middle region. This region is fine to coarse cancellous and is characterized by scattered secondary osteons of varying orientation. They may possess wide Haversian canals. The primary bone matrix consists of homogeneous parallel-fibered bone.

Internal cortex. The internal cortex is composed of parallel-fibered bone. It is well vascularized by different layers of primary vascular canals and primary osteons.

3.3.17. *Labidosaurus hamatus* (Amniota, Eureptilia, Captorhinidae)

Many parareptiles and basal eureptiles possess distinctly sculptured dermal bones, similar to those of temnospondyls (KISSEL et al. 2002; MODESTO et al. 2007; WITZMANN, unpublished data). From the captorhinid *Labidosaurus hamatus* COPE, 1895, a 5 mm thick bone fragment of the skull table with a reticular sculpture has been sectioned. The internal cortex is eroded in this specimen.

External cortex. This region is mainly composed of coarse parallel-fibered bone (Fig. 13e). The majority of the well mineralized, long Sharpey's fibers can be found in the sculptural ridges, whereas the sculptural valleys are nearly devoid of them. The diameter of most Sharpey's fibers varies between 16 and 29 μm . Vascularization is low and consists of scattered simple primary canals and primary osteons in the interior portion of the external cortex, whereas the external portion is almost avascular.

Middle region. The middle region is coarse cancellous and is populated by numerous secondary osteons that course in different directions (Fig. 13f). Locally, Haversian tissue is formed. Mostly fine, homogenous parallel-fibered bone constitutes the primary bone matrix. The bone cell lacunae are generally elongate. Canaliculi are not visible, probably due to poor preservation.

The histological features of the investigated taxa are summarized in Tables 2–4.

4. Discussion

4.1. Growth of bony tubercles and ridges, and remodeling of the outer bone surface

Among extant tetrapods, growth of dermal bony tubercles and ridges has been studied in the osteoderms of squamates and in dermal skull bones and osteoderms of crocodiles. In squamates, the presence of pits and ridges on the external surface of osteoderms follows from both local resorption and growth of bone (ZYLBERBERG & CASTANET 1985; LEVRAT-CALVIAC & ZYLBERBERG 1986), whereas in crocodile dermal bones, DE BUFFRÉNIL (1982) stated that sculpture is mainly the result of local resorption. In contrast, VICKARYOUS & HALL (2008) found no evidence for morphogenesis of bone sculpture by resorption in *Alligator mississippiensis* and presumed that sculptural ridges develop by preferential bone growth. Concerning basal tetrapods, BYSTROW (1935, 1947) showed that the development of bone sculpture in the temnospondyls *Benthosuchus*, *Platyoposaurus* and *Dvinosaurus* took place solely by growth of the bony ridges and tubercles, and resorptive processes were not involved.

The thin sections of the dermal bones of skull and pectoral girdle in the basal tetrapods investigated here corroborate BYSTROW'S findings and show that the dermal sculpture did not develop by local resorption of the bone surface, comparable to the pattern in basal tetrapod osteoderms (WITZMANN & SOLER-GUJÓN 2008). The growth marks follow clearly the pattern of sculptural saddles and valleys. In general, the sculptural saddles in basal tetrapods are characterized by a much greater number of Sharpey's fibers than the valleys (see below). The presence of these anchoring fibers can induce preferential growth of the mineralized tissue or bone around them (BOYDE 1972; SIRE 1985, 1986; MOWBRAY 2005), and this might have contributed to the formation of the bony tubercles and ridges that constitute the dermal sculpture in basal tetrapods (see also WITZMANN & SOLER-GUJÓN 2008). Nevertheless, resorptive structures are visible on the bone surface in the sculptural saddles in some taxa: the better vascularized secondary bone lies discordantly on the primary bone and is separated from it by a distinct resorption line that is often interiorly convex. Very similar cases of remodeling in the external cortex have been reported by SCHEYER & SÁNCHEZ-VILLAGRA (2007) in the shell bones of two turtle taxa, the extant *Podocnemis erythrocephala* (SPIX, 1824) and the fossil *Taphrosphys sulcatus* (LEIDY, 1856), where this phenomenon is interpreted as a reaction of bone to infection or trauma. The remodeling structures on the bone surface in the basal tetrapods investigated here might result from similar reasons and can be regarded as unusual bone growth that did not contribute to the formation of dermal bone sculpture.

The fact that morphogenesis of bony ridges and tubercles took place by preferential growth in all investigated taxa of basal tetrapods strongly suggests that dermal sculpture evolved once in the finned stem-tetrapods after the reduction of the dermal components (odontodes) and was basically retained in all lineages of basal tetrapods including early amniotes (see below).

4.2. Vascularization of the external and internal cortex

BYSTROW (1935, 1947) found a network of capillaries in the external cortex of the stereospondyls *Benthosuchus* and *Wetlugasaurus* that he named the 'rete vasculosum'. He suggested that this network carried blood capillaries into the overlying dermis. In the temnospondyls *Platyoposaurus* and *Dvinosaurus*, and in the seymouriamorph *Enosuchus*, the same author found this network to be absent and the cortex rather avascular. For BYSTROW (1947), this finding was of great palaeobiological significance. He called those forms that possess the 'rete vasculosum' the 'hydrophilous labyrinthodonts' and concluded that they were water-dwellers that breathed primarily through their wet skin; in contrast, those basal tetrapods in which this network is absent were considered as 'xerophilous labyrinthodonts' that lived mainly terrestrially and relied primarily on lung-breathing rather than on cutaneous respiration, since the integument was interpreted to be less vascularized. BYSTROW (1947) regarded the temnospondyl *Dvinosaurus* as an exception since it lived aquatically and lacks the 'rete vasculosum'. This discrepancy, however, was explained by the fact that *Dvinosaurus* possessed gills throughout its lifetime and therefore, cutaneous respiration was not necessary for gas exchange (BYSTROW 1947).

The thin sections of basal tetrapod dermal bones investigated here show that the external cortex varies in the density of vascularization (Tab. 2). In taxa such as the presumably semi-terrestrial *Edops*, *Chenoprosopus* and *Eryops*, and the rather terrestrial *Acheloma*, *Pantylus* and *Labidosaurus*, the external cortex is poorly vascularized or almost avascular. In most other taxa investigated, a moderate to high number of primary vascular canals is present in the more interior part of the cortex where they may anastomose and form a 'rete vasculosum' sensu BYSTROW (1935, 1947). However, there is a drop in vascularization towards the bone surface, and thus the more external portion of the cortex is populated by sparsely distributed primary canals, or the bone is even avascular. In some specimens of the aquatic *Mastodonsaurus*, the external cortex is throughout well vascularized by primary canals and even more by primary osteons that are arranged in layers and may anastomose. Towards the external surface of the bone, however, many of the canals get

Tab. 2. Summary of histological data concerning the external cortices of the dermal bones investigated. ** indicates that the Sharpey's fibers are not mineralized. Abbreviations: int., interior; mod., moderate. For further abbreviations, see text.

Taxon	Bone tissue	Vascularization	Sharpey's fibers		Growth marks
			Ø in µm	density	
Porolepiform and stem-tetrapods					
<i>Laccognathus</i>	fine PFB, odontodes	high	2**	loose	not visible
<i>Panderichthys</i>	fine PFB	moderate	5–6	mod. dense	not visible
<i>Acanthostega</i>	fine to coarse PFB	mod. to high	3–5	loose	not visible
<i>Greererpeton</i>	coarse PFB	mod. to high	3–7	loose	not visible
Temnospondyls					
<i>Edops</i>	coarse PFB > ISF	low	21	mod. dense	distinct
<i>Chenoprosopus</i>	coarse PFB > ISF	low	8–17	dense	distinct
<i>Eryops</i>	coarse PFB > ISF	low	21–29	dense	distinct
<i>Acheloma</i>	fine PFB	low	15–31	dense	weak
<i>Sclerocephalus</i>	?	moderate to low	?	?	distinct
<i>Archegosaurus</i>	fine PFB	mod. to high (int.)	?	?	not visible
<i>Kupferzellia</i>	coarse PFB > ISF	moderate (int.)	5–16	loose	weak
<i>Mastodonsaurus</i>	coarse PFB, ISF	mod. to high	25–28	loose	distinct
<i>Mastodonsaurus</i> (juv.)	coarse PFB	high	?	?	not visible
<i>Metoposaurus</i>	fine PFB	mod. to high (int.)	17–25	mod. dense	distinct
<i>Plagiosuchus</i>	coarse PFB > ISF	mod. to high	22–26	dense	distinct
<i>Plagiosternum</i>	coarse PFB > ISF	mod. to high (int.)	17–26	dense	distinct
<i>Gerrothorax</i>	fine /coarse PFB > ISF	mod. to high (int.)	8–11	mod. dense	distinct
Lepospondyls					
<i>Diplocaulus</i>	coarse PFB, ISF	high (int.)	11–13	mod. dense	distinct
<i>Pantylus</i>	fine PFB	low	13–21	dense	distinct
Seymouriamorpha					
<i>Seymouria</i>	coarse PFB	mod. to high (int.)	21–32	loose	not visible
Eureptilia					
<i>Labidosaurus</i>	coarse PFB	low	16–29	mod. dense	not visible

distinctly smaller in their diameter. A similar pattern is also visible in the Berlin specimen of the aquatic *Plagiosternum* (MB.Hi.1714). The fact that the primary vascular canals that may or may not form a network are mostly restricted to the more interior portion of the cortex renders a connection between cutaneous respiration and vascularization of the bone doubtful. Furthermore, even when the canals extend to the external portion of the cortex and to the bone surface as in the mentioned specimens of *Mastodonsaurus* and *Plagiosternum*, they constitute a very irregular and thus less effective route for the blood to reach the soft-tissue integument, as correctly pointed out by COLDIRON (1974).

The primary vascular canals in the external cortex rather had the function to supply the bone during its growth. Their varying density, presence or absence might be explained with different growth rates in bone during ontogeny. In the compacta of long bones, the density of vascular canals is closely connected with the apposition rate of bone, i. e., a dense or sparse vascularization means a higher or lower growth rate, respectively (CHINSAMY 1993; STEYER et al. 2004; KLEIN & SANDER 2008, and references therein). The higher growth rate requires a dense vascularization since faster growing bone has higher energy demands. With increasing age of the animals, vascularization and growth rate of the long bone cortices decreased, and the diameter of the vascular spaces becomes increasingly smaller due to their infilling with bone (KLEIN & SANDER 2008). Although these studies focused on growth rates in long bone compacta, a similar connection between vascularization and bone growth can also be assumed in dermal bones. The better vascularization of the more interior than the more external part of the external cortex in the dermal bones investigated here might suggest that the bone growth was faster in an earlier ontogenetic stage and slowed down later. It is not possible that the vascular canals developed after the formation of the bone, since primary canals are incorporated into the bone during its deposition (FRANCILLON-VIEILLOT et al. 1990; CHINSAMY-TURAN 2005).

In this connection, it is interesting to regard the thin section of the clavicle of the small, juvenile *Mastodonsaurus*. The external cortex is penetrated by an anastomosing network of numerous primary osteons. In contrast to more advanced specimens of the same taxon, neither the density nor the diameter of the vascular spaces decrease towards the bone surface, and the organization of the vascular network is irregular compared to the succession of primary osteons parallel to the external surface in the older specimens. The presence of numerous primary osteons through-

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Tab. 3. Summary of histological data concerning the internal cortices of the dermal bones investigated. For abbreviations, see text.

Taxon	Bone tissue	Vascularization	Extraneous fibers
Porolepiform and stem-tetrapods			
<i>Laccognathus</i>	isopedine	avascular	fine, perpendicular to bone surface
<i>Panderichthys</i>	isopedine	low	fine, perpendicular to bone surface
<i>Acanthostega</i>	PFB, isopedine	low	fine, perpendicular to bone surface
<i>Greererpeton</i>	isopedine	low	fine, perpendicular to bone surface
Temnospondyls			
<i>Edops</i>	coarse PFB	avascular	not visible
<i>Eryops</i>	coarse PFB > ISF	low	fine, oblique to bone surface
<i>Acheloma</i>	fine PFB	avascular	fine, oblique to bone surface
<i>Sclerocephalus</i>	?	low	?
<i>Archegosaurus</i>	coarse PFB	low	not visible
<i>Kupferzellia</i>	coarse PFB	low	not visible
<i>Mastodonsaurus</i>	coarse PFB > ISF	medium to low	fine, oblique to bone surface
<i>Mastodonsaurus</i> (juv.)	coarse PFB	high	not visible
<i>Metoposaurus</i>	fine PFB	avascular	not visible
<i>Plagiosuchus</i>	coarse PFB	high	fine, oblique to bone surface
<i>Plagiosternum</i>	coarse PFB	high (interior)	fine, oblique to bone surface
<i>Gerrothorax</i>	coarse PFB	low	coarse, oblique to bone surface
Seymouriamorpha			
<i>Seymouria</i>	fine PFB	high	not visible

out the external cortex of the small specimen suggests a rather rapid formation of the bone (MARGERIE et al. 2002). However, the bone matrix proper in this specimen consists of parallel-fibered bone that has an intermediate growth rate between the slow-growing lamellar and the fast-growing woven or fibrous bone (FRANCILLON-VIEILLOT et al. 1990), so that the growth rate cannot be compared e. g. with that of fast growing archosaurs (see e. g. CHINSAMY-TURAN 2005). However, the parallel-fibered bone is rather poorly organized in this specimen, indicating a higher growth rate than in well ordered parallel-fibered bone.

In the thin sections investigated here, the vascularization pattern of the internal cortex is similar to the external one in that the more interior portion is mostly better vascularized by primary vascular canals and primary osteons, whereas the internal portion is poorly vascularized or avascular (Tab. 3). In the small *Mastodonsaurus* specimen, the complete internal cortex is well vascularized, corresponding to the external cortex.

The secondary bone in the external cortex of *Edops*, *Eryops*, *Pantylus* and *Mastodonsaurus* that formed possibly after trauma or infection (see above) is much better vascularized than the adjacent primary bone. This could be explained by the enhanced physiological need for blood supply during bone repair.

4.3. Bone texture and implications for the mode of life

The middle region of the investigated dermal bones exhibits varying degrees of vascularization, resorption

and secondary bone growth (Tab. 4). *Laccognathus* and the stem-tetrapods investigated here have a cancellous middle region that may show large erosion spaces in some areas, with irregular and rather thick trabeculae. Secondary remodeling is present, but Haversian tissue is not formed. Crown-group tetrapods like *Edops*, *Chenoprosopus*, *Eryops*, *Metoposaurus*, *Gerrothorax*, *Kupferzellia* and *Mastodonsaurus* are heavily ossified, and the middle region possesses numerous secondary osteons (often forming Haversian tissue) and stout, thick trabeculae. In contrast, *Plagiosuchus* shows very little secondary remodeling in its dermal bones, and a clear diploë structure is not present since the rather compact middle region is populated mostly by small primary vascular canals and primary osteons, similar to the osteoderms of this plagiosaurid (WITZMANN & SOLER-GUJÓN 2008). All these crown-group tetrapods lived primarily aquatically and were probably not rapid and agile swimmers but rather ambush predators, and the weight of the skeleton would have helped them to dive and to stay under water. DE RICQLÈS & DE BUFFRÉNIL (2001) found osteosclerosis in the ribs of *Mastodonsaurus* and pachyostosis in the ribs of *Gerrothorax*, which fits into this interpretation. Only the postcranial skeleton of *Eryops* has adaptations for larger land excursions (PAWLEY & WARREN 2006), although this animal was certainly still feeding in water (SCHOCH 2009) where it was lurking for prey.

Archegosaurus has more lightly built dermal skull bones since the middle region is trabecular with large erosive spaces. This gharial-like temnospondyl is interpreted as an active swimmer searching for fishes in the

Tab. 4. Summary of histological data concerning the middle region of the dermal bones investigated. Abbreviation: trab., trabecular. For further abbreviations, see text.

Taxon	Primary tissue	Vascularization	Bone texture	Haversian tissue
Porolepiform and stem-tetrapods				
<i>Laccognathus</i>	fine PFB	high (PO and SO)	coarse cancellous (trab.)	absent
<i>Panderichthys</i>	fine PFB	high (PO and SO)	coarse cancellous	absent
<i>Acanthostega</i>	fine PFB	high (PO and SO)	coarse cancellous	absent
<i>Greererpeton</i>	fine PFB	high (PO and SO)	fine to coarse cancellous	absent
Temnospondyls				
<i>Edops</i>	PFB > ISF	high (SO and PO)	fine to coarse cancellous	present
<i>Chenoprosopus</i>	PFB > ISF	high (SO)	fine to coarse cancellous	present
<i>Eryops</i>	PFB > ISF	high (SO)	coarse cancellous (trab.)	present
<i>Acheloma</i>	fine PFB	high (SO and ER)	trabecular	absent
<i>Sclerocephalus</i>	?	high (SO and ER)	trabecular	absent
<i>Archegosaurus</i>	fine PFB	high (SO)	trabecular	absent
<i>Kupferzellia</i>	PFB > ISF	high (SO)	coarse cancellous	absent
<i>Mastodonsaurus</i>	PFB, ISF	high (SO and PO)	coarse cancellous (trab.)	present
<i>Mastodonsaurus</i> (juv.)	coarse PFB	high (SO and PO)	fine to coarse cancellous	absent
<i>Metoposaurus</i>	fine PFB	high (SO)	coarse cancellous	present
<i>Plagiosuchus</i>	ISF, PFB	high (PVC, PO, ER)	fine cancellous	absent
<i>Plagiosternum</i>	fine PFB	high (SO, ER)	trabecular	absent
<i>Gerrothorax</i>	PFB, ISF	high (PO, SO, ER)	coarse cancellous to trab.	present
Lepospondyls				
<i>Diplocaulus</i>	PFB, ISF	high (SO, ER)	trabecular	absent
<i>Pantylus</i>	fine PFB	high (SO, ER)	trabecular	absent
Seymouriamorpha				
<i>Seymouria</i>	fine PFB	moderate (SO, PO)	fine to coarse cancellous	absent
Eureptilia				
<i>Labidosaurus</i>	fine PFB	high (SO)	coarse cancellous	present

open water (WITZMANN & SCHOCH 2006). The dermal bone of the subadult *Sclerocephalus* skull investigated here has a similar microstructure. At least the juvenile and subadult individuals of this taxon can be interpreted as rather agile predators, as indicated by their slender body outline, the long, deep swimming tail and the flexible gastral scales (WITZMANN 2007; SCHOCH & WITZMANN 2009).

The nectridean *Diplocaulus* shows a completely different microstructure of its dermal skull bones compared to the above mentioned temnospondyls. The cortices are much reduced and the extended middle region is composed of large erosive cavities that are framed by very thin, regularly arranged trabeculae. This highly porous structure is the result of extensive erosion and remodeling, and it can be designated as an 'osteoporotic-like condition' in the sense of DE RICQLÈS & DE BUFFRÉNIL (2001). The histological data of the dermal skull of *Diplocaulus* and the implication of skeletal lightening is in accordance with the palaeobiological hypothesis concerning the mode of life of this animal by CRUICKSHANK & SKEWS (1980). These authors showed on the basis of wind tunnel tests that the expanded posterolateral 'horns' of the flat, boomerang-shaped skull of *Diplocaulus* served as a hydrofoil that produced positive lift in slowly moving water of streams, that enabled this animal to rise rapidly of the substrate towards the prey in the water column. The reduced skeletal

mass observed in the *Diplocaulus* skull certainly enhanced the agility of the animal as well as its capability to accelerate quickly. However, to gain a more integrated picture, it would be interesting to investigate also the postcranial elements of *Diplocaulus* (ribs, vertebrae, limb bones) concerning their microstructure in the future.

The new skull reconstruction of *Plagiosternum* by GASTOU (2007) shows that this plagiosaurid has a skull shape that is strikingly similar to that of *Diplocaulus*, and a corresponding function as a hydrofoil is well possible. This is supported by the fact that the dermal bones of *Plagiosternum* investigated here are also lightly built with extensive erosion cavities in the middle region. Unfortunately, the postcranial anatomy of *Plagiosternum* is too poorly known to gain further information about its mode of life.

4.4. Implications of bone histology for the soft tissue dermis

4.4.1. Metaplastic bone

Metaplastic bone develops via direct transformation of pre-existing, dense connective tissue (HAINES & MOHUID-DIN 1968). Since a periost and thus osteoblasts are absent

during metaplastic ossification (but not always, see SCHEYER et al. 2008), fibroblasts take over the role of osteoblastic cells (VICKARYOUS & HALL 2008). According to HAINES & MOHUDDIN (1968), metaplastic bone is a dense fibrous tissue whose coarse fibers are interwoven, and the bone cell lacunae are arranged irregularly and have mostly short or stumpy canaliculi. In accordance, the interwoven structural fibers described here in the dermal bones of skull and pectoral girdle of basal tetrapods can be interpreted as metaplastic in origin. However, none of the dermal bones investigated are composed completely of interwoven structural fibers. Interwoven structural fibers are found often as islets or larger areas in the more interior part of the external cortex, whereas the more external part consists often of parallel-fibered bone. As pointed out by MAIN et al. (2005), there exist many intermediate states between the periosteal bone of 'normal intramembraneous bone' and the metaplastic bone, and transitions from metaplastic to periosteal tissue can be observed in the same section (e. g., interwoven structural fibers to parallel-fibered bone; see also GOODWIN & HORNER 2004, SCHEYER & SÁNCHEZ-VILLAGRA 2007 and WITZMANN & SOLER-GIJÓN 2008). Apart from the basal tetrapods described in this study, metaplastic tissue has been found within the periosteal bone in the skull of pachycephalosaur dinosaurs (GOODWIN & HORNER 2004), in the ornamentation of abelisaurid theropod skulls (HIERONYMUS & WITMER 2008), in dermal bones of the turtle shell (SCHEYER & SÁNCHEZ-VILLAGRA 2007) and in osteoderms of several tetrapod taxa such as chroniosuchians and temnospondyls (WITZMANN & SOLER-GIJÓN 2008), extant squamates (ZYLBERBERG & CASTANET 1985; LEVRAT-CALVIAC & ZYLBERBERG 1986), fossil and extant archosaurs (e. g., DE RICQLÈS et al. 2001; MAIN et al. 2005; SCHEYER & SANDER 2004; VICKARYOUS & HALL 2008), and extant anurans (RUIBAL & SHOEMAKER 1984). Whereas VICKARYOUS & HALL (2006) found no evidence of metaplasia in the dermal armour of the extant armadillo *Dasyus*, HILL (2006) demonstrated characteristics of metaplastic tissue in fossil and extant xenarthran osteoderms.

The prerequisite for metaplastic development of bone is a dense connective tissue, e. g. articulation facets, attachment sites of tendons and ligaments, or a dense dermis (HAINES & MOHUDDIN 1968). Because metaplastic bone develops via direct transformation of preexisting connective tissue, its occurrence in dermal bones of several basal crown-group tetrapods investigated here might indicate that their dermis was rather dense and composed of an interwoven network of strong collagenous fiber bundles. A mechanical advantage of metaplastic bone is a firm connection between bone and overlying soft-tissue, since the collagen fibers of the attached soft tissue are confluent with the collagen fibers within the metaplastic bone (HAINES & MOHUDDIN 1968).

4.4.2. Sharpey's fibers

The often closely packed, well-mineralized Sharpey's fibers are numerous especially in the ridges and tubercles, and support the assumption of a rather dense integument in most investigated basal tetrapods. Sharpey's fibers represent pre-existing fibers of the dermis that became progressively incorporated in the external cortex during its growth. A very similar pattern of Sharpey's fibers has been reported in the shell bones of many turtles, in which dense connective tissue is tightly anchored to the sculptural projections of the dermal bones (SCHEYER & ANQUINETIN 2008). Also HILL (2006) described closely spaced, ossified Sharpey's fibers that extend perpendicular to the external bone surface of xenarthran osteoderms and interweave with the collagen-fibers of the overlying dermis. Similarly, extraneous fibers firmly connect the scales of many teleosts (SIRE 1985, 1986) or the osteoderms of squamates (ZYLBERBERG & CASTANET 1985; LEVRAT-CALVIAC & ZYLBERBERG 1986) with the overlying integument. In these forms, the anchoring fibers extend uninterrupted from the bone into the dermis and continue until to the basement membrane of the epidermal-dermal boundary.

In general, the mineralization of Sharpey's fibers themselves can vary considerably, and the degree of their mineralization is probably associated with their mechanical effectiveness (JONES & BOYDE 1974; SILVA & MERZEL 2004). The mineralized fibers in basal tetrapods, especially when they have attained a large diameter, suggest a tight anchorage of the dermis to the external bone surface, particularly to the sculptural ridges and tubercles, which served as the main points of anchorage for the skin.

4.5. Dermal bone histology and the fish-tetrapod transition

4.5.1. The bone structure

Dermal sculpture that consists of bony tubercles and ridges is no acquisition of basal tetrapods, but developed already in their finned stem-forms after the reduction of the dental components (odontodes) in the dermal bones (see below). The basic morphology of the dermal sculpture, its morphogenesis by preferential growth, and its association with Sharpey's fibers was retained during the fish-tetrapod transition and was basically conserved in the different lineages of basal tetrapods including basal amniotes. In this respect, the dermal bones of basal tetrapods are highly conservative, and this applies also to the diploë-structure with compact external and internal cortices framing a cancellous to trabecular middle region that is affected by secondary remodeling to varying degrees.

The dermal bones of the limbed stem-tetrapods *Acan-*

thostega and *Greererpeton* are more 'fish-like' compared to those of the crown-group tetrapods in the possession of isopedine in the internal cortex, a tissue that has so far not been demonstrated in limbed tetrapods, and in the thinner Sharpey's fibers within the external cortex. Similar to the finned sarcopterygians, the primary bone matrix of external cortex and middle region is mainly composed of parallel-fibered bone. However, limbed stem-tetrapods are more 'tetrapod-like' in that the bony tubercles and ridges (the 'pit and ridge-sculpture') are more pronounced and form a stronger relief.

In crown-group tetrapods, the sculpture is generally even more pronounced, what surely led to an increased consolidation of the bone-dermis contact, and also the Sharpey's fiber morphology shows differences. In the porolepiform *Laccognathus*, the Sharpey's fibers that penetrated the bone surface between the odontodes were unmineralized, whereas the fibers are well mineralized in the basal tetrapods investigated here. Interestingly, the Sharpey's fibers are distinctly larger in diameter in most basal crown-group tetrapods than in *Laccognathus* and stem-tetrapods (Tab. 2), and often more densely arranged. Compared to the finned sarcopterygians and stem-tetrapods, the degree of remodeling and the number and density of secondary osteons are generally higher, with the exception of *Plagiosuchus*, in which secondary osteons are very scarce and thus gives a 'juvenile' impression. Furthermore, the cancellous to trabecular middle region occupies a proportionally larger space in most investigated basal crown-group tetrapods with respect to the compact cortices. The primary bone matrix in basal crown-group tetrapods consists to a large degree of parallel-fibered bone, and this holds true also for the internal cortex, where isopedine is completely reduced. However, also primary interwoven structural fibers can be recognized in the dermal bones, in contrast to *Laccognathus* and stem-tetrapods. The ability of the tetrapod dermis to form this metaplastic tissue might have evolved somewhere before the split into the amphibian- (temnospondyl-) and amniote lineage in a stem-tetrapod more crownwards than *Greererpeton*. This is in accordance with the study of SIRE & HUYSSEUNE (2003), who found a 'normal' periosteal development without evidence of metaplasia in the postcranial armour plates of extant fishes.

4.5.2. The soft-tissue integument

If the interpretations based on the occurrence of metaplastic tissue and Sharpey's fiber morphology outlined in chapter 4.4. are correct, then many basal crown-group tetrapods had a more consolidated integument compared to *Laccognathus* and the stem-tetrapods investigated, that might be associated with their different modes of life. Like

finned sarcopterygians, *Acanthostega* and *Greererpeton* probably possessed internal gills (CLACK 2000; LEBEDEV & COATES 1995). They were primarily water dwellers that were nevertheless probably able to crawl on the shore, but not to walk effectively on land (CARROLL et al. 2005). In contrast, the earliest known temnospondyls of the Carboniferous are suggested to be capable of larger land excursions (MILNER & SEQUEIRA 1994; HOLMES et al. 1998). Therefore, a denser integument might have been required to reduce the extent of water loss in air and to withstand mechanical friction and abrasion during locomotion on land. The fact that the number and density of Sharpey's fibers are generally reduced in the external cortex of *Mastodonsaurus* could be explained with the larger amount of interwoven structural fibers in the external cortex of this taxon. As outlined by HAINES & MOHUIDDIN (1968), soft tissue is tightly anchored to metaplastic bone because the collagen fibers course uninterrupted between bone and soft-tissue. This can also be assumed for external cortex and overlying dermis of these capitosauroids, rendering a larger number of Sharpey's fibers unnecessary. In contrast, *Metoposaurus* has an external cortex that is solely composed of well-ordered parallel-fibered bone with no metaplastic tissue, and numerous clusters of densely arranged Sharpey's fibers connected the integument to the bone surface.

4.6. Odontodes and bony sculpture

4.6.1. Spatial arrangement of odontodes and bony ridges and tubercles

The presence of dental tissue (dentine and enamel/enameloid) on the external surface of dermal bones as either tubercles or ridges (odontodes; see description of *Laccognathus* above) can be regarded as plesiomorphic for osteichthyans and even for vertebrates in general (e.g., ØRVIG 1968, 1977; REIF 1982; SMITH & HALL 1993; JANVIER 1996). These dental components of the exoskeleton were reduced during the evolution of distinct vertebrate lineages, and also independently within actinopterygians and different groups of finned sarcopterygians. Also in tetrapods and their immediate stem-forms from tristichopterids (including *Eusthenopteron*) crownwards, all non-oral dental elements were lost, and the tubercles and ridges on the dermal bone surface consist completely of bone (BYSTROW 1939; GROSS 1957; ØRVIG 1977; REIF 1982; JANVIER 1996).

In thin sections of odontode-bearing dermal bones of several 'ostracoderms', arthrodiros, actinopterygians and finned sarcopterygians, different generations of odontodes are frequently visible within the external cortex, with the older generations being buried within the growing bone matrix (e.g., PANDER 1860; GROSS 1930; BYSTROW 1939;

ØRVIG 1977; SMITH 1977) (see also Fig. 2c). A very similar pattern of superpositional growth is shown by the sculptural tubercles or ridges that consist completely of bone, e. g. in the basal tetrapods and their stem-forms investigated here (Figs. 2e, 11d). 'Buried' bony tubercles of earlier generations are generally readily visible in the bone matrix of the external cortex, closely resembling the spatial arrangement of successive generations of odontodes. A further similarity is that the odontodes/bony tubercles of successive generations are generally larger than those of preceding generations (e. g., BYSTROW 1935, 1939; ØRVIG 1977; this study). This similarity in arrangement, spatial distribution and outer morphology of the bony sculpture and the odontodes suggests that the bony tubercles and ridges have taken over parts of the functional role of the odontodes. This is supported by the histology of the dermal tubercles e. g. in the Devonian fish-like sarcopterygian *Holoptychius*. BYSTROW (1939, fig. 10a, b) investigated thin sections of dermal skull bones of this porolepiform and found the sculptural tubercles to be composed of both bone and dentine, and noted the absence of enamel. He interpreted this as an evolutionary 'transformation' (Verwandlung) of dermal teeth (odontodes) into bony tubercles within 'crossopterygians' (BYSTROW 1939: 303; see also ØRVIG 1977).

4.6.2. Functional considerations and the reduction of odontodes

The dentinous tissue of the odontodes was formed during ontogeny in a dental papilla (consisting of mesenchymal soft tissue) in the dermis directly below the epidermal-dermal junction, and enamel was produced by the adjoining dental organ (consisting of epidermis cells) in the basal part of the epidermis (ØRVIG 1977; REIF 1982). In contrast to odontodes, which arose always in the superficial part of the dermis, the supporting, comparatively thick dermal bone developed in the middle and internal parts of the dermis (ØRVIG 1968). By the interactions of epidermal and ectomesenchymal tissue in the production of the odontodes, and their development above (enamel) and below (dentine and bone) the epidermal-dermal junction, the outer skeletal surface might have been well integrated with both dermis and epidermis via the odontodes. Furthermore, because of the superficial position of the odontodes within the skin (the enamel cap might have extended beyond the soft-tissue integument, or it was covered solely by epidermis cells; see ØRVIG 1977, fig. 1), they stabilized the integument and served for mechanical protection (e. g. against abrasion) of the soft-tissue including the vessels and nerves that arose from the bone surface in the 'valleys' between the odontodes.

The epidermal (and superficial dermal) portion of the

exoskeleton was lost when the odontodes were reduced and replaced by bony tubercles and ridges. As indicated by the occurrence of the mostly densely arranged Sharpey's fibers, these bony sculptural elements laid deeper in the integument than the odontodes and were covered by the dermis, and there are no indications that they extended until to the epidermis. REM studies reveal no imprints of epithelial cells as visible e. g. in the cosmine covering of dermal bones in fossil lungfishes (SMITH 1977; BEMIS & NORTH CUTT 1992). Analogous to certain fishes and squamates (see above), it is hypothesized here that the bundles of Sharpey's fibers, that are found mainly and most closely packed in the bony tubercles and ridges, still maintained an association between the outer surface of the dermal bone and the superficial parts of the dermis and epidermal-dermal junction, respectively. These extrinsic fibers led to a strengthening of the integument and its tight connection to the bone surface. Like the odontodes, the bony ridges and tubercles certainly also protected the numerous blood vessels mechanically that coursed in furrows or pits between them. The difference, however, is that the bony tubercles and ridges were embedded deeper within the dermis and did not extend to or beyond the epidermis (see above). This might be the reason why the skin became more dense and was more tightly bound to the bone surface by Sharpey's fibers after the odontodes were reduced; this difference is well visible between the odontode-bearing *Laccognathus* with loosely arranged, unmineralized Sharpey's fibers (Fig. 2a, c) and *Panderichthys*, that has a bony sculpture and stronger, mineralized extrinsic fibers (Fig. 2e).

5. Conclusions

The thick, well mineralized Sharpey's fibers and the presence of metaplastic tissue suggest that the first crown-group tetrapods had attained a denser integument than their stem-forms. The more consolidated integument probably provided a better resistance against water loss and mechanical damage such as abrasion during locomotion on land. Additional to this, there is also evidence that the epidermis in basal tetrapods was more similar to amniotes in being more strongly cornified and more complex compared to lissamphibians (MADDIN et al. 2007). These implications for the soft-tissue integument, the presence of well-ossified scales in the majority of Palaeozoic basal tetrapods (WITZMANN 2007) and the often large size of these animals strongly suggest that cutaneous respiration was not as substantial as in extant salamanders and anurans. It might have been comparably important in small-growing, newt-like forms like branchiosaurids (BOY 1993) or the miniaturized lepospondyls (SCHOCH & CARROLL 2003). The thin, moist integument of extant amphibians, which is suitable to large-scale cutaneous gas exchange, can there-

fore probably be regarded as derived and is an adaptation to their small size, as already suggested by ROMER (1972). The 'rete vasculosum' did not serve for the purpose of cutaneous respiration as proposed by BYSTROW (1947), but rather for supply of the dermal bone during its growth.

6. References

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