Mandible histology in *Metoposaurus krasiejowensis* (Temnospondyli, Stereospondyli) from the Upper Triassic of Poland (#62020)

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Mandible histology in *Metoposaurus krasiejowensis* (Temnospondyli, Stereospondyli) from the Upper Triassic of Poland

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Recent studies which have systematically augmented our knowledge of dermal bones of the Late Triassic temnospondyl amphibian *Metoposaurus krasiejowensis* have been mostly focused on the shoulder girdle elements and the skull. So far histological data on the mandible are still scant. For the present study, two mandibles have been examined, using 50 standard thin sections. Dermal bones of the mandible reveal a uniform diploë structure, with the external cortex consisting of moderate vascularised, parallel-fibred bone, as well as distinct alternation of thick zones and thinner annuli. Dense bundles of well-mineralised Sharpey’s fibres are seen in the external cortex over the entire length of the mandible. The trabecular middle region is highly porous and well vascularised, showing small primary vascular canals and more numerous secondary osteons; irregular erosion spaces occur in large numbers as well. The thin and poorly vascular internal cortex consists of parallel-fibred bone. Solely the articular is not a dermal bone in origin, being formed of a thin layer of avascular cortex and a very extensive, trabecular middle region. In contrast to the dermal bones of the mandible, the articular developed from a cartilagenous precursor, as evidenced by numerous remains of calcified cartilage in the central parts of the bone. Histological variability is extremely high along the mandible as well as microstructure of dermal bones. Its anterior part is characterised by high compactness and biomechanically good resistance in contrast to the posterior and highly porous parts. Distinct variations of thickness of the bones and degree of their porosity in specific areas of the mandible, may refer to local biomechanical condition during feeding activity. Microstructure of the mandible confirms previous study of active and ambush predation strategy in metoposaurids.

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ABSTRACT

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INTRODUCTION

Temnospondyli were a large clade of extinct amphibians which appeared during the Early Carboniferous; in the Permian and Triassic they achieved a peak of radiation and diversity and went extinct in the Early Cretaceous (Milner, 1990). Metoposaurids belong to cosmopolitan temnospondyls during the Late Triassic (Carnian-Norian) which occupied freshwater ecosystems (Schoch & Miller 2000; Schoch, 2013). Fossil remains of these large amphibians are known from North America (Hunt, 1993; Lucas et al. 2007; Lucas, 2015, Gee et al. 2017), Africa and Madagascar (Dutuit, 1976, 1978; Hunt, 1993), India (Sengupta, 1992, 2002) and western and central Europe (von Meyer, 1842; Schoch & Milner, 2000; Sulej, 2002, 2007; Brusatte et al. 2015). Characteristic features of their anatomy were dorso-ventrally flattened body, short limbs and huge parabolic skull with anterio-lateral position of the orbits (e.g., Schoch & Miller 2000). Since the publication of the first paper on the genus *Metoposaurus* (von Meyer, 1842), the knowledge of its ecology has been constantly growing (see e.g., Hunt 1933; Ochev 1966; Howie 1970; Dzik et al. 2000; Sulej 2007; Konietzko-Meier & Sander 2013; Konietzko-Meier et al. 2013; Fortuny et al. 2017). *Metoposaurus krasiejowensis* (Sulej, 2002) belongs now to the best known temnospondyli being studied from the point of view of osteology (Dzik & Sulej, 2007; Sulej 2007; Barycka, 2007, Antczak & Bodzioch, 2018), histology (Konietzko-Meier & Sander 2013; Konietzko-Meier and Sander, 2013; Konietzko-Meier et al. 2012; Gruntmejer et al. 2016; Teschner et al. 2018) and the functional biomechanics (Fortuny et al. 2017; Konietzko-Meier et al. 2018; Gruntmejer et al. 2019a).

Current histological studies on metoposaurids focus mainly on characteristic of long bones, e.g. femora (Konietzko-Meier & Sander, 2013) or humeri (Teschner et al., 2018;

Teschner et al., 2020) and, ribs (Gądek, 2012) and vertebra (Konietzko-Meier et al., 2013; Konietzko-Meier et al., 2014; Danto et al. 2016; Gee et al. 2017).

Histology of dermal bones is still poorly known in temnospondyls. First description was provided by Gross (1934) for *Mastodonosaurus*, *Metoposaurus* and *Plagiosternum*. More detailed characteristics of dermal bones were presented decades later for a wider group of early tetrapods (Witzmann, 2009; De Buffrénil et al., 2016). Based on these studies it was concluded that dermal bones represent metaplastic origin and exhibit diploë structure with well-differentiated external cortex, middle region and internal cortex. Witzmann (2009) also provided a short description of thin sections of few dermal bone fragments of *Metoposaurus,* among other republishing the section mentioned by Gross (1934). However, it is not known if examined bones belonged to the skull or pectoral girdle (Witzmann, 2009). Preliminarly histological characteristic of the clavicle of *Metoposaurus krasiejowensis* was presented by Gądek (2012). Histological analysis of the skull of *Metoposaurus krasiejowensis*, additionally supported by Computational Modeling (CM) and Finite Element Analysis (FEA), put a new insight about the knowledge of dermal bone microstructure, origin and ecological implications in metoposaurids (Gruntmejer et al., 2016 with supplementary material; Konietzko-Meier et al., 2018; Gruntmejer et al., 2019a). Gruntmejer et al. (2016) provided detailed characteristics of almost all cranial bones with preliminary data of their biomechanical resistance. Further studies revealed that dermal bones microstructure is not only limited to a concrete bone, but relates to specific area of the skull (Konietzko-Meier et al. 2018). Dominance within skull roof, a thick and moderate porous bone with numerous, densely arranged Sharpey's fibres show that the skull was a robust structure which enabled the animal to bite actively on prey. Computational simulation of the skull of *Metoposaurus krasiejowensis* using FEA (Fortuny et al., 2017) and histological analysis of cranial sutures (Gruntmejer et al., 2019a) revealed that metoposaurids specialised in direct biting during ambush and active hunting. In contrast to the skull, histology ~~of~~ the mandible of *Metoposaurus* has been studied only briefly up till now (Gruntmejer, 2015). Only histological analysis of mandibular sutures, additionally bridged by dense clusters of Sharpey's fibres at bony edges, suggests that lower jaw was at the influence of complex loading regime during feeding activities (Gruntmejer et al., 2019b). Thus, presentation of detailed histological characteristic of mandible bones may help for better understanding of metoposaurids ecology in the Late Triassic ecosystems. Abundant accumulation of *Metoposaurus krasiejowensis* fossils in the Upper Triassic bone-bearing bed in Krasiejów (southwest Poland) allows us to conduct histological analyses in more detailed way than usual. Histology is an invasive technique of research, thus, detailed investigations from individual specimen have never been done before in any taxa.

The pursued goals of this study are to: 1) present for the first-time the mandible histology of serially sectioned specimens; 2) compare histological variability of the mandible among two individuals; 3) provide a preliminary interpretation of the mandible biomechanics based on histological framework.

MATERIAL AND METHODS

Material

The examined material comes from a former claypit near the village of Krasiejów in the Opole voivodship (Upper Silesia, southwest Poland). Geologically, this region is located along the south-easterly edge of the Fore-Sudetic Homocline and sedimentary formations at Krasiejów belong to the Upper Triassic – Norian according to stratigraphical data (Racki & Szulc 2014;

Szulc et al. 2015a, b, 2017; Jewuła et al. 2019) or Carnian according to biochronological studies (Dzik & Sulej, 2007, 2016; Lucas et al. 2007; Lucas 2015).

Two mandibles of *Metoposaurus krasiejowensis* were studied histologically. Both specimens are stored in the collections of the University of Opole, Institute of Biology, Laboratory of Palaeobiology (abbreviation: UOPB). UOPB 01145 was a complete (38 cm in length), well-preserved left ramus (Fig. 1) and UOPB 01027 is an almost complete (34 cm in length) right hemimandible (Fig. 2).

Methods

In total, 50 thin sections of the mandibles of *Metoposaurus krasiejowensis* were studied histologically. UOPB 01145 was completely sectioned at less than 10-mm distances. In this way, 45 samples were prepared from a single specimen (Fig. 1). UOPB 01027 was sectioned in 5 specific areas of the mandible (symphyseal region, medial and postglenoid area) in order to compare histological variability among the two specimens.

Thin sections were prepared at the Institute of Geology, Adam Mickiewicz University (Poznań, Poland). According to standard petrographical procedures (Lamm, 2013), thin sections were ground and polished to a thickness of 60-80 μm using wet SiC grinding powders (SiC 600, 800). Microscopic observations were conducted using LEICA DMLP light microscope in plane-, cross-polarised light and gypsum filter, and were supplemented by using scanning electron microscope (SEM) Hitachi S-3700N and binocular microscope Olympus SZH10 and SZ61.

The histological nomenclature used in this study follows ~~the one in~~ Francillon-Vieillot et al. (1990), Witzmann (2009) and Lamm (2013). Histological characteristic of the mandible of *Metoposaurus* was conducted and compared based on previous work regarding cranial bone histology of this taxon (Gruntmejer et al., 2016). Preliminary interpretation of biomechanical function of examined bones was also based on the study of the skull by Konietzko-Meier et al. (2018). Due to a lot of thin sections and high histovariability along the mandible of *Metoposaurus krasiejowensis*, it would be difficult to describe histology of each bone individually. Their histology and microstructure are shortly presented in Table 1. Thus, in this study we provide the description of the histological variability along the entire mandible arch.

Some other problematic issues can be raised to understand correctly the histological description of some bone components, i.e. external and internal cortices. The mandible of *Metoposaurus* is a tube-like structure, where several bones (dentary, splenial, postsplenial and angular) possess variable shape along their length. In many places they become U-shaped in cross section, thus, recognizing the position of external and internal cortices may be difficult. In this study, it was assumed that term ‘external cortex’ refers to parallel-fibred bone which occurs in the uppermost and ornamented parts of the bones at labial side and similarly in the uppermost and unornamented parts of the same bones at lingual side. Analogically, ‘internal cortex’ refers to parallel-fibred bone which consists of opposite and unornamented margin of bones, both at the labial and lingual side.

For the most representative cross sections (No. 4, 14, 22, 29, 36, 39, 41, 43) the porosity of the bones was calculated using the software `bw-counter` developed by Peter Göddertz from Institute of Geoscience, University of Bonn. That software allows us to describe the bone porosity mathematically by calculating the number of white and black pixels representing, respectively, bone tissue and cavities. All cross sections were calculated as a one sample record, without distinguishing individual bones. Only the articulare visible in two last sections was always calculated separately because of the different origin and structure.

RESULTS

The mandible of *Metoposaurus* is a longitudinal, tubular in shape and structure, forming of a conglomerate of 10 bones various in sizes and shapes (Fig. 1 and Fig. 2). With the exception of articular, all mandibular bones are dermal in origin which ossifies directly within the dermis without a cartilaginous predecessor. Their external surface is ornamented by grooves and longitudinal ridges, similar to those of skull bones and pectoral girdle. Dermal bones show a diploë structure in cross section with a well-differentiated compact external and internal cortex which are separated by a wide and porous middle region. Bone thickness varies from around 2 millimeters to over 10 millimeters along the mandible even within the same bones, e.g. angular or surangular (Tab. 1). The exception is articular bone which undergo endochondral ossification process.

Histology of dermal bones

External cortex consists usually of compact parallel-fibred bone with thickness that reaches to around 2 millimeters (Fig. 3A-B). In some areas, Interwoven Structural Fibres (ISF) are visible in external cortex (Fig. 3C). Growth marks structures appear as thick and well-vascularised zones, separated by thinner and avascular annuli (Fig. 3D-F), in both, sculptural ridges (labial side) and unornamented parts of external cortex (lingual side), especially in dentary and angular. Typical lines of arrested growth (LAG) do not occur. ~~Very~~ numerous, well-mineralised and dense packed ~~in~~ bundles Sharpey's fibres occur along the whole mandible length and are present in all dermal bones. However, they are the most abundant on the labial side of the mandible, mainly in ornamented parts of dentary, angular and surangular (Fig. 3G-H). In these areas Sharpey's fibres are very long and penetrate into deeper parts of external cortex (Fig. 3I-K). In bones of the lingual side of the mandible, especially in precoronoid, intercoronoid, coronoid and postsplenial, Sharpey's fibres are shorter and thinner.

External cortex is poorly vascularised. High number of vascular canals and small primary osteons occur only in thick zones, mainly in dentary and splenial. At labial side, sculptural ridges are almost avascular in postsplenial and angular, and the alternations of older generation of ridges are present (Fig. 4A-C). Osteocyte lacunae with branched canaliculi occur numerously along external cortex in all examined bones (Fig. 4D).

External cortex clearly transits into extensive middle region which occupies the largest parts of every bone in cross section (Fig. 4E-F). Vascular network in the middle region varies from low to well-developed. Small secondary osteons and primary vascular canals occur numerously next to the border between middle region and external cortex (Fig. 4G-I). In many areas, the dense clusters of small osteons creates the beginning of the Haversian tissue. These ~~structures~~ are clearly seen, mainly in the posterior part of dentary (Fig. 4G), anterior areas of angular and occasionally in splenial and postsplenial (Fig. 4H-I). Deeper parts of the middle region are occupied by larger secondary osteons (50-200 µm in diameter) which create dense clusters mainly in the posterior parts of postsplenial, angular and surangular (Fig. 5A-B). The middle region is highly remodelled and the most various is the presence of large and irregular erosion cavities along the mandible. The degree of porosity may drastically change even along a single bone, e.g. angular at its anterior part is relatively thin and low porous, whereas at its further parts it becomes thicker and highly porous as well (Fig. 5C-E). A similar pattern represents prearticular (Fig. 5F-G) and surangular (Fig. 5H-I). The middle region at the posterior part of these bones is almost absent, and erosion cavities could exceed 3.000 µm in length.

Internal cortex consists of parallel-fibred bone and its thickness usually reaches around one millimeter (Fig. 5J). Vascularization is moderate: longitudinal primary vascular canals are very numerous (Fig. 5K) small secondary osteons are less common and filled with a thin layer of lamellar bone. Sharpey's fibres are long, dense and packed in bundles; they occur along subsurface and in the deeper part of internal cortex, especially in dentary and angular (Fig. 5L). Osteocyte lacunae are numerous as well. Growth marks structures are not visible.

The histological variability of the mandible

In the lower jaw of *Metoposaurus krasiejowensis*, bone microanatomy and histological framework are highly variable. Symphyseal and ~~further~~ anterior parts of the mandible represent a compact bony structure (calculated porosity below 20% - Tab. 1; Fig. 7) being a conglomerate of low porous bones i.e., dentary, splenial, precoronoid and the anterior part of intercoronoid and postsplenial. At labial side, dentary, precoronoid and splenial possess well developed vascular network (Fig. 3D-F; Fig. 4D) and abundant clusters of Sharpey's fibres (Fig. 3G-K). In medial part, the mandible is formed by the tube-like structure with large Meckelian canal (sectioning samples no. 17-32 in UOPB 01145). The thickness of bones varies across these mandible part. Dentary thickness reaches from 1 to 5 millimeters, the same as in the coronoid case, whereas in postsplenial and angular it reaches from 2 millimeters to almost 1 centimeter (Tab. 1). The porosity of these bones is low to moderate (between 20% – 30%, Tab. 1; Fig. 7), however the most variable is the degree of vascularization. Dense clusters of large, secondary osteons are visible in the thickest parts of postsplenial and angular (Fig. 5A-B). Distinct variations in the thickness of bones and their compactness begin in the area of glenoid foramen (sectioning samples no. 33-45 in UOPB 01145). The average thickness of surangular and angular is around 4 millimeters, however at the upper part of surangular and posterior area of the angular, thickness of these bones can reach even to 10 milimeters. Prearticular thickness varies from 2 to 8 millimeters. The porous degree of all these bones becomes very high in contrast to anterior and medial areas of the mandible. Extensively remodelled middle region consists of large and irregular erosion cavities which can reach to around 3 millimeters in length. Microanatomical variability could be easily follow, e.g., in angular (Fig. 5C-E), prearticular (Fig. 5F-G) and surangular (Fig. 5H-I). Anteriormost parts of these bones characterize with allow thickness and high compactness, whereas further became much thicker and highly porous. ~~Due to the presence of such a high level of porosity, detailed histological characteristic of glenoid and postglenoid area is difficult to perform.~~

Histology of ~~endochondral bone~~

The articular consists of an extensive spongy bone, which is surrounded by thin cortex (Fig. 6A-B). Poorly preserved and avascular cortex consists of parallel-fibred bone. Growth marks and Sharpey's fibres are not visible. The spongy consists of an extensive spongy area with large cavities between trabeculae (Fig. 6C-D). Within bony trabeculae, numerous and elongated osteocyte lacunae are present and ~~very numerous~~ remains of calcified cartilage are visible (Fig. 6E-F).

Microstructure of mandible bones

The overall thickness of bone-walls increases along the mandible from symphysial to the postglenoid area (Tab. 1). The symphysial part is a tube-like structure, relatively massively build with only few, small cavities. The calculated porosity in that area equals about 19% (Fig. 7). The highest compactness is observed in the slide 14, counted to 89 %. Posteriorly, the diameter of the entire mandible ramus growths rapidly, with the increase of the size of inner cavities and the decrease of the bone thickness. Simultaneously, the bone porosity growths, achieving 42% in the slide 43 (Fig. 7). The articular shows different structure, with very loose framework, the bone porosity up to 51% in slide 41 and over 73% in slide 43.

DISCUSSION

Skeletochronology

In contrast to long bones where the growth marks structure could be easily determined and follow (Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013; Teschner et al. 2018~~; Teschner et al.~~ 2020), dermal bones are not a good source of skeletochronological information (Gruntmejer et al. 2016). Growth mark structures appear in the skull of *Metoposaurus* as resting lines and alternation of thick zones and annuli. Typical lines of arrested growth (LAGs) also could not be found (Gruntmejer et al., 2016). Similar skeletochronological patters occur along mandibles of *Metoposaurus*. Lines of arrested growth and resting lines are not visible. However, very common is the alternation of thick zones, separated by thinner and avascular annuli (Fig. 3D-F). The presence of this alternation is not constant, but clear to follow along the dentary and angular. Vascularised zones are associated with faster ontogeny of an organism which refers to favourable environmental conditions with high water level and food availability (Konietzko-Meier & Sander, 2013). Avascular annuli are related to less beneficial season when life activity and the body growth was slower (Konietzko-Meier & Sander, 2013). Due to the lack of continuity of growth marks along mandible bones and high bone remodelling, it is difficult to assess individual age of investigated specimens; the same situation is with the skull (Gruntmeier et al., 2016).

Ossification processes of the mandible

Dermal bones develop directly from the soft tissue i.e., the deep parts of dermis without periost, osteoblasts and osteoidand, via ~~metaplactic~~ ossification (Francillon-Vieillot et al., 1990; Vickaryous & Hall, 2008). In temnospondyls, dermal bones form the skull, mandible and pectoral girdle (two clavicles and interclavicle). Their external surface is ornamented by grooves, ridges and polygonal pits (e.g., von Meyer, 1858; Fraas, 1889; Fritsch, 1889; Zittel, 1911; Witzmann, 2009; Witzmann et al., 2010; De Buffrénil et al., 2016). In cross section, dermal bone shows a diploë structure. Their external surface creates compact layer of intramembranous component which appears as ~~i.e.,~~ parallel-fibred bone, lamellar bone or interwoven structural fibres (Scheyer & Sander, 2004; Scheyer & Sánchez-Villagra, 2007). ~~Eternal~~ cortex gradually passes into extensive and highly porous middle region, usually with numerous clusters of secondary osteons (Witzmann, 2009). Internal cortex also consists of intramembranous, lower part of bone. In mandibles of *Metoposaurus* (UOPB 01145 and UOPB 01027), dermal bones also represent diploë combination in cross section. External and internal cortices usually consist of a compact layer of the parallel-fibred bone (Fig. 3A-C; Fig. 5J). Its metaplastic origin additionally confirms the presence of interwoven structural fibres (ISF) in the subsurface part of the cortex and at sutural edges of the surangular and prearticular (Gruntmejer et al., 2019b). The middle region is highly remodelled and it composes the most portion of bone (Fig. 5C-I).

Endochondral bones ossify throughout the cartilage predecessor and consist of a trabecular region, surrounded usually by a thin layer of cortex. In the skull of *Metoposaurus*, the quadrate and exoccipital belong to endochondral bone (Gruntmejer et al., 2016). In the mandible case, the articular do not constitute a dermal bone in origin, being formed of a thin layer of avascular cortex and a very extensive, trabecular region (Fig. 6A-D). The remnants of calcified cartilage show an endochondral development of articular bone (Fig. 6E-F).

Sharpey's fibres

Dense clusters of two types of Sharpey's fibres were recognised in long bones of *Metoposaurus* (Konietzko-Meier & Sander, 2013). Thick and long fibres indicate a point of attachment of strong skeletal muscles and tendons, whereas shorter one presents the areas where the periosteum is connected to the bone. Similar distribution of Sharpey's fibres can be observed within the skull of *Metoposaurus* (Gruntmejer et al., 2016). Short fibres are rare, but they appear along the length of the skull and may indicate a delicate, soft tissue attachment. More numerous and thick Sharpey's fibres occur in the posterior part of the skull in tabular and occipital condyle. The presence of well mineralised and dense bundles in these areas suggests a strong skeletal muscle attachment of the skull to the vertebral column (Gruntmejer et al., 2016). Moreover, numerous clusters of short Sharpey's fibres occur at sutural edges between adjacent bones (Gruntmejer et al., 2019a). Their presence at lateral edges of dermal bones refers to the occurrence of collagen fibres within sutural morphospace which bridged and increased the connections of adjacent bones (Rafferty & Herring, 1999).

In the mandibles of *Metoposaurus* (UOPB 01145 and UOPB 01027), both types of Sharpey's fibres are present as well. However, long and short fibres occur together along the whole length of the mandible at the labial side (Fig. 3G-K). Their presence was noted in sculptural ridges and unornamented part of bones where longer Sharpey's fibres infiltrate into deeper parts of external cortex. Thinner fibres are present along lingual side of the mandible and in internal cortex of several bones (Fig. 5L). Dense clusters of two types of Sharpey's fibres along labial part of the mandible suggests ~~the~~ abundant attachment of skeletal muscles, tendons and ligaments at this side of lower jaw. On the other hand, the occurrence of shorter fibres along the lingual part of mandible may relate to delicate and soft tissue attachment which filled the inner surface of the mouth. Similarly to the skull case, short and numerous Sharpey's fibres were also noted at the sutural edges between adjacent bones of the mandible (Gruntmejer et al., 2019b). Moreover, their orientation is an important indicator ~~of deduce~~ of stress distribution during feeding activity. Sutural morphology and crucial orientation of Sharpey's fibres in anterior part of the dentary and at the sutural contact between articular, surangular and prearticular suggest tensile stress at these areas. Tensile loading regime at symphyseal and postglenoid region could be an adaptation to open the jaw very wide during predation (Gruntmejer et al. 2019b).

Biomechanical condition of dermal bones in the mandible

Histological studies of dermal skull bones in *Metoposaurus krasiejowensis* revealed that such parameters like bone thickness and porosity are the most variable along the skull and play~~s~~ an important role in its biomechanics (Konietzko-Meier et al. 2018). Bone thickness and compactness are real responses to the stress distribution, i.e., bones lose strength and stiffness with increasing porosity, however this can be partly compensated for the increase of the structure thickness. In addition to this, the histological properties are not related only to the bone, but strictly depend on the particular sectioning-plane (Gruntmejer et al., 2016; Konietzko-Meier et al., 2018). In the skull of *Metoposaurus krasiejowensis* the bones from sagittal axis like jugal and postorbital, sectioned in the sutural contact, represent the same histological framework and very good biomechanical properties to resist stresses. Another example can be the squamosal sectioned in its anterior part and next to the otic notch which showed different histological levels. Bones situated on the palatal side (e.g. vomer and pterygoid) represent the weaker biomechanical resistance, characterised by low bone thickness and extreme porosity (Gruntmejer et al. 2016). This suggests that the histological framework is not specifically bone-limited, but it show the specific areas of the skull which probably were involved during the feeding (Konietzko-Meier et al., 2018).

High variability of microstructure of the mandible bones of *Metoposaurus krasiejowensis* may also provide preliminary data on its biomechanics. Similarly to the skull, the microstructure of the mandible is also not limited to a single bone, but refers to specific area of the mandible. The angular, sectioned in different areas of its length, show completely various histological framework, from low thickness and high compactness to high thickness and extremely high degree of porosity (Fig. 5C-E). Similar microstructural pattern could be observed in the prearticular (Fig. 5F-G). Moreover, some bones e.g., the angular and surangular sectioned at sutural contact represent the same histological framework (i.e. degree of bone thickness and compactness) which varies in further parts of these bones (Fig. 5H-I).

Based on such high histovariability along the mandible of *Metoposaurus*, the preliminary interpretation of its biomechanics can be put on forward. Symphyseal and other anterior parts of the mandible are characterised by low porosity of the bones which creates a thick conglomerate without large cavity (Meckelian canal) between them (Fig. 7). Such microstructure may represent good biomechanical resistance of anteriormost area of the mandible. Stabile histological framework, accompanied by sutures mostly related to tensile loading (Grunmejer et al., 2018), made of the symphyseal part of the lower jaw, a structure well adapted to resist stress created during feeding. The most stable structure occurs on the level of slide 14, with the lowest porosity of dentary, splenial and postsplenial and complex structure without large inner cavity. It makes from that part of the mandible is a key point with the highest loading. It the midline areas, the thickness of the bones is low, reaches to around 2-5 millimeters, but increases to even one centimeter at sculptural regions. However, compactness of these bones is lower than in the anterior part, thus biomechanical resistance of central parts of the mandible can be assesed as moderate. Distinct increase of bones porosity begins in the glenoid area, whereas in postgleonoid parts, all bones become extremely porous (up to 42% in slade 43) at a thickness from 5 millimeter to 1 centimeter. However, the high level of porosity caused that biomechanical parameters of these bones can be assumed from moderate to low. Based on such various microstructure among dermal bones, the mandible in general appears as not such a strong structure. However, seemingly weak bones (caused by low compactness) could be strengthened by connections of strong skeletal muscles and other soft tissues. Dense clusters of thick and long Sharpey’s fibres support this assumption. Moreover, five types of sutures adapted to resist different stresses (tension vs compression) have been noted along the mandible (Gruntmejer et al., 2019b). One of the biomechanical roles of sutures is to minimalize loading regimes acting within the skull or the mandible during feeding. Thus, the complexity of sutural morphology and the abundance of Sharpey’s fibres along the mandible may compensate for relatively weak microstructure of dermal bones of the mandible. These preliminary interpretations of the mandible biomechanics should be improved and supplemented in further studies e.g., by computational modelling using finite element analysis.

CONCLUSIONS

Dermal bones have already been studied histologically in temnospondyls' ~~case~~, however not in serially sectioned specimens. The histology of cranial bones and pectoral girdle in metoposaurids was presented by several authors, but up till now, knowledge about the mandible microstructure was unknown. In the present study, a detailed histological description of the mandible of *Metoposaurus krasiejowensis* have been presented. All bones represent metaplastic origin with uniform diploë structure, typical for dermal bones, with the exception of the articular. External cortex consists of relatively thick parallel-fibred bone with well differentiated growth marks structure and long Sharpey's fibres. Extensive middle region represents high level of bone remodelling with very numerous secondary osteons and larger erosional cavities. Internal cortex consists of almost only of avascular parallel-fibred bone. The articular represents endochondral development with trabecular region and numerous cartilage remains. The same histological framework in concrete areas of the mandible was confirmed in two specimens compared.

General histology of the mandible of *Metoposaurus krasiejowensis* represents similar microanatomy to the one recognised in the skull, but with some differences. ~~As stated in previous works, growth mark structures appear in~~ dermal bones ~~as~~ cyclicall~~y~~ ~~repeated~~ thick and well vascularised zones separated by thinner and avascular annuli. However, ~~the same case as in the skull, they are difficult to follow along the mandible~~ and they are not good source to deduce the skeletochronological information. Sharpey's fibres are very long and occur in dense bundles along the whole mandible, both on labial and lingual side. Such a clusters an abundant occurrence of fibres suggests strong muscles and other soft tissues attachment. Highly variable porosity of all bones starting from the symphyseal to articular region also confirms previous results that bone microstructure is associated to the specific areas of the mandible as an answer to local biomechanical condition. Anterior part of the mandible is characterised by low bone porosity, thus these areas were heavily loaded during prey capture in contrast to highly porous bones in the posterior and articular region. The histology of mandibular sutures supports this assumption. Sutures located at the anterior and medial parts of the mandible were capable to resist various stresses acting together (compression vs tension) which was helpful during feeding activity. On the other hand, in the posterior and articular areas of the mandible only compressive-resisted suture has been noted. Such type of suture and additionally high amount of long Sharpey's fibres may reinforce and compensate for relatively weak microstructure of those bones.

To summarize, the histology of the mandible presented in this work significantly supplements and confirms previous histological and computational FE investigations about the ecology of metoposaurids . It is known that these temnospondyls specialised both in active and ambush predation. However, histological data suggest that the skull was used for laterally or bilaterally biting, whereas the mandible played a role in holding down the struggling prey.

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FIGURE CAPTIONS

Fig. 1 Mandible of *Metoposaurus krasiejowensis* (UOPB 01145) and schematic drawings with marked locations of sectioning planes (after Gruntmejer et al. 2019b). Grey colour indicates cleaned up parts of the mandible; yellow colour refers to areas covered by sediment. Scale bar equals 5 cm. Abbreviations: An, angular; Ar, articular; C, coronoid; D, dentary; Ic, intercoronoid; Par, prearticular; Pc, precoronoid; Psp, postsplenial; Sa, surangular; Sp, splenial; fma, anterior Meckelian foramen; fmp, posterior Meckelian foramen.

Fig. 2 Mandible of *Metoposaurus krasiejowensis* (UOPB 01027) and schematic drawings with marked locations of sectioning planes (after Gruntmejer et al. 2019b). Grey colour indicates cleaned up parts of the mandible; yellow colour refers to areas covered by sediment. Scale bar equals 5 cm. Abbreviations: An, angular; Ar, articular; C, coronoid; D, dentary; Ic, intercoronoid; Par, prearticular; Psp, postsplenial;; Sp, splenial.

Fig. 3 Histology of the external cortex of the mandible bones of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027). (A) Thick layer of parallel-fibred bone in ornamented part of the dentary; (B) Compact external cortex of the splenial with several vascular canals (VC); (C) Alternation of parallel-fibred bone (PFB) and interwoven structural fibres (ISF) of the splenial; (D-F) Growth marks structure (indicated by arrows) visible as thick and vascular zones, separated by avascular annuli along the dentary; (G-H) Two types of well mineralised Sharpey's fibres (indicated by arrows) of the dentary; (I) Long Sharpey's fibres (indicated by arrows) in gypsium filter; (J-K) Sharpey's fibres (indicated by arrows) in subsurface and deeper part of the external cortex of the angular. Abbreviations: A, annulus; EC, external cortex; ISF, interwoven structural fibres; PFB, parallel-fibred bone; VC, vascular canals; Z, zone.

Fig. 4 Histology of the external cortex and middle region of the mandible bones of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027). (A) Alternation of growth rate pattern (indicated by arrows) within sculptural ridges of the splenial; (B) the same, postsplenial; (C) the same, angular; (D) Vascular canals and numerous osteocyte lacunae in the deeper portion of external cortex; (E) Sharp transition from external cortex into the middle region of the dentary (indicated by dashed line); (F) Same as in E, postsplenial; (G-I) Dense clusters of small secondary osteons in the upper areas of middle region. Abbreviations: EC, external cortex; LB, lamellar bone; MR, middle region; OL, osteocyte lacunae; SO, secondary osteons; VC, vascular canals.

Fig. 5 Histology of the middle region and internal cortex of the mandible bones of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027). (A) Highly remodelled and well vascularised parts of the surangular; (B) Dense clusters of large secondary osteons of the angular; (C-E) Microstructural variability along the angular; (F-G) Microstructural variability along the prearticular; (H-I) Microstructural variability at the sutural contact between angular and surangular; (J) Internal cortex with well-differentiated parallel-fibred bone of the angular; (K) Longitudinal vascular canals within internal cortex; (L) Dense clusters of short Sharpey's fibres (indicated by arrows) along the internal cortex of the angular. Abbreviations: ER, erosion cavities; IC, internal cortex; PFB, parallel-fibred bone; SO, secondary osteons; VC, vascular canals.

Fig. 6 Histology of the articular of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027). (A) General microstructure of UOPB 01027 specimen; (B) and of UOPB 01145 specimen; (C-D) Bone trabeculae in the central part of the articular; (E-F) Numerous remains of calcified cartilage visible in the trabeculae (arrowed). Abbreviations: TR, bone trabeculae.

Fig. 7 General microanatomy of selected thin sections of specimen UOPB 01145 and estimated biomechanical loading reconstructed on the basis of the microstructural characteristics of the *Metoposaurus krasiejowensis* mandible. Black and white images of selected thin sections show calculated composition of bone thickness and its compactness. Colour frames and scale bar represent estimated values of stress distribution in different parts of the mandible, but they only suggest a contractual stress regime (higher or lower). ~~As was stated in Konietzko-Meier et al. 2018, it is impossible to calculate the objective amount of stress in case of histological thin section.~~ Black arrows indicate places underwent various stresses (tensile-compressive) caused by mandible suture mechanics, ~~followed by~~ Gruntmejer et al. 2019b. Black scale bar equals 4 cm.

Table 1(on next page)

General histology of *Metoposaurus krasiejowensis* mandible of UOPB 01145 and UOPB 01027 specimens.

Table 1 General histology of *Metoposaurus krasiejowensis* mandible of UOPB 01145 and UOPB 01027 specimens.

Bone	Bone thickness	Ornamentation	Growth marks	Sharpey's fibers	Vascularization	Bone remodelling
Angular (thin sections no. 22-45) UOPB 01145	2 millimeters to 10 millimeters	high ridges (5 millimeters)	alternation of vascularised zones and avascular annuli	very numerous; two types: 1) long and thick, 2) thin and short	low (almost avascular in the middle part of the bone) to very high (numerous secondary osteons in posterior part of the bone)	low (numerous erosion cavities but in small sizes) to very high (numerous and large erosion cavities)
Angular (thin sections no. 1e and 1f) UOPB 01027	3 millimeters to 10 millimeters	high ridges (5 millimeters)	visible thick zones and thinner annuli	very numerous; two types: 1) long and thick, 2) thin and short	low (almost avascular in the middle part of the bone) to very high (numerous secondary osteons in posterior part of the bone)	low (numerous erosion cavities but in small sizes) to very high (numerous and large erosion cavities)
Articular (thin section no. 41-44) UOPB 01145	over 10 millimeters at the widest place	lack	not visible	not visible	low (simple vascular canals and secondary osteons)	highly porous trabecular region
Articular (thin section no. 1e) UOPB 01027	around 10 millimeters	lack	not visible	not visible	low (simple vascular canals and secondary osteons)	highly porous trabecular region
Coronoid (thin sections no. 22-31) UOPB 01145	2-8 millimeters	lack	not visible	very short and rare	moderate (several secondary osteons)	low (presence of few and small erosion cavities)
Coronoid (thin section no. 1d) UOPB 01027	1-3 millimeters	lack	not visible	very short and rare	moderate (several secondary osteons)	low (presence of few and small erosion cavities)
Dentary (thin sections	2 millimeters to 10 millimeters	generally lack; only three ridges at	alternation of vascularised zones and	very numerous; two types: 1) long and thick, 2) thin	high (numerous secondary osteons and vascular	moderate (numerous

no. 1-29) UOPB 01145		symphyseal region	avascular annuli	and short	canals)	erosion cavities but in small sizes)
Dentary (thin sections no. 1a, 1c and 1d) UOPB 01027	3-6 millimeters	generally lack; only two ridges at symphyseal region	visible thick zones and thinner annuli	very numerous; two types: 1) long and thick, 2) thin and short	high (numerous secondary osteons and vascular canals)	moderate (numerous erosion cavities but in small sizes)
Intercoronoid (thin sections no. 15-21) UOPB 01145	3 millimeters	lack	not visible	very short and rare	moderate (several secondary osteons)	low (presence of few and small erosion cavities)
Intercoronoid (thin section no. 1c) UOPB 01027	3 millimeters	lack	not visible	very short and rare	moderate (several secondary osteons)	low (presence of few and small erosion cavities)
Prearticular (thin sections no. 26-44) UOPB 01145	1 millimeter to 10 millimeters	lack	not visible	short and numerous	low to moderate (several secondary osteons)	moderate (numerous erosion cavities but in small sizes) to very high (numerous and large erosion cavities)
Prearticular (thin sections no. 1e and 1f) UOPB 01027	4-8 millimeters	lack	not visible	not visible	low to moderate (several secondary osteons)	moderate (numerous erosion cavities but in small sizes) to very high (numerous and large erosion cavities)
Precoronoid (thin sections no. 8-14) UOPB 01145	4 millimeters	lack	not visible	very short and rare	moderate (several secondary osteons)	low (presence of few and small erosion cavities)
Precoronoid (thin section no.	3 millimeters	lack	not visible	very short and rare	moderate (several secondary osteons)	low (presence of few and

1a) UOPB 01027						small erosion cavities)
Postsplenial (thin sections no. 16-28) UOPB 01145	2-8 millimeters	medium high ridges (3 millimeters)	alternation of vascularised zones and avascular annuli	very numerous; two types: 1) long and thick, 2) thin and short	moderate to high (numerous secondary osteons and vascular canals)	moderate (numerous erosion cavities but in small sizes)
Postsplenial (thin sections no. 1c and 1d) UOPB 01027	3-6 millimeters	medium high ridges (2 millimeters)	alternation of vascularised zones and avascular annuli	very numerous; two types: 1) long and thick, 2) thin and short	moderate to high (numerous secondary osteons and vascular canals)	moderate (numerous erosion cavities but in small sizes)
Splenial (thin sections no. 4-16) UOPB 01145	2-7 millimeters	moderate high ridges (3 millimeters)	not visible	visible but not numerous; thin and short	low to moderate (simple vascular canals and secondary osteons)	low to moderate (simple erosion cavities)
Splenial (thin section no. 1a) UOPB 01027	4 millimeters	lack	not visible	visible but not numerous; thin and short	low (simple vascular canals and secondary osteons)	low (lack of erosion cavities)
Surangular (thin sections no. 31-44) UOPB 01145	2 millimeters to 10 millimeters	generally lack; simple medium high ridges (3 millimeters)	alternation of vascularised zones and avascular annuli	very numerous; two types: 1) long and thick, 2) thin and short	low (almost avascular in the middle part of the bone) to very high (numerous secondary osteons in upper part of the bone)	low (presence of few and small erosion cavities) to very high (numerous and large erosion cavities)

Figure 1

Mandible of *Metoposaurus krasiejowensis* (UOPB 01145) and schematic drawings with marked locations of sectioning planes (after Gruntmejer et al. 2019b).

Grey colour indicates cleaned up parts of the mandible; yellow colour refers to areas covered by sediment. Scale bar equals 5 cm. Abbreviations: An, angular; Ar, articular; C, coronoid; D, dentary; Ic, intercoronoid; Par, prearticular; Pc, precoronoid; Psp, postsplenial; Sa, surangular; Sp, splenial; fma, anterior Meckelian foramen; fmp, posterior Meckelian foramen.

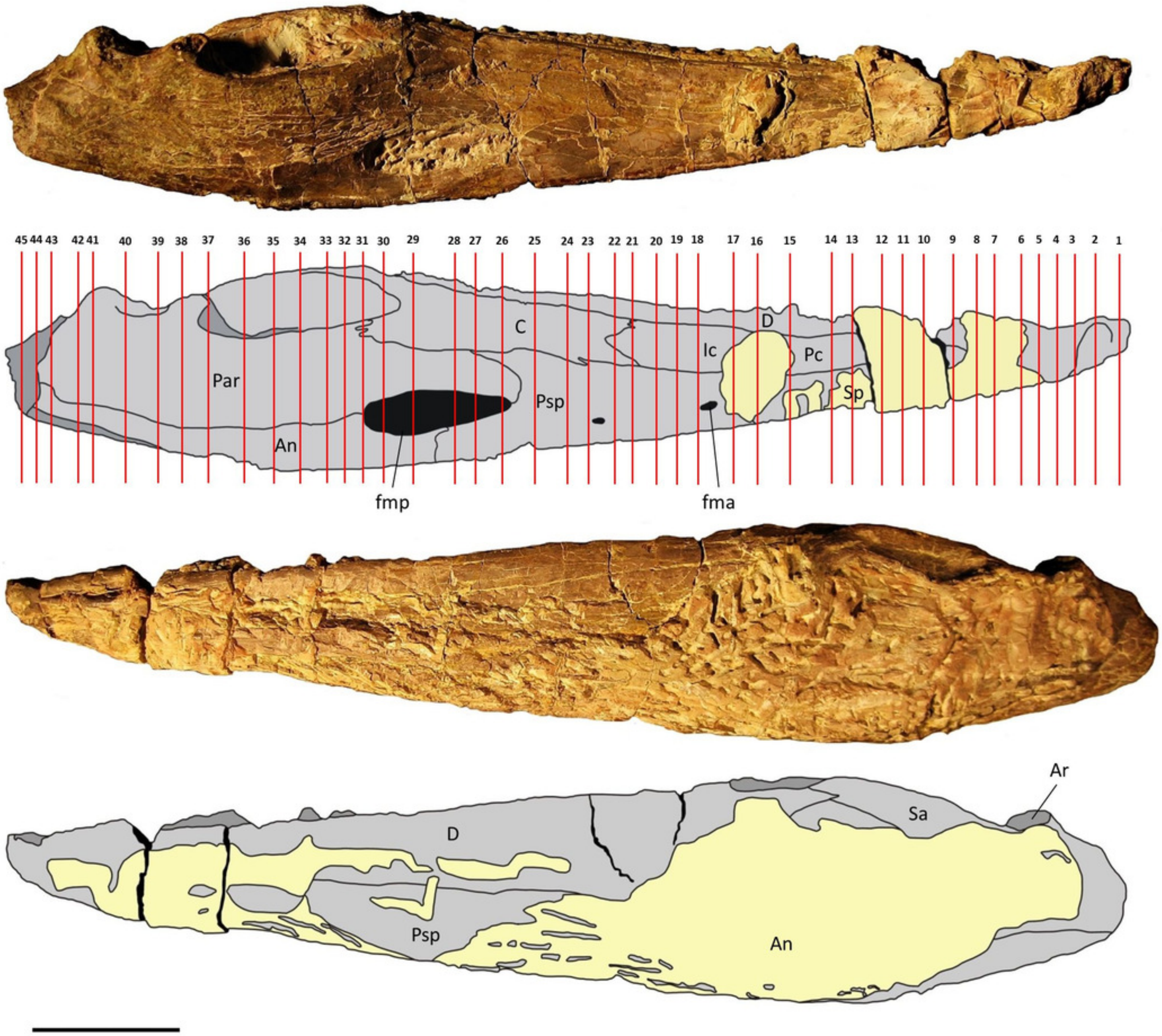

45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
C
D
Ic
Pc
Par
Psp
Sp
An
fmp
fma
Ar
Sa
D
Psp
An

Figure 2

Mandible of *Metoposaurus krasiejowensis* (UOPB 01027) and schematic drawings with marked locations of sectioning planes (after Gruntmejer et al. 2019b).

Grey colour indicates cleaned up parts of the mandible; yellow colour refers to areas covered by sediment. Scale bar equals 5 cm. Abbreviations: An, angular; Ar, articular; C, coronoid; D, dentary; Ic, intercoronoid; Par, prearticular; Psp, postsplenial;; Sp, splenial.

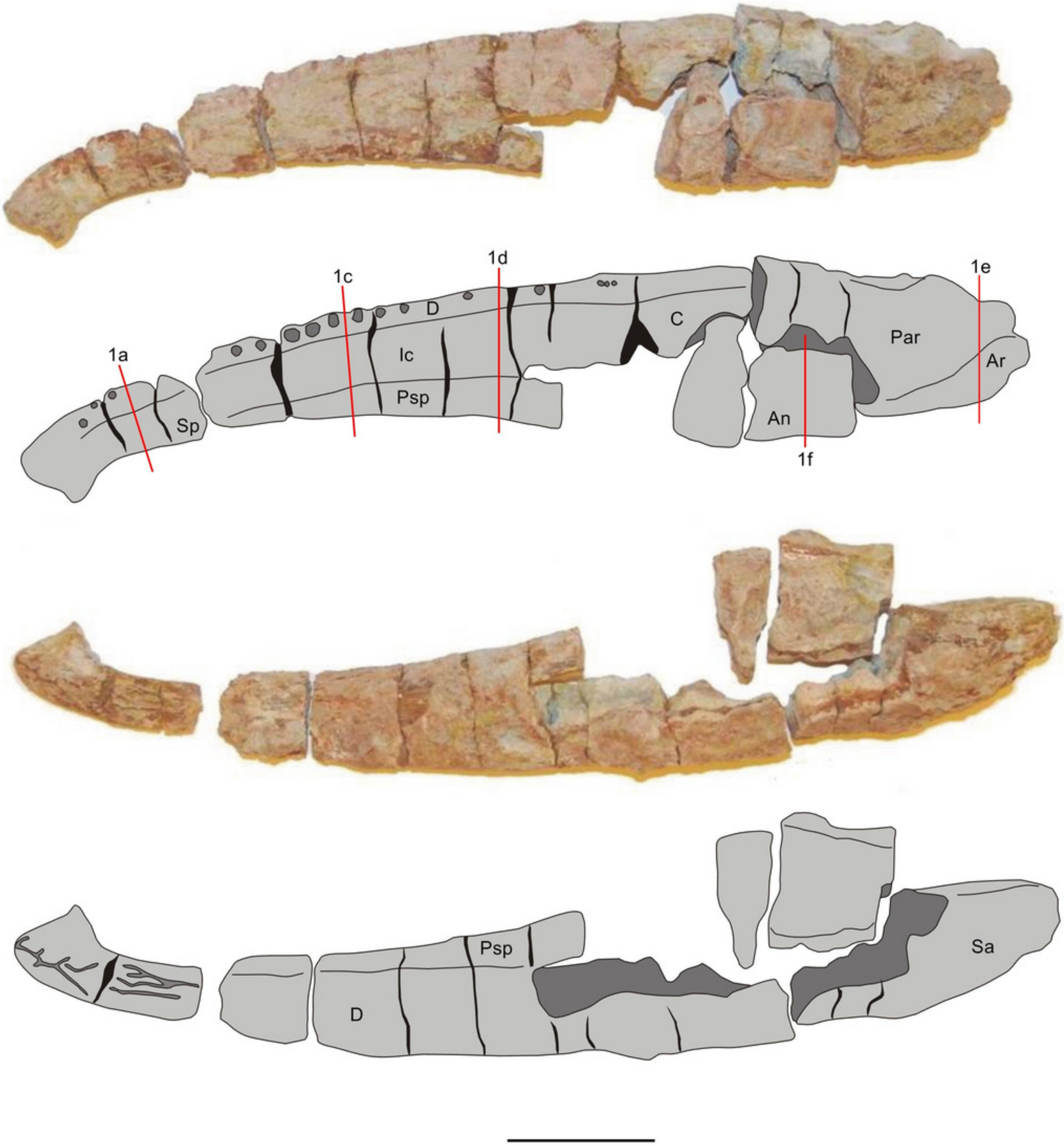

1d
1c
1e
D
C
Par
Ic
1a
Ar
Psp
Sp
An
1f
Psp
Sa
D

Figure 3

Histology of the external cortex of the mandible bones of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027).

(A) Thick layer of parallel-fibred bone in ornamented part of the dentary; (B) Compact external cortex of the splenial with several vascular canals (VC); (C) Alternation of parallel-fibred bone (PFB) and interwoven structural fibres (ISF) of the splenial; (D-F) Growth marks structure (indicated by arrows) visible as thick and vascular zones, separated by avascular annuli along the dentary; (G-H) Two types of well mineralised Sharpey's fibres (indicated by arrows) of the dentary; (I) Long Sharpey's fibres (indicated by arrows) in gypsium filter; (J-K) Sharpey's fibres (indicated by arrows) in subsurface and deeper part of the external cortex of the angular. Abbreviations: A, annulus; EC, external cortex; ISF, interwoven structural fibres; PFB, parallel-fibred bone; VC, vascular canals; Z, zone.

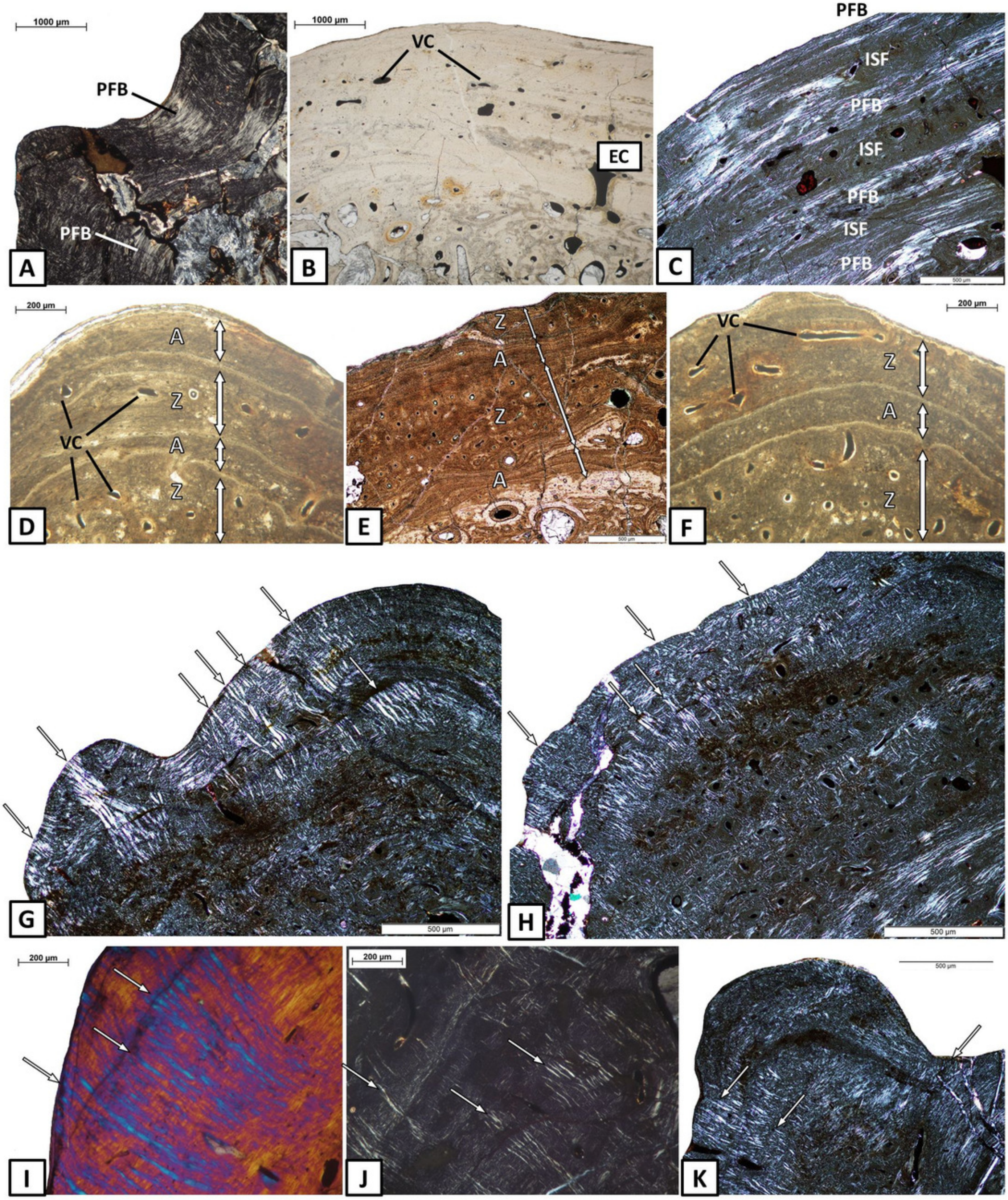

1000 µm
PFB
PFB
A
1000 µm
VC
EC
B
PFB
ISF
PFB
ISF
PFB
ISF
PFB
C
500 µm
200 µm
A
Z
VC
A
Z
D
Z
A
Z
A
E
500 µm
VC
200 µm
Z
A
Z
F
G
500 µm
H
500 µm
200 µm
I
200 µm
J
500 µm
K

Figure 4

Histology of the external cortex and middle region of the mandible bones of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027).

(A) Alternation of growth rate pattern (indicated by arrows) within sculptural ridges of the splenial; (B) the same, postsplenial; (C) the same, angular; (D) Vascular canals and numerous osteocyte lacunae in the deeper portion of external cortex; (E) Sharp transition from external cortex into the middle region of the dentary (indicated by dashed line); (F) Same as in E, postsplenial; (G-I) Dense clusters of small secondary osteons in the upper areas of middle region. Abbreviations: EC, external cortex; LB, lamellar bone; MR, middle region; OL, osteocyte lacunae; SO, secondary osteons; VC, vascular canals.

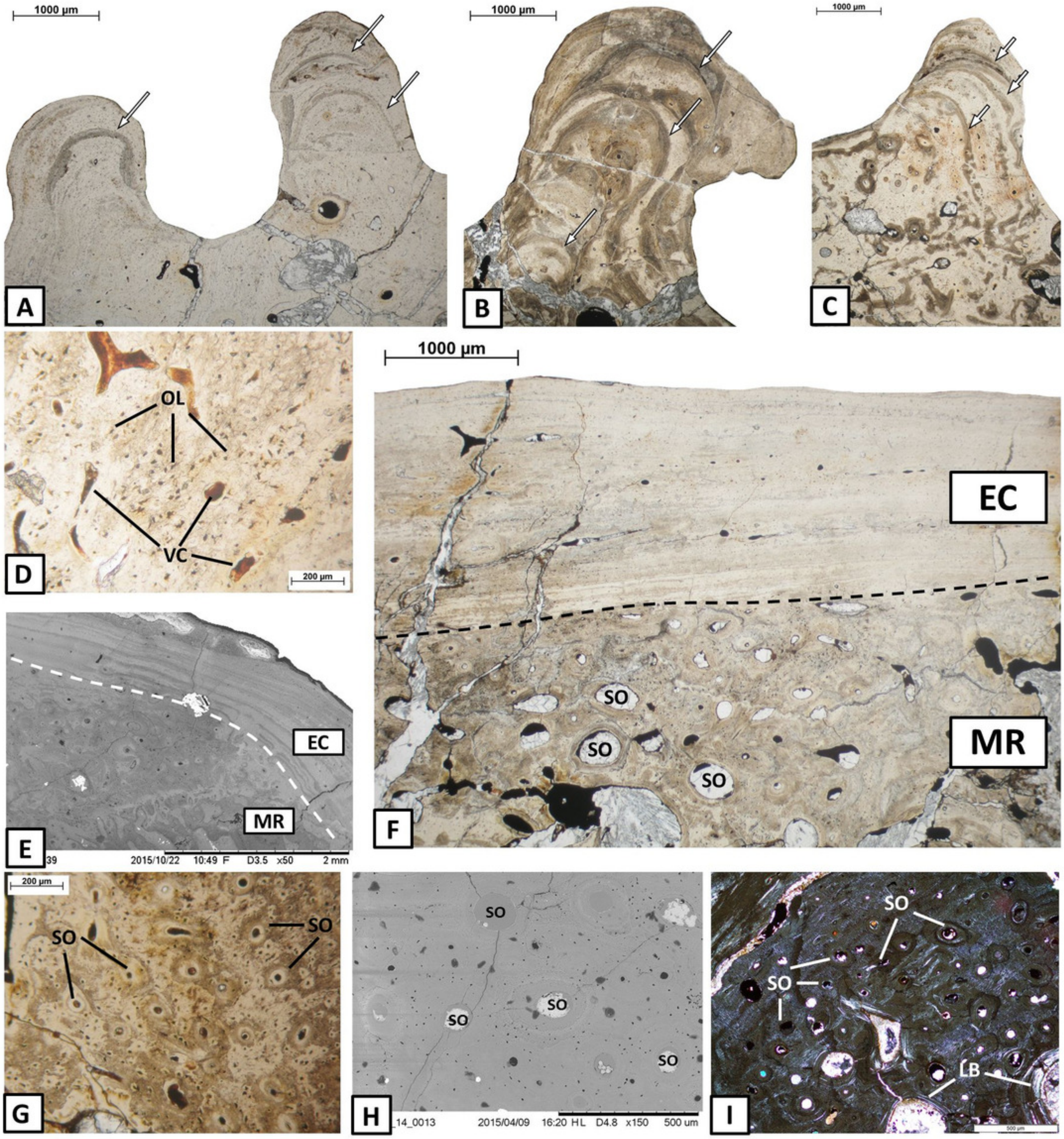

1000 µm
A
1000 µm
B
1000 µm
C
OL
VC
200 µm
D
1000 µm
EC
MR
SO
SO
SO
F
EC
MR
E
39 2015/10/22 10:49 F D3.5 x50 2 mm
200 µm
SO
SO
G
SO
SO
SO
SO
H
_14_0013 2015/04/09 16:20 HL D4.8 x150 500 um
SO
SO
LB
500 µm
I

Figure 5

Histology of the middle region and internal cortex of the mandible bones of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027).

(A) Highly remodelled and well vascularised parts of the surangular; (B) Dense clusters of large secondary osteons of the angular; (C-E) Microstructural variability along the angular; (F-G) Microstructural variability along the prearticular; (H-I) Microstructural variability at the sutural contact between angular and surangular; (J) Internal cortex with well-differentiated parallel-fibred bone of the angular; (K) Longitudinal vascular canals within internal cortex; (L) Dense clusters of short Sharpey’s fibres (indicated by arrows) along the internal cortex of the angular. Abbreviations: ER, erosion cavities; IC, internal cortex; PFB, parallel-fibred bone; SO, secondary osteons; VC, vascular canals.

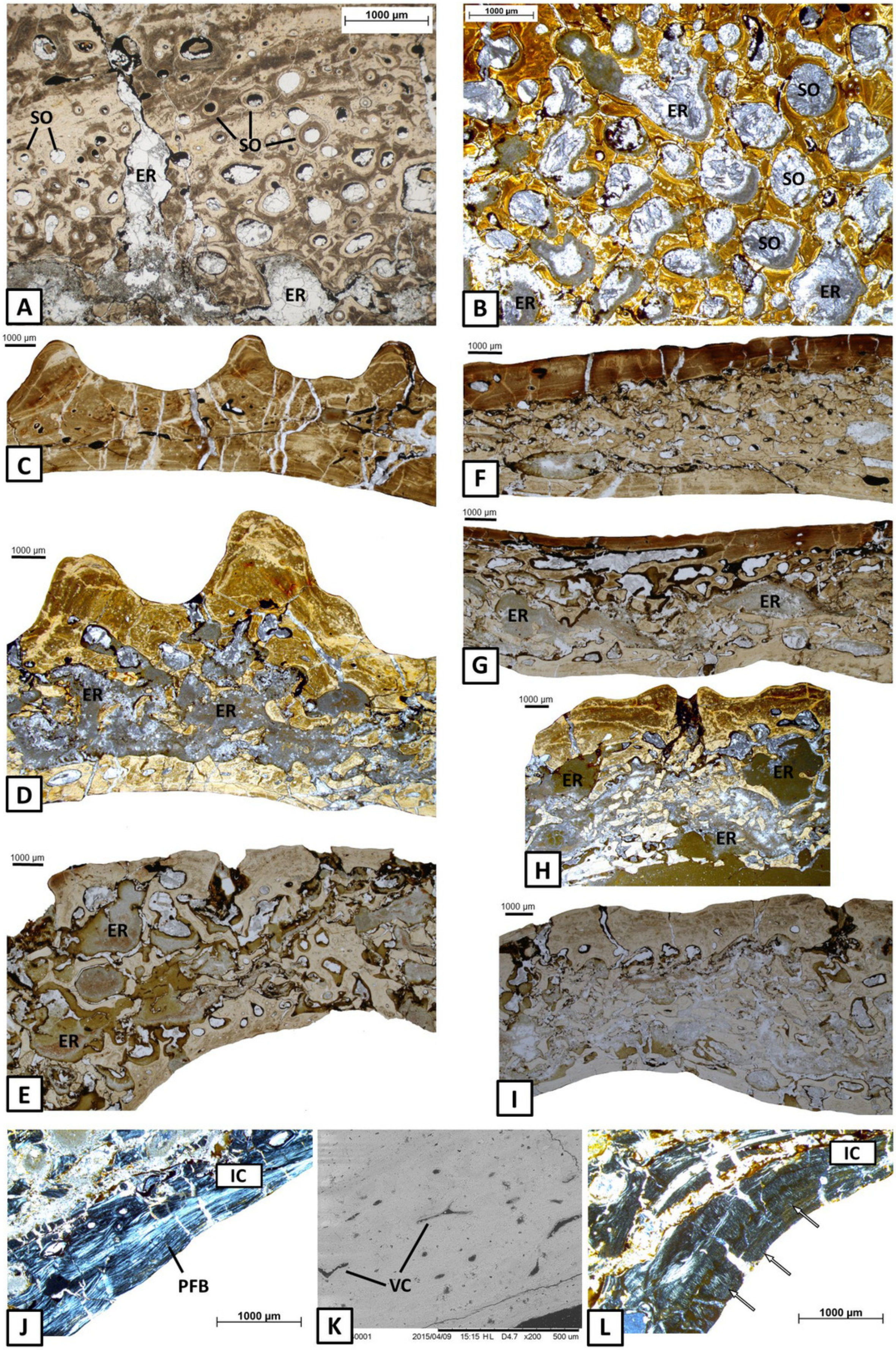

1000 µm
SO
SO
ER
ER
A
1000 µm
SO
ER
SO
SO
SO
ER
ER
B
1000 µm
C
1000 µm
F
1000 µm
ER
ER
D
1000 µm
ER
ER
G
1000 µm
ER
ER
ER
H
1000 µm
ER
ER
E
1000 µm
I
IC
PFB
1000 µm
J
VC
0001 2015/04/09 15:15 HL D4.7 x200 500 um
K
IC
1000 µm
L

Figure 6

Histology of the articular of *Metoposaurus krasiejowensis* (UOPB 01145 and UOPB 01027).

(A) General microstructure of UOPB 01027 specimen; (B) and of UOPB 01145 specimen; (C-D) Bone trabeculae in the central part of the articular; (E-F) Numerous remains of calcified cartilage visible in the trabeculae (arrowed). Abbreviations: TR, bone trabeculae.

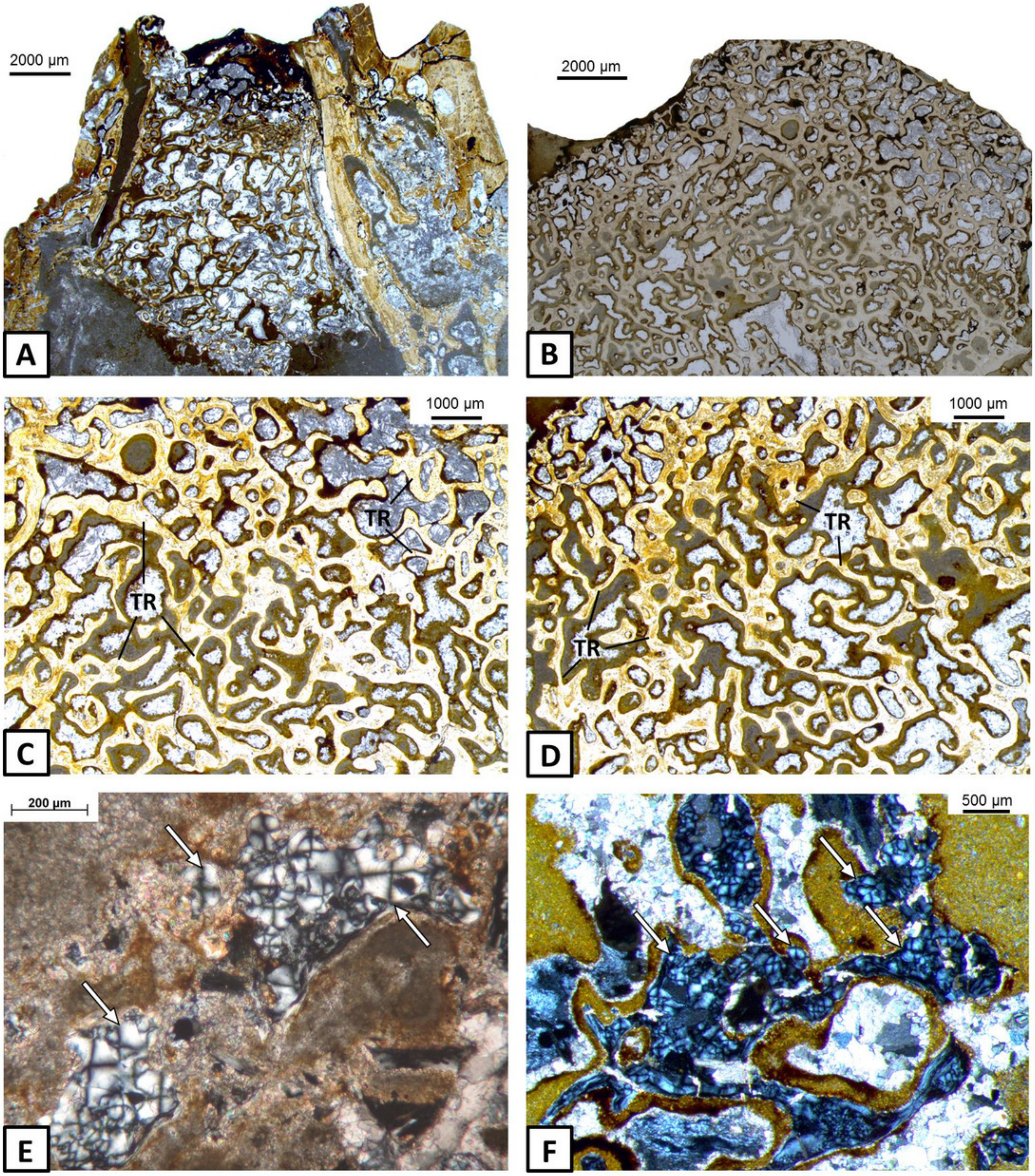
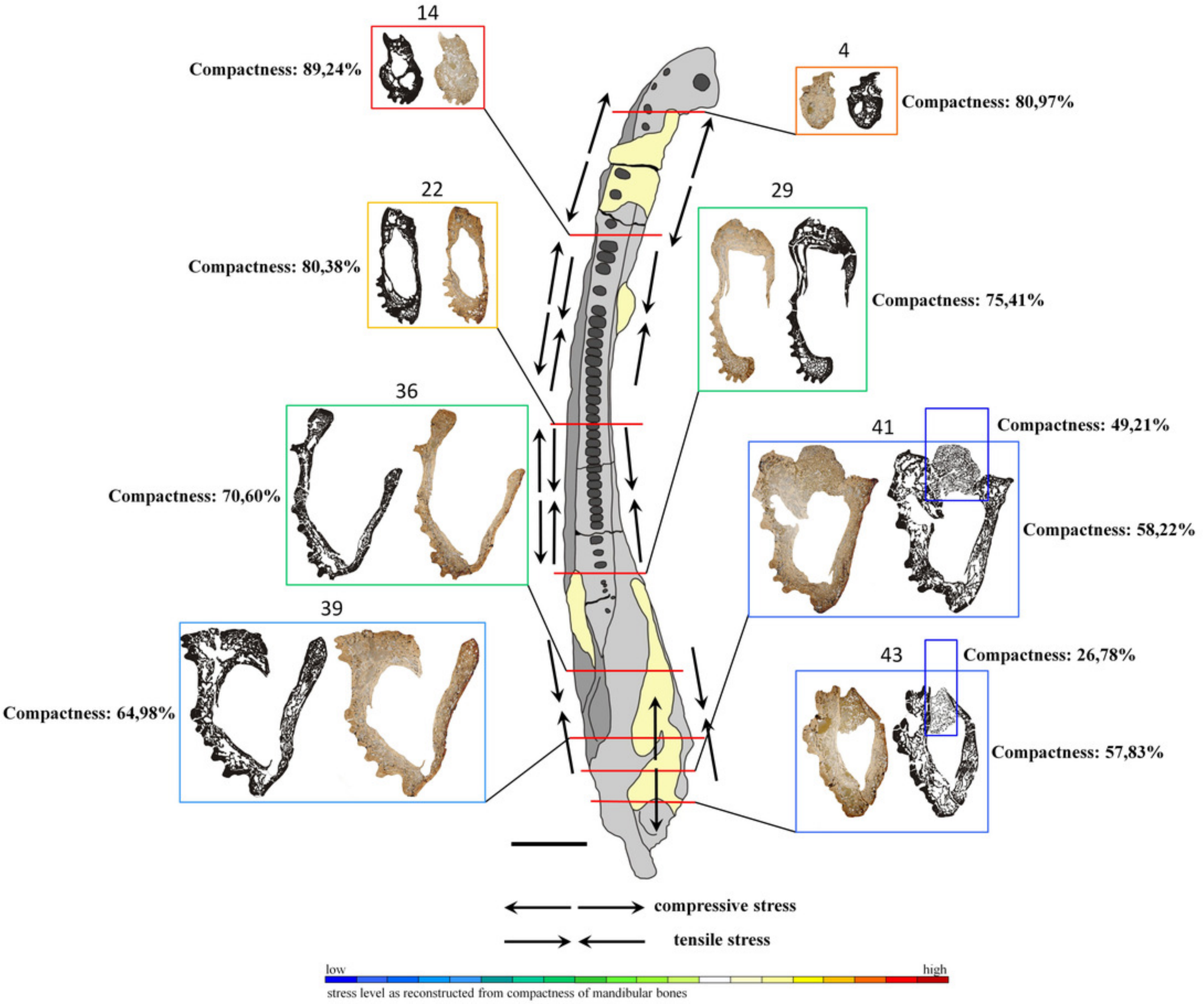

2000 µm
A
2000 µm
B
1000 µm
TR
TR
C
1000 µm
TR
TR
D
200 µm
E
500 µm
F

Figure 7

General microanatomy of selected thin sections of specimen UOPB 01145 and estimated biomechanical loading reconstructed on the basis of the microstructural characteristics of the *Metoposaurus krasiejowensis* mandible.

Black and white images of selected thin sections show calculated composition of bone thickness and its compactness. Colour frames and scale bar represent estimated values of stress distribution in different parts of the mandible, but they only suggest a contractual stress regime (higher or lower). As was stated in Konietzko-Meier et al. 2018, it is impossible to calculate the objective amount of stress in case of histological thin section. Black arrows indicate places underwent various stresses (tensile-compressive) caused by mandible suture mechanics, followed by Gruntmejer et al. 2019b. Black scale bar equals 4 cm.


14
Compactness: 89,24%
4
Compactness: 80,97%
22
Compactness: 80,38%
29
Compactness: 75,41%
36
Compactness: 70,60%
41
Compactness: 49,21%
Compactness: 58,22%
39
Compactness: 64,98%
43
Compactness: 26,78%
Compactness: 57,83%
compressive stress
tensile stress
low
high
stress level as reconstructed from compactness of mandibular bones