

Merging cranial histology and 3D-computational biomechanics: a review of the feeding ecology
of a Late Triassic temnospondyl amphibian

Dorota Konietzko-Meier^{1,2,*}, Kamil Gruntmejer^{2,3}, Jordi Marcé-Nogué⁴, Adam Bodzioch², Josep
Fortuny^{5,6}

¹Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany

²Department of Biosystematics, Opole University, Oleska 22, 45-052 Opole, Poland

³European Centre of Palaeontology, Oleska 48, 45-052 Opole, Poland

⁴Centre of Natural History (CeNak), University of Hamburg, Martin-Luther-King-Platz 3,
20146 Hamburg, Germany

⁵Institut Català de Paleontologia Miquel Crusafont, ICTA-ICP Building, c/ de les Columnes, s/n,
08193 Cerdanyola del Vallès, Spain

⁶Centre de Recherches en Paléobiodiversité et Paléoenvironnements, Muséum national d'Histoire
naturelle, Bâtiment de Paléontologie, CP38, 8 rue Buffon, 75005 Paris, France

* Address for correspondence (E-mail: dorotam@uni.opole.pl)

ABSTRACT

A Finite Element Analysis is a useful method for understanding form and function in Finite Element Analysis. However, modelling of fossil taxa invariably involves assumptions as a result of preservation-induced loss of information in the fossil record. To test the validity of such assumptions ~~a sensitive method is needed, e.g., bone and suture microstructure. different analysis~~ additional analyses are needed. In the current study a new concept of using bone microstructure as a prediction of stress distribution in the skull during feeding is presented and a correlation between bone microstructure and computational biomechanics (FEA) results is done. The bony framework is a product of biological optimisation; bone structure is created to meet local mechanical conditions. Thus, bone microstructure can be used to recalculate/predict local stress and these results can be combined with used to check the predictions of the Finite Element models. To test this scenario, the early tetrapod group of Temnospondyli is an excellent case-study. This clade ranks amongst the most important groups of extinct amphibians during the Early Carboniferous to late Early Cretaceous. In spite of the fact that they have been intensively studied during the last century a half their biology and mode of life still are debated. A crucial issue is their feeding mode; did they suction feed or employ direct biting, or both. The genus *Metoposaurus*, which is very common in Upper Triassic strata, is a good model for testing the various hypotheses about feeding strategies. A crucial issue is their feeding mode; did they suction feed or employ direct biting, or both? Metoposaurids have previously been characterised either as active hunters or passive bottom dwellers. In order to assess assumptions required for Finite Element Analyses, two skulls of *Metoposaurus krasiejowensis* from the Upper/Late Triassic of southwest Poland were tested accordingly and microscopical observations of 17 dermal bone/bones microstructure and suture morphology in 39 thin sections were added/analysed. For the first time, three/two independent models were merged in a revision of the feeding strategy

of *Metoposaurus*. *Metoposaurus* appears to have been an aquatic animal that was little only slightly specialised concerning feeding behaviour. This taxon may have used two foraging techniques in hunting; an ambush strategy, mainly using bilateral biting, or active hunting, using and lateral strikes of the head, in lesser way. However, microscopic data suggest that lateral biting was commoner more frequent than can be observed in suggested by Finite Element Analysis only. The (FEA). One of the potential main factors that determined its mode of life probably was may have been water levels. During optimum water conditions, metoposaurids were more active ambush predators capable of lateral strikes of the head. The dry season required a less active mode of life with when the bilateral biting is particularly efficient bilateral biting and,. This combined with their characteristically anteriorly positioned orbits, was optimal for ambush strategy. This ability for alternative modes of food acquisition, independent of environmental conditions, could be the key to explain the very common occurrence of metoposaurids during the Late Triassic.

KEY WORDS

bone histology, dermal bone, FEA, feeding strategy, *Metoposaurus*, skull, suture morphology, Temnospondyli

INTRODUCTION

Reconstruction of the behaviour and function of ancient organisms is one of the most interesting tasks in palaeobiology, but at the same time the most hypothetical as the direct evidences are only very rarely preserved. There are three possible ways to inferring function and behavior from fossils - empirical evidence, comparison with modern analogs, and biomechanical modeling. Evidences about biology of extinct taxa might be collected based on the morphological, anatomical or microscopic characters of fossils themselves, but also important sources of the information about lifestyle are sediments, associated fossils or any traces. In the ideal model the function or behavior proposed based on the collected evidences should be testable in extant taxa. However, sometimes implications are limited as in the case of e.g., Temnospondyli (*Sanchez et al.*, 2010), the giant terrestrial sauropod dinosaurs (e.g., *Erickson*, 2005; *Sander et al.*, 2011), or some marine reptiles (*Chen et al.*, 2014a, b; *Cheng et al.*, 2014; *Chun Li et al.*, 2011, 2013, 2016;

Klein et al., 2015a,b; Houssaye, Sander & Klein, 2016; Klein et al., 2016) because of lack of modern analogues. In this case might be helpful phylogenetic bracket where the presence of some characters and thus indirect the function could be deduced from the phylogenetic relation (*Witmer, 1995*). However, it is possible only for groups with well-known evolutionary history and rich fossil records. The last way to gather information about moving parts and skeletons are various biomechanical models (*Benton, 2010*), which flourished during last years thank to develop of computing technologies.

Nevertheless, the main limitation of all studies on the fossilized animal is an inability to test the created model 'in vivo' and thus each modelling implies assumptions and simplifications which should be taken into account in the interpretation of results. Because of the influence of simplifications to model construction has not yet been fully examined and is therefore poorly understood (i.e., *Ross et al., 2005; Kupczik et al., 2007; Wang et al., 2010, 2012; Cox et al., 2011; Wood et al., 2011; Bright, 2012; Fitton et al., 2012*) the validation and testing the reliability of results using sensitivity (*Walmsley et al., 2013; McCurry, Evans & McHenry, 2015*) and validity analysis (*Bright & Rayfield, 2011*) is necessary. These procedures however remain difficult to realise for most of extinct groups because the amount of preserved information in fossilised state is limited. This is why it is extremely and highly recommended to merge and compare each available type of information sources for a well-known taxon, but so far no previous studies have done this.

In this sense, *Metoposaurus krasiejowensis* (*Sulej, 2002*) from the Upper Triassic of southwest Poland provides an excellent case study, in view of the sheer number of excellently preserved specimens recovered as well as the extensive data set for this taxon (*Sulej, 2002, 2007; Konietzko-Meier & Sander, 2013; Konietzko-Meier & Klein, 2013; Gruntmejer, Konietzko-Meier & Bodzioch, 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017*).

A useful method to understand form-function relationships, rapidly increased during last years thanks to fast updating of computing technologies, is Finite Elements Analysis (FEA). Over recent years, FEA has been intensively used. Temnospondyls belong to Temnospondyli, one of the most diverse groups of early tetrapods, which flourished worldwide during the Carboniferous, Permian, and Triassic periods, and survived the Triassic-Jurassic extinction as relics in eastern Asia and Australia until the Early Cretaceous (*Holmes & Carroll, 1977; Milner, 1990; Warren, Rich & Vickers-Rich, 1997; Schoch, 2013*). The most characteristic and widely known part of the temnospondyl skeleton is the skull. It is a flat structure with only a few fenestrae on the skull roof (for nares, orbits and, in some capitosaurids, for closed otic notch); the palatal side has many more openings: large subtemporal windows, interpterygoid vacuities and choanas. Despite the fact that temnospondyls have been studied for over 150 years (huge teeth with a labyrinthodont structure were described by *Jaeger* 1824, 1828), the extremely large fossil records, numerous queries as to their biology and mode of life remain. One of the crucial issues concerns their mode of feeding. Temnospondyls were carnivorous, but whether they mainly used suction feeding and/or direct biting is still unclear (*Milner & Sequeira, 1998; Warren, 2000; Steyer et al., 2006; Witzmann, 2006; Damiani et al., 2009; Maganuco et al., 2009; Fortuny et al., 2011*). Suction feeding was possibly present in almost all larval temnospondyls, and many adult temnospondyl taxa with well-ossified hyobranchial skeletons, i.e. plagiosaurs (*Damiani et al., 2009; Fortuny et al., 2011; Witzmann & Schoch, 2013*). Other clades of temnospondyls (e.g. edopoids, eryopids and stereospondylomorpha, including Archegosauriformes and Stereospondyli) have been hypothesized to be feeding analogous to the crocodiles (*Milner & Sequeira, 1998; Warren, 2000; Steyer et al., 2006; Witzmann, 2006; Maganuco et al., 2009; Fortuny et al., 2011, 2012*). These interpretations are mostly inferred from morphological characters of skull, dentition and i.e. presence of hyobranchial skeletons. Up to date only few very promising attempts of computer

modeling (finite element analysis and geometric morphometrics) were done (*Stayton & Ruta, 2006; Fortuny et al., 2011, 2012, 2016, 2017*). Despite the interesting conclusions it is important to remember that, the computing models require a lot of methodological assumptions (see next chapter) and the influence of the simplifications on the final model can lead to inaccuracies or misinterpretations. Thus in the present study is for the first time correlation of histological and cranial suture morphology results with computational biomechanics (FEA) is done. Merging these three sources of data will first test the correctness of the biological reconstructions generated by FEA and second give the new insights into the feeding ecology of Temnospondyli in greater detail.

TESTING FEEDING

Methodological approach to Finite Element Analysis

A method which could help to understand the ecomorphological patterns of feeding is 3D Finite Element Analysis (FEA). FEA documents deformation and distribution of strains and stresses in these skulls that are related to different ecomorphologies (*Fortuny et al., 2011, 2012, 2016, 2017; Lautenschlager, Witzmann & Werneburg, 2016*). Over recent years, FEA has been used intensively to study the biomechanical behaviour of a wide array of vertebrates, providing new insights into exploration of function, morphological evolution, particular adaptation and biological structure constraints (*Rayfield, 2007*). FEA enables to obtain stress distribution patterns that can be interpreted in order to understand either biomechanical behaviour or evolutionary adaptation (*Witzel et al., 2011*). It also allows to analyse and interpret parameters such as stress and strain patterns indifferently on a qualitative comparative framework using models of different shapes and sizes. It is important to note, that in FE analyses the stresses,

which is a physical quantity that expresses the internal forces that neighbouring particles of a continuous material exert on each other, is described. However in the literature very often interchangeably occurs the term strain, which is the measure of the deformation of the material. This is possible and correct because both parameters are proportionally related by Hooke's Law when linear properties of materials are assumed (see *Timoshenko*, 1976). However, computational modelling requires numerous methodological assumptions and simplifications which can lead to inaccuracies or misinterpretations. It is especially important for fossils taxa because of an inability to test the scenario 'in vivo'. A common simplification is the limited amount of biomechanical scenarios tested (see *Fortuny et al.*, 2015 for a discussion). It is important for complex functions as i.e. feeding, because for complicated behaviour probably scenarios additional to these performed in FEA analyses occurred. ~~Next~~ A further problem are simplifications concerning boundary conditions and mechanical bone characters as i.e. elastic linear, homogeneous material properties, which are calculated by using stable values for the entire structure (*Anderson et al.*, 2012; *Bright*, 2014). For fossils taxa without modern analogues these variables moreover have to be assume based on the taxa with a similar Bauplan, but sometimes far phylogenetically (*Anderson et al.*, 2012) as it is i.e. for Temnospondyli where commonly the *Crocodylus* is used as a proxy (see *Fortuny et al.*, 2016 for a discussion). The influence of these simplifications on model construction has not yet been fully examined and is therefore poorly understood, thus the validation and testing the reliability of results using sensitivity analyses is necessary (i.e., *Ross et al.*, 2005; *Kupczik et al.*, 2007; *Wang et al.*, 2010, 2012; *Bright & Rayfield*, 2011; *Cox et al.*, 2011; *Wood et al.*, 2011; *Bright*, 2012; *Fitton et al.*, 2012; *Walmsley et al.*, 2013; *McCurry, Evans & McHenry*, 2015).

FEA studies could be approached from two different perspectives: deductive or inductive. The deductive approach assumes a close relationship between form and function. This type of

analysis allows to manipulate FEA models digitally in order to alter the loading conditions or add/ remove biological geometries, i.e., bone or pieces of bone or fills of any structure (e.g., *Marcé-Nogué et al.*, 2015). Alternatively, the inductive approach aims to test the relationship between form and function, being able to test the assumption that form and function are tightly linked (*Strait et al.*, 2005). However, a common limitation of FEA is the paucity of biomechanical scenarios tested for each FEA (see *Fortuny et al.*, 2015 for a discussion), because the behaviour of these animals probably included scenarios additional to the ones performed there. Moreover, for any biological modelling which implies assumptions to perform any analysis, these assumptions should be as minimal as possible and taken into account in the interpretation of results. Furthermore, it should be borne in mind that modelling fossil taxa implies even more assumptions as a result of the lack of data in the fossil record (*Anderson et al.*, 2012). Despite the mentioned problems, FE analyses are non-invasive, and thus irreplaceable and crucial for examinations of the function of fossilized animals.

Bone histology as a tool to test function

AnotherA useful approach to ~~ensure reliable~~increase the confidence in the results and problem solving is the use of may be bone histology. The bony framework is a product of biological optimisation and the bone structure is created to meet local mechanical conditions. Thus and thus, bone microstructure can be used to estimate local stress. Bone histology seems to be an effective tool to reconstruct the biomechanical loading on the structures; however it is a highly limited method because of its invasive nature.

Biomechanical properties of bone and biological implications have been extensively analysed histologically for a long time (i.e., *Martin*, 1991; *Currey*, 2003, 2006, 2012; *Currey*, *Pitchford & Baxter*, 2007; *Zioupou, Hansen & Currey*, 2008; *Mishra*, 2009; and references

therein). Bone microstructure is related directly to loads and can be modified during the animal's life time (short-term adaptation) and/or ~~on~~ in the long term, as an evolutionary adaptation. The mechanical properties of bone are the result of a compromise between the need for a certain stiffness (i.e., to reduce stress and achieve more efficient kinematics) and the need for enough ductility to absorb impacts (i.e., to reduce the risk of fracture and minimise skeletal weight), but at with the same biological safety factors that need to be maintained (*Biewener, 1993*).

Bone properties can be studied at four different levels: nanoscale (mineralised collagen fibres and extrafibrillar minerals), microscale (microscopically visible structure), mesoscale (in particular the relationship between cancellous and cortical bone) and the whole-bone scale (*Currey, 2012*). In addition, biomechanical properties of bone may be described by different variable indicators, such as Young's modulus of elasticity E , bending strength, determined in tension, tensile strength or impact energy absorption of slotted specimens (*Currey et al., 2007*) and these depend directly of various biological and ecological factors during an animal's life. In view of the fact that vertebrates are able to adapt their bone structure to imposed loading; this is a highly complex issue (i.e., *Martin, 1991; Currey, 2003, 2006, 2012; Currey et al., 2007; Zioupos et al., 2008; Mishra, 2009*). With strong simplification, the strength of a structure is the product of organisational and compositional features (*Currey, 2012*). With regard to the mesoscale levelbone microstructure, the most important organisational feature is porosity, because bone loses strength and stiffness with increased porosity. This is explained by the fact that soft tissues have essentially no strength or stiffness with respect to non-hydrostatic stresses (*Martin, 1991*). However, high cortical thickness can in part compensate for low resistance of bone tissue (*Carrier & Leon, 1990; Margerie et al., 2004*). Compact bone is associated with high strength in tension, but accompanied by a lack of strength in compression, which is higher for trabecular bone (*Martin, 1991; Currey, 2003; Rhee et al., 2009; Achrai & Wagner, 2013*). Considering

composition, lamellar bone with a regular orientation of collagen fibres is stronger than woven bone. In lamellar bone the longitudinal fibres are associated with strength in tensions, while transverse fibres are associated with strength in compression (*Martin, 1991; Currey, 2003; and refernces therein*).

A significant portion of the early amphibian skeleton is consisted of dermal bone (skull, mandible, clavicle and interclavicle), either intramembranous or metaplastic in origin. Dermal bone, as a specific combination of trabecular and cortical bone, forms a “sandwich-type” or plywood structure which is well known in engineering for its optimum structural properties (*Currey, 2006*). In large flat bones which are bent along their shortest dimension, the cancellous bone forms the middle of a sandwich, with the compact shell bearing the major loads and the cancellous bone keeping the walls of the shell apart, and dealing with any shearing loads that may arise. Dermal bone texture provides, moreover, a substantial increase in strength and stiffness that is accompanied by a relatively small increase in mass (*Witzmann, 2009; Rinehart & Lucas, 2013*). Calculations have demonstrated that there is a property/mass advantage, albeit modest, in having cancellous bone in the middle, rather than having a solid, though overall thinner bone (*Currey, 2006, 2012*). A mechanical advantage of metaplastic bone is a firm connection between bone and overlying soft tissue, since the collagen fibres of the attached soft tissue are confluent with the collagen fibres within the metaplastic bone (*Haines & Mohiiddin, 1968*).

Role of the cranial suture in skull biomechanics

The next important factor which should be taken into account during biomechanical analysis of a skull is the type of cranial sutures. Cranial sutures are deformable joints between adjacent bones, bridged by collagen fibres, and provide an ontogenetic and biomechanical function (*Jasinoski & Reddy, 2012*). Their main purpose is to absorb or disperse stresses and strains in compression and

tension which act inside the skull or directly on its surface during activities related with feeding, i.e., biting, mastication, holding struggling prey in the jaw and suction. Moreover, cranial sutures resist stress rise during birth (mainly in mammals), during expansion of skull and soft tissues, and absorbing impact forces (e.g., such as head butting in goats). The sutural morphology is also an important indicator for deduction of the type of feeding (Markey, Main & Marshall, 2006).

Markey *et al.* (2006) distinguished three types of suture: interdigitated, overlapping (or scarf) and abutting (or butt-ended). Each of these is responsible for counteracting specific stress.

Interdigitated sutures occur mainly in areas that experience compressive forces, abutting (or butt-ended) sutures are associated with tensile strain, and variable strains (tension or compression)

counteract overlapping sutures (Jasinowski, Rayfield & Chinsamy, 2010). Rafferty and Herring

(1999) distinguished complex interdigitated sutures (associated with compressive strain) and

shallowly interdigitated or butt-ended sutures (associated with tensile strain). Mechanical

properties of cranial sutures have frequently been studied *in vivo* in extant vertebrates, even in phylogenetically widely diverging groups that are adapted to life in different environments (i.e.,

Rafferty & Herring, 1999; Markey & Marshall, 2007a,b). Markey and Marshall (2007a)

investigated cranial suture mechanics in the extant, suction-feeding fish *Polypterus* and compared

their results with cranial suture morphology in fossil vertebrates such as the Devonian

osteolepiform *Eusthenopteron*, the Devonian tetrapod *Acanthostega* and the Triassic

temnospondyl *Phonerpeton*. *Polypterus* exhibits tension-resistant sutures in the anterior part of

the skull (interfrontal suture) and compression-resistant sutures along the posterior skull region

(interparietal suture). *Eusthenopteron* shows the same pattern – tension-resistant suture between

frontals and compression-resistant suture between parietals, which suggest suction feeding for

this group (Markey & Marshall, 2007b). On the other hand, the terrestrial, bite-feeder

Phonerpeton, and the fully aquatic *Acanthostega*, exhibit similar compression-resistant sutures

between frontals and parietals (*Markey and Marshall, 2007b*). This suggests that even the fully aquatic *Acanthostega* was adapted to feeding by biting (*Markey and Marshall, 2007b*).

Interpretation of feeding behaviour of metoposaurids up to date

Metoposaurids were common temnospondyls that were confined to the Upper Triassic, with records from several continents (*Sulej, 2007*). To conclude if models created by FEA and the histological results provide similar results it is recommended to merge and compare these information sources for a well-known taxon. In this sense, the early tetrapod *Metoposaurus krasiejowensis* (*Sulej, 2002*) (Metoposauridae, Temnospondyli) from the Late Triassic of southwest Poland provides an excellent case study, in view of the great number of excellently preserved specimens recovered as well as the extensive data set for this taxon (*Sulej, 2002, 2007; Barycka, 2007; Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013; Gruntmeier, Konietzko-Meier & Bodzioch, 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017; Teschner, Sander & Konietzko-Meier, 2017*). Metoposaurids belong to Temnospondyli, one of the most diverse groups of early tetrapods, which flourished worldwide during the Carboniferous, Permian, and Triassic periods, and survived the Triassic-Jurassic extinction as relics in eastern Asia and Australia until the Early Cretaceous (*Holmes & Carroll, 1977; Milner, 1990; Warren, Rich & Vickers-Rich, 1997; Schoch, 2013*). The most characteristic and best known part of the temnospondyl skeleton is the skull. It is a flat structure with few fenestrae on the skull roof (nares, orbits and, in some capitosaurids, the closed otic notch); the palatal side has many more openings: large subtemporal windows, interpterygoid vacuities and choanae. Despite the long-term studies and large fossil records, numerous queries about temnospondyls biology and mode of life still remain unclear. One crucial issue concerns their mode of feeding. Temnospondyls were carnivorous, but whether they mainly used suction feeding and/or direct biting is still

unclear (Milner & Sequeira, 1998; Warren, 2000; Steyer *et al.*, 2006; Witzmann, 2006; Damiani *et al.*, 2009; Maganuco *et al.*, 2009; Fortuny *et al.*, 2011). Up to date a number of studies have used computational biomechanical analyses to address the question of feeding strategies among Temnospondyli (Stayton & Ruta, 2006; Fortuny *et al.*, 2011, 2012, 2016; Marcé-Nogué *et al.*, 2015; Lautenschlager, Witzmann & Werneburg, 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017). FEA documents deformation and distribution of strains and stresses in the skulls that are related to different ecomorphologies (Fortuny *et al.*, 2011, 2012, 2016; Marcé-Nogué *et al.*, 2015; Lautenschlager, Witzmann & Werneburg, 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017). However, Temnospondyli belongs to one of the groups for which modern ecological analogues does not exist (Sanchez *et al.*, 2010; Fortuny *et al.*, 2016). It drive to make assumptions regarding bone properties and moreover calculations are simplified (*see Bright, 2014; Fortuny et al., 2015* and references therein for discussion). The histological studies of the metoposaurid skull have shown that the histological framework of skull bones is very variable (Gruntmejer, Konietzko-Meier & Bodzioch, 2016), which is never taken into consideration during FEA analysis of fossil taxa.

In the current study a new concept of using bone microstructure as a prediction of stress distribution in the skull during feeding is presented and a correlation between bone microstructure and computational biomechanics (FEA) results is done. Merging these sources will test first the predictions generated by FEA and help to evaluate the influence of methodological assumptions and simplifications onto the final interpretation and second give the new insights into the feeding ecology of Temnospondyli.

Despite their common occurrence and well-known *Bauplan*, the mode of life of metoposaurids still remains controversial. Earlier they were either considered to have been passive bottom-dwellers in lakes and rivers, lying in wait for prey using the passive “death-trap” model (Ochev,

1966; Murry, 1989), mid-water feeders, comparable to temnospondyl capitosaurians (Howie, 1970; Chernin and Cruickshank, 1978; Hunt, 1993) or active swimmers that used limbs (Sulej, 2007) or tail (Konietzko-Meier, Bodzioch & Sander, 2013) for propulsion.

A cranial computational biomechanics approach based on Finite Element Analysis -

The results and a discussion of FE models of the skull of *Metoposaurus krasiejowensis* have recently been published by Fortuny *et al.* (2017). However, for easier understanding the discussion a brief summary of the main results is included below.

Under bilateral biting, the model has showed moderate to low-level stresses on most parts of the skull, with just a few peak stress levels in the posterior part (Fig. 1A). Small spots of stress were present on the dorsal portion of the supratemporal and posterior part of the squamosal, but mainly in ventral portions of the jugals and supratemporal and the posterior ramus of the pterygoid. Of particular interest is the absence of stress around the premaxilla, the posterior part of the maxilla and lacrimal and the naso-frontal region. Stress slightly increased around the orbits. On the palate, a few peak levels of stress were present nearing the choanas, with no levels of stress on the premaxilla, nor on most of the cultriform process and the parasphenoid.

The general pattern during lateral loading revealed low or absent levels of stress on the skull roof; on the quadratojugal stress was slight (Fig. 1B). It is particularly significant that the antorbital region had extremely low levels of stress. However, on the palate, the general stress levels increase: low or moderate levels were seen on the vomer and premaxilla, while the cultriform process presented low levels in its anterior part, being moderate in its posterior part and absent from the central part. As far as the posterior part of the skull is concerned, high stress levels were present on the posterior branch of the pterygoid and quadratojugals, while the anterior part of the pterygoid had low or very low stress levels under lateral loading, while its central area

(adjacent to the parasphenoid) revealed moderate levels of stress. The major part of the parasphenoid had moderate and high levels of stress, increasing on the posterior part of the parasphenoid and in the exoccipitals.

The simulation of the skull raising system showed that the stress values are very low along nearly the entire skull (Fig. 1C). The stress values increase only significantly in the interorbital region, the regions around the otic notches, the central part of the cultriform process and posterior rami of the pterygoids (Fig. 1C). Lower, but still measurable, stress is indicated in the anterior rami of the pterygoid, ectopterygoid and in the vomer (Fig. 1C).

A 3D Finite Element Analysis of the metoposaur skull has revealed thus that the bottom dweller and active predator hypotheses may in part be joined (Fortuny et al., 2017). Metoposaurids preferred rapid bilateral biting which would confirm the ambush strategy – resting on the bottom in wait for passing prey. However, the relatively low stress level that is seen along the skull under lateral strike indicates that lateral strike of the head was possible, even if this was not preferred (Fortuny et al., 2017). The FEA results also demonstrated clearly that unilateral biting was avoided because the skull would experience a comparatively high stress level, probably due to the absence of a secondary palate (Fortuny et al., 2016, 2017).

However, how it was mentioned above the FEA analysis has a limitation concerning the amount of tested scenario. The results confirm the presence of direct lateral and bilateral biting, but not exclude other combinations, except of unilateral biting, simple because of lack of models.

Microscopic studies - Cranial suture morphology and its predicted function for *Metoposaurus* have been studied histologically in preliminary fashion (Gruntmejer, 2012). Most of the sutures were defined as complex interdigitated which served a compression-resistant purpose. Moreover, a shallowly interdigitated suture (prefrontal-lacrimal) has been observed,

which resisted tensile strains and two samples of probably overlapping sutures (maxilla-nasal and frontal-postfrontal), which counter variable strains forces, have also be noted (*Gruntmejer, 2012*). Based on these facts, a predominant feeding mode of direct biting was concluded for *Metoposaurus*. However, because of the presence of overlapping sutures in the anterior part of the skull, capture of prey by suction could not be ruled out (*Gruntmejer, 2012*).

MATERIAL AND METHODS

Material

Two skulls of *Metoposaurus krasiejowensis* housed in the collections of Opole University (UOPB) were analysed. One of these (UOPB 01029; 400 mm in length) was studied histologically, while the second (UOPB 00124; 290 mm in length) was CT scanned for 3D-Finite Element Analysis., while the second (UOPB 01029; 400 mm in length) was studied histologically (Fig. 1). Both specimens were collected at Krasiejów (southern Poland) from- the Upper Triassic locality in southern Poland (Norian according to recent stratigraphical studies: *Racki and Szulc, 2015; Szulc, Racki & Jewula, 2015; Szulc et al., 2015*), lower bone bearing horizon (*sensu Dzik and Sulej, 2007*), and are housed in the collections of Opole University (UOPB2015).

Methods

Finite Elements Analysis – A skull of *Metoposaurus krasiejowensis* (Sulej, 2002) (UOPB 124; 29 cm in length) was CT scanned at the Hospital Mutua de Terrassa (Catalonia, Spain) using a medical CT scanner Siemens Sensation 16. The specimen was scanned at 140 kV and 150 mA, obtaining a 0.576 mm pixel size and an output of 512X512 pixels per slice with an interslice space of 0.3 mm. The specimen corresponds to a complete skull completely filled with

sediment. After segmentation, a 3D model only of the skull was generated. During this last step, the surface irregularities were repaired using refinement and smoothing tools from Rhinoceros 5.0 software and imported into ANSYS 16.2 software to perform FEA (see *Fortuny, Marcé-Nogué & Konietzko-Meier, 2017* for further details).

A Structural Static Analysis to evaluate the biomechanical behavior during biting was performed using the Finite Element Package ANSYS 16.2 on a Dell Precision™ Workstation T7600 with 32 GB (4X8GB) and 1600 MHz. Elastic, lineal and homogeneous material properties were assumed for the bone using the following values: E (Young's modulus): 6.65 GPa and ν (Poisson's ratio) 0.35 (*Currey, 1987*), from frontal bone of *Crocodylus*. The skull of *Metoposaurus krasiejowensis* was meshed with an adaptive mesh of hexahedral elements (*Marcé-Nogué et al., 2015*). The mesh of the model was around 2.2 million elements and 3.1 million nodes. A gape angle of 10° was used, although was tested also under 20°, obtaining a very similar distribution pattern (see *Fortuny, Marcé-Nogué & Konietzko-Meier, 2017* for comparison).

Four loading cases were analyzed considering bilateral, unilateral, lateral prehension/bite and the skull-raising system (Fig. 2). The bilateral case simulates a bilateral bite on both left and right sides of the skull whereas the unilateral case simulates the same bite only on the right side. The lateral case simulates a lateral loading direction to generate a within-plane lateral bend of the snout and simulate movement of the head through the water, considering that *Metoposaurus* could hunt prey by using a rapid sideways sweep of the head during active swimming. The skull-raising case considered the motion of the skull (relative to the lower jaw) when the mouth opens. All the cases are described in Figure 2 and further explained in *Fortuny, Marcé-Nogué & Konietzko-Meier, 2017*.

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Displacements at the jaw joint were restricted in the y-direction simulating the contact with the jaw and near the double-headed occipital condyle in the x-direction simulating the presence of the vertebral column.

For the bilateral and the unilateral case, as loading conditions, the Adductor Mandibulae Internus (AMI), the Adductor Mandibulae Externus (AME) and the Adductor Mandibulae Posterior (AMP) were considered in the model according to this soft tissue reconstruction based on several authors (e.g. *Carroll and Holmes*, 1980; *Sulej*, 2007; *Steyer et al.*, 2010; *Witzmann and Schoch*, 2013; *Marcé-Nogué et al.*, 2015; *Fortuny et al.*, 2016, *Fortuny, Marcé-Nogué & Konietzko-Meier*, 2017). The muscular insertion areas of AMI, AME and AMP were defined in the model in order to apply the forces of the muscular contraction during the different prehension/bites. The direction of these forces was defined by the line that joins the centroid of the insertion area in the skull with its correspondence in the insertion area of the lower jaw. According to *Alexander* (1992), a value of 0.3 MPa was assumed as muscular contraction pressure. To simulate biting, a fixed boundary condition in the three dimensions (x, y and z) was applied in the bite location to simulate the moment that skull and mandibles contact the prey.

For the lateral case, an arbitrary force of 100 N was applied in the z-direction at the position of the fangs in the palate. Finally, for the skull-raising case, a muscular force was applied on the cleidomastoideus muscle creating null displacement of the tip of the snout when the overall weight of the skull is applied.

Thin-sections — The histological study of skullcranial bones of *Metoposaurus krasiejowensis* Skull (UOPB 01029) has indicated a relatively stable collagen fibre pattern with parallel-fibred bone constructing the grooves and inner cortex and lamellar bone present in the troughs/grooves of the skull (*Gruntmejer et al.*, *Konietzko-Meier & Bodzioch*, 2016). In contrast, microstructural characters (thickness and compactness) change very clearly (*Gruntmejer et al.*,

Konietzko-Meier & Bodzioch, 2016), and thus may be used as a proxy to estimate the mechanical loading. However, the detailed studies were not performed to analyse the relations between the thicknesses, compactness and estimated biomechanical loading. It may be assumed then that these characters influence the results of estimation significantly. This is why these two features, based on the same thin-sections collection (Fig. 2) as published by *Gruntmejer et al., Konietzko-Meier & Bodzioch (2016)* are widely analysed here and only these two were taken into account in biomechanical simulation. Additionally, the thin-sections from the various border regions were prepared to test the morphology of sutures (Fig. 2)..

UOPB 01029 was sectioned in 3916 places, inclusive of 1917 flat dermal bones (Fig. 23; Table 1), according to standard petrographic procedures (*Chinsamy & Raath, 1992*). Non-dermal bones such as the exoccipital and quadratojugal were not analysed, because of their endochondral origin and different shape. Cross-sectional shape morphology of cranial sutures was conducted on 26 thin sections (Table 1; green and purple lines in Fig. 2). The bone microstructure was studied in 16 thin sections (Table 2; red and purple lines in Fig. 2). Subsequently, the thin sections were studied under a LEICA DMLP light microscope in normal and polarised light. Additionally, cranial sutures were qualitatively analysed in Scanning Electron Microscope (SEM) to assess their morphology.

In the thin sections, the average thickness of the entire bone was estimated, expressed as an arithmetical average from three measurements of the thickness of the entire bone. The average thickness of the bone was measured three times over the distance between the ventral side of the bone and the bottom of troughs/grooves, and three times as the distance to the top of ridges. The mathematical average was calculated from these measurements.

To estimate bone porosity the thin sections were scanned by using an Epson Scanner and transformed into black and white images (Fig. 3).. The analysis of compactness was done by using software Bone Profiler (*Girondot & Laurin, 2003*).

In the prefrontal, squamosal 2 and parasphenoid, on account of the strongly variable bone thickness, the significantly thinner parts of these bones (labelled in Figures 3 and 4 and in the text as -b, as opposed to the thicker part named -a), were calculated separately (Fig. 3I,M and O)..

RESULT

A cranial computational biomechanics approach based on Finite Elements Analysis - Skull UOPB 00124 (290 mm in length) was CT scanned for 3D-**Finite Element Analysis**. A Structural Static Analysis to evaluate the biomechanical

Values of equivalent Von Mises stresses and their distribution were recorded in order to compare their behaviour during under the effect of loads and constraints in the bilateral, unilateral, lateral biting and skull -raising was performed using the Finite Element Package ANSYS 14.5 in a Dell Precision™ Workstation T7600 with 32 GB (4X8GB) and 1600 MHz.for simulating feeding behaviour. The detailed methodology was results and a discussion of FE models of the skull of *Metoposaurus krasiejowensis* have recently been published by *Fortuny et al., Marcé-Nogué & Konietzko-Meier (2017)*. In this study the generated models (*Fortuny et al., 2017*; for summary see also chapter III) were reformulated in order to get information about sutures function.

Under bilateral biting, the model showed moderate to low-level stresses on most parts of the skull, with just a few peak stress levels in the posterior part (Fig. 4A). Small spots of stress were present on the dorsal portion of the supratemporal and posterior part of the squamosal, but

mainly in ventral portions of the jugals and supratemporal and the posterior ramus of the pterygoid. Of particular interest is the absence of stress around the premaxilla, the posterior part of the maxilla and lacrimal and the naso-frontal region. Stress slightly increased around the orbits. On the palate, a few peak levels of stress were present near the choanae, with no levels of stress on the premaxilla, nor on most of the cultriform process and the parasphenoid.

Simulating unilateral biting reveals a different stress pattern for left and right part of skull with the significant higher high levels of stress on the right side (Fig. 4B). The preorbital region presents moderate to high levels of stress in the region of anterior part of the right maxilla and increasing of loading in the interorbital region. The extremely high level of stress is reconstructed in the posterior part of the parietals and the postparietals as well as the otic notch (posterior part of the squamosal) till the quadratojugal. Predicted stress level for the palate is even higher and refers to the quadratojugal-quadrato region, most of the pterygoid and is being particularly very high in the plate of the parasphenoid, and most of the cultriform process, as well as the exoccipitals (Fig. 4B).

The general pattern during lateral loading revealed low or absent levels of stress on the skull roof; on the quadratojugal stress was low (Fig. 4C). It is particularly significant that the antorbital region had extremely low levels of stress. However, on the palate, the general stress levels increase: low or moderate levels were seen on the vomer and premaxilla, while the cultriform process presented low levels in its anterior part, being moderate in its posterior part and absent from the central part. As far as the posterior part of the skull is concerned, high stress levels were present on the posterior branch of the pterygoid and quadratojugals, while the anterior part of the pterygoid had low or very low stress levels under lateral loading, while its central area (adjacent to the parasphenoid) revealed moderate levels of stress. The major part of the

parasphenoid had moderate and high levels of stress, increasing on the posterior part of the parasphenoid and in the exoccipitals.

The simulation of the skull raising system during jaw opening showed that the stress values are very low along nearly the entire skull (Fig. 4D). The stress values increase only significantly in the interorbital region, the regions around the otic notches, and the central part of the cultriform process as well as posterior rami of the pterygoids (Fig. 4D). Lower, but still measurable, stress is indicated in the anterior rami of the pterygoid, ectopterygoid and in the vomer (Fig. 4D).

Biomechanical loading approach from thin-section analysis

RESULTS

Biomechanical loading approach from thin-section analysis

Bone microstructure — The average thickness of dermal bones varies from 2 to 10 mm (Table 21, Figs 35 and 46). In the posterior part of the skull, bones are the thickest (postparietal and tabular), with the thickness of up to 10 mm with a compactness varying between 80 and 82%. The microstructural characters indicate suggest a very high biomechanical loading on this part of the skull (Table 21; Fig. 45). The postorbital and jugal represent a similar average thickness (close to 7 mm), but the compactness varies from 83% to 88%, respectively. These bones show (Table 1; Fig. 5). Bone microstructure predicts a lower loading, compared to the posterior part of skull, but still have high stress level. Further decrease of the strength is observed for the lacrimal, quadratojugal, frontal and pterygoid bones, in which the thickness oscillates

around 6 mm and the compactness varies from 73 to 80% (Table 21; Figs 35 and 46). The postfrontal, squamosal 1, posterior part of -1, squamosal -2-a, parietal and supratemporal(-a) present thicknesses of around four4 mm, with the compactness changing from 88 to 95% (Table 21; Figs 35 and 46). The nasal, prefrontal and parasphenoid(-a) with a relatively limited thickness and compactness received low biomechanical loads (Table 21; Figs. 3 5 and 46). The vomer is extremely porous, with a compactness of only about 55%, accompanied by limited thickness and possibly free of stress (Table 21, Figs 3 and 4). Markedly thinner are also medial parts of the supratemporal and parasphenoid (Fig.on Figures 3 I and O). In these bones the thinnest fragments are 4 marked as -b) reaching about 2 mm thickof thickness, contrary to the remaining partparts (supratemporal-a and parasphenoid-a) with an average thickness of about 4 mm (Table 21, Figs 35 and 46). In the squamosal -2 the decreasechange in bone thickness is more gradual (Fig. 3M). In5). The supratemporal-b, parasphenoid-b and squamosal-2-b are the thinnest among all these three bones thebones, however extremely compact, over 90% (Table 1; Fig. 5). In sum, there is a linear relationship (Fig. 6) between compactness increases alongand average bone thickness, with thickness decreasing, reaching more than 90% in the thinnest region. Despite theonly exception of vomer, being an outlier. Bones with high compactness these portions of bones are very weak, in view of their extreme thinness (Table 2, Figs 3 and 4).have low values of thickness and bones with low values of compactness have higher values of thickness.

Cranial biomechanical loading approach from bone microstructure — The microstructural bone characters suggest a high biomechanical resistance of the posterior part of the skull; this is moderate in the preorbital and along the lateral edges of the skull roof, with a tendency to decrease in the otic notchesnotch region and postorbital area (Fig. 46). A slight increase of biomechanical loading is present only next to the posterior margin of the orbits (Fig.

46). The squamosal-2-b which is the anterior part of squamosal 2 this bone and the deep trough/groove a narrow valley that represents a lateral canal in the supratemporal (supratemporal-b) are considerably weaker than in the remaining part of these bones. However, in the supratemporal there is a narrow valley that represents a lateral canal (Fig. 3I6). The squamosal -2 shows a gradual decrease/increase in mechanical resistance in an anterior/posterior direction, indicating low/predicting slightly higher loading on the lateroposterior part (squamosal-2-a) of the skull. (Fig. 6). The postfrontal, squamosal -1, posterior part of squamosal 2,-2 (squamosal-2-a), parietal and supratemporal(-a) are thinner, but significantly more compact than the lacrimal, quadratojugal and as well as frontal, but significantly more compact and thus represent only a slight decrease of final biomechanical strength. With the same values in respect of thickness as in the prefrontal, nasal and parasphenoid-a, the postfrontal, squamosal-1, squamosal-2-a, parietal and supratemporal-a are more compact and thus able to resist higher stress (Fig. 6).

The microstructure of bones from the palatal side represents/suggests moderate or low stress levels. Extremely weak are the The vomer and the medial part of the parasphenoid (Fig. 4),6 – parasphenoid-b) appear to be extremely weak, whereas the anterior branch of the pterygoid shows a greater biomechanical resistance.

Cranial suture morphology - All sutures studied here are recognised as interdigitated. The presence of this suture type has been noted in the anterior and posterior parts of the skull, both on the skull roof and on the palatal side (Figs 5 and 6). Distinct clumps of Sharpey's fibres occur along the lateral edges of bones (Fig. 7).

Biomechanical role of sutures obtained from the FE analysis - Under a bilateral loading, results obtained for *Metoposaurus* reveal that the posterior sutures of the supratemporal,

in conjunction with the tabular, parietal and postparietal, and to a lesser extent the squamosal, plays an important role in the absorption, flexion and distribution of stress in the posterior part of the skull, where stresses are greater. With regard to the palate, the lateral extension of the jugal to the anterior branch of the pterygoid, as well as the quadratojugal suture, probably also played an important role in stress dissipation. To a lesser extent, the pterygoid-parasphenoid and sutures around the choana played a minor role.

DISCUSSION

New insights into skull biomechanics – merging methods

Bone histology vs computational biomechanics – how does bone structure correlate with Finite Element Analysis? - Values of equivalent Von Mises stresses and their distribution were recorded in order to compare their behaviour under the effect of loads and constraints in the bilateral and lateral cases. The Von Mises criterion is the most accurate for predicting fracture location when isotropic material properties are used in cortical bone (*Doblaré, García & Gomez, 2004*). As stated previously, the von Mises stress patterns of the models could be used indifferently with strain patterns, allowing to compare qualitatively these results with the compactness obtained from histological thin sections.– As a proxy to test predictions created during FEA simulation the bone microstructure was used. In this context, low levels of Von Mises stress appear in the thin and compact bones and these levels increase when the compactness of the bone is higher and the thickness lower. As a general trend, high values of von Mises stress appear in thicker bones.

The histological framework confirms mostly the stress distribution pattern obtained during FE analyses. The histological characters support the FEA results demonstrated that metoposaurids preferred rapid bilateral biting along with lateral strikes of the head, even if the ~~second~~ latter behaviour was not preferred (Fortuny, Marcé-Nogué & Konietzko-Meier, 2017). Based on FEA results, unilateral biting was avoided because the skull would experience a comparatively very high stress level, probably due to the absence of a secondary palate (Fortuny et al., 2016; Fortuny, Marcé-Nogué & Konietzko-Meier, 2017). The histological framework confirms a very close stress distribution pattern obtained during FE analyses (Fig. 7), including the fact that it was very unoptimal and not efficient for metoposaurs to perform unilateral biting in any scenario (Fig. 7A). ~~Only a case when~~ The only case, where histological model and unilateral FEA loading show the same tendency is a high loading present in the posterior part of skull (Fig. 7A) whereas under bilateral and lateral FEA loadings, this skull region receives a low or moderate level of stress (Fig. 7B and C). However, in this case the similar signal in unilateral and histological models is only a methodological artefact. The microstructural analysis reveals for the tabular and the postparietal that these elements are biomechanically adapted to receive high amounts of stress (Figs 5 and 6). Moreover, these bones are strongly metaplastic, which suggest a tight connection to muscles or ligaments (Gruntmejer, Konietzko-Meier & Bodzioch, 2016). The reason ~~effor~~ the presence of extremely resistant bones in this region is not directly connected with feeding actives, but other variables, which are related to skull raising, affect the tabular and parotic process, otic notch and mainly the cleidomastoideus muscles and could explain the strength and biomechanic capabilities found in the histological analysis. A slight increasing of stress level in the FEA model of skull raising (Fig. 7D) reinforces the support to this hypothesis.

The microstructural characters confirm that the nasal and prefrontal are relatively weak bones; thus, the biomechanical loading in these regions was relatively low. In both simulations (bilateral and lateral) the same tendency is observed, with a slight increase of stress level in the prefrontal (Fig. 8A7B and BC), which is also thinner (Fig. 45). In the frontal region, under a bilateral case, the estimated stress level exceeds that in the prefrontal and nasal (Fig. 8A7B). Histologically, the frontal is a relatively massive bone in comparison to the nasal and prefrontal. This indicates that loading on the frontal region was probably high. The postfrontal, squamosal -2(-a), parietal and squamosal -1 are thinner than the frontal, but more compact and thus the loading could be the same or only slightly lower as on the frontal (Figs 3A-B5 and 46). The same tendency is observed in bilateral and lateral FEA cases (Fig. 8A-B7B and C). Squamosal 2 is of special interest as the FE models suggest a change of stress value from the posterior to the anterior part of this element, receiving high to low levels, respectively (Fig. 87). Interestingly, the histological results also reveal this change in the thickness of the cortex as well as in the porosity across the bone (Fig. 46). Squamosal -2(-b) in both FEA cases (bilateral and lateral) show barely any stress anteriorly (Fig. 8A-B7B and C); moreover, histologically, squamosal -2(-b) is a very thin bone, indicating that the mechanical loading of this part of skull was very low, only slightly increasing posteriorly (Fig. 4). In its entirety⁵). As an entire bone, the supratemporal is adapted to moderate loading (Fig. 46), which is visible also in bilateral and lateral FEA cases (Fig. 87). The histological framework of the supratemporal suggests that the most sensitive part of this bone, which represents a drastically reduced strength, is the lateral line canal (Fig. 46). The increase in bone compactness visible in the canal might partially compensate a decrease of bone thickness in this place. The lamellar bone visible at the bottom of the canal (*Gruntmejer et al., Konietzko-Meier & Bodzioch, 2016*) is associated with marked strength of this region but accompanied by low resistance in compression (*Martin, 1991; Currey, 2003; Rhee et al., 2009; Achrai & Wagner,*

2013). The significant change of microstructural conditions, and thus biomechanical properties, shows that the lateral line canals might be crucial structures for the biomechanical function of the skull; especially for metoposaurids with extremely deep system of lateral canals. The increased compactness of the bone on the bottom of the canals might be an adaptation reaction to preserve the optimal strength of the bone with minimal thickness. However, it could have some side-effect as a compact bone is associated with a high strength in tension (Martin, 1991; Currey, 2003; Rhee et al., 2009; Achrai & Wagner, 2013), thus lateral canals could serve as tensile members that are subjected to axial tensile forces occurred in the skull.

The microstructure of the lacrimal, jugal and quadratojugal suggest a significantly high loading on the lateral margins of the skull. The same tendency is visible in the lateral FEA case (Fig. 8B7C), where an increase of stress level is suggested. It seems to be clearly connected with the presence of tooth rows on the ventral side of these bones. The histological results in this case suggest a commoner more frequent occurrence of lateral biting than is concluded only from Finite Element Analysis.

For the tabular and postparietal, the histological analysis reveals that these elements are biomechanically adapted to receive high amounts of stress (Fig. 4). Moreover, these bones are strongly metaplastic, which suggest a tight connection to muscles or ligaments (Gruntmejer et al., 2016). Under bilateral and lateral FEA loadings, the skull region receives a low or moderate level of stress (Fig. 8A-B). However, it should be noted that other variables affect tabular and parotic process, otic notch and mainly the cleidomastoideus muscles related to skull raising (Fig. 8C). All these variables possibly could affect the biomechanical properties of this element, and explain the strength and biomechanic capabilities found in the histological analysis.

With regard to the palatal side, the Finite Element loading cases suggest low stress for the pterygoid, and slightly higher for the parasphenoid, which is in agreement with the

microstructural results (Figs. 4 6 and 87). Additionally, the histological framework suggests that the parasphenoid was loaded more next closer to the external edges than near the central axis, where the bone is thinnest. *Marcé-Nogué et al.* (2015) pointed out that during skull raising relatively high stress affected the cultriform process. The histological results obtained herein do not appear to support the idea of any high loading on the palatal side of the skull. However, the section was done only from the very posterior part of the parasphenoid; the cultriform process itself was not sectioned. Taking into account the high microstructural variability of skull bones (*Gruntmejer et al., Konietzko-Meier & Bodzioch, 2016*) it cannot be ruled out that the anterior part of this bone is highly metaplastic. This, along with large increased width of the process, might significantly increase the biomechanical strength of this bone. To confirm this hypothesis more sections are needed. Otherwise, the Finite Element lateral case shows a stress increase in the vomer (Fig. 8C7C), but this stress pattern is not supported by the histological framework. The, which suggest that the vomer is the weakest bone of the entire skull (Fig. 46).

The exoccipital and quadratojugal have an endochondral origin and develop via a cartilage precursor. Histologically, both bones resemble the structure of vertebrae with a highly trabecular domain area surrounded by a thin, more compact cortex (*Konietzko-Meier et al., 2013*). Between the trabeculae the remains of calcified cartilage are visible suggesting slow ossification of the endochondral region (*Konietzko-Meier et al., 2013; Gruntmejer et al., Konietzko-Meier & Bodzioch, 2016*). However, in both bones very strong Sharpey's fibres are present (*Gruntmejer et al., Konietzko-Meier & Bodzioch, 2016*). Large concentrations of long, well-mineralised Sharpey's fibres in the exoccipital appear to represent the remains of strong muscular attachments and ligaments that connect the skull to the vertebral column that may have played a role during skull rising.

The role of sutures in skull biomechanics - All microscopically analysed cranial sutures in an adult skull of *Metoposaurus* were defined as interdigitated, which served a compression-resistant purpose. *Gruntmejer* (2012) previously, albeit erroneously, interpreted the morphology of some sutures to be overlapping and shallowly interdigitated. However, the present histological analysis reveals that all sutures are interdigitated (Figs. 5-7). Sutural morphology, unlike the very variable bone histology, does not change along the skull. The histological results of cranial suture morphology in *Metoposaurus* are the same as in the case of *Acanthostega*, i.e., the presence of compression-resistant sutures both in the anterior and posterior parts of the skull (Fig. 6). The absence of tension-resistant sutures between the frontals (commonly occurring in aquatic suction-feeders) and a predominance of interdigitated sutures along the skull of *Metoposaurus*, demonstrates that it had a biting behaviour.

The histological data confirm the estimates made for sutures on the basis of FEA analysis. As previously discussed, FE results also reveal that unilateral strikes of the head were probably not performed by metoposaurids (*Fortuny et al.*, 2017). In this respect, a correlation of stress patterns and sutures also enforces this idea. Under unilateral biting (*Fortuny et al.*, 2017), the high stress patterns correlate with the tabular-squamosal-supratemporal suture and, to a lesser extent, with the postparietal and parietal but under this loading main stresses are seen in the central part of the cultriform process, where no sutures are present. Moreover, this structure is one of the most fragile ones of the metoposaurid skull. Finally, high stress levels under unilateral loading are present in the parasphenoid plate whereas the parasphenoid-exoccipital suture could have played a role, although great stress around the endocranial region suggests that this loading was usually avoided. Lastly, under a lateral strike of the head, the high amount of stress correlated with the quadrate-jugal, quadrate-pterygoid and parasphenoid-exoccipital sutures. This

loading was possibly less usual than the bilateral but most probably more optimal than unilateral loading, in consideration of the suture pattern.

New interpretation of mode of life

Metoposaurids were common temnospondyls confined to the Late Triassic, with records from several continents (Sulej, 2007). Despite their common occurrence and well-known *Bauplan*, the mode of life of metoposaurids still remains controversial. In the past they were either considered to have been passive bottom-dwellers in lakes and rivers, lying in wait for prey using the passive “death-trap” model (Ochev, 1966; Murry, 1989), mid-water feeders, comparable to temnospondyl capitosaurids (Howie, 1970; Chernin and Cruickshank, 1978; Hunt, 1993) or active swimmers that used limbs (Sulej, 2007) or tail (Konietzko-Meier, Bodzioch & Sander, 2013) for propulsion.

A 3D FEA of the metoposaur skull has revealed thus that the bottom dweller and active predator hypotheses are the best supported ones (Fortuny, Marcé-Nogué & Konietzko-Meier, 2017). Metoposaurids preferred rapid bilateral biting, which according to this study, would confirm the ambush strategy – resting on the bottom in wait for passing prey. The relatively low stress level found along the skull under lateral strike indicates that lateral strike of the head was possible, even if this was not preferred and connected with the active predatory (Fortuny, Marcé-Nogué & Konietzko-Meier, 2017). However, as was mentioned above the FEA analysis has a limitation concerning the amount of tested scenario. Merging threetwo different approaches (Finite Element Analysis, and bone histology and cranial suture morphology) provides data from different perspectives on skull biomechanics that, when correlated, yield, a clearclearer image of the feeding behaviour of *Metoposaurus*. *Metoposaurus* This genus appears to have been an aquatic animal that could adapt to various environmental conditions and was less specialised in

their mode of feeding than assumed previously (Ochev, 1966; Murry, 1989; Howie, 1970; Chernin & Cruickshank, 1978; Hunt, 1993; Sulej, 2007). As suggested by Fortuny *et al.* (2017), on the basis of Finite Element Analyses, metoposaurs could have used two foraging techniques in hunting; an ambush strategy using bilateral biting was commonest, but active hunting using lateral strikes of the head was also possible. However, on the basis of FE loading cases (Fortuny *et al.*, 2017), unilateral biting was most probably excluded. The morphology of sutures clearly indicates that suction feeding did not occur in *Metoposaurus*. The histological results confirm the presence of direct lateral and bilateral biting, but not exclude other combinations, except of unilateral biting, and may reinforcing the idea that lateral strike was also performed under an ambush strategy and not only as active swimming.

The microstructural structure of cranial bones mostly support the bilateral Finite Element loading case, with the exception of the system of lateral canals, which does not appear to be well adapted for handling high stress levels (Figs. 3I and 4).

However, microscopic data that indicate significantly high loading on the lateral margins of the skull, suggest a commoner more frequent occurrence of lateral biting than is concluded from the Finite Element Analysis only (Fig. 87). The main biting forces are connected with long rows of teeth along the skull margin. These rows actively occlude with the tooth row in the dentary, which is supported by the presence of sharp cutting edges on the tooth margin in dentary teeth (Konietzko-Meier & Wawro, 2007). Important also crucial is the role of the vomer tusk. As histology reveals, the vomer is a very weak bone; on the basis of FEA, there was stress increase in the vomer during lateral biting (, but absent under bilateral biting).. At first view, this is contradictory. However, it may indicate that the vomer tusks only played an active role in bilateral biting, but not in lateral biting because it could easily have snapped.

The main factor that determines the mode of life probably is may be water level. The two-season climate during the Late Triassic, with high and low water levels in local lakes and periodic rivers (*Bodzioch & Kowal-Linka, 2012*) requires ecological changing ecologic strategies in order to survive the unfavourable part (i.e., dry season) of the year.. Among amphibians, the common strategy is to wait out the dry or cold season is (aestivation/hibernation.). However, the growth pattern preserved in long bones (revealed by histology) of *Metoposaurus* does not show distinct, seasonal Lines of Arrested Growth (LAGs) at all, but only zones and unusually thick annuli, which point to a reduced growth rate for a certain period (*Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013*). The numerous lines present in annulus indicate that animals reduced their activity for several shortershort periods but did not aestivate for the entire unfavourable time (*Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013*). Growth, even slow, requires a regular access to energy. Because of seasonally variable high and low water levels, also the feeding strategies had to be adequate to counter environmental conditions. During favourable water conditions metoposaurids may have been ambush and active predators capable of lateral strikes of the head. The dry season required a less active mode of life with particularly efficient bilateral biting, together with their characteristically anteropositioned orbits, optimal infor ambush strategy.

Interestingly, the same feeding strategies were suggested for the small metoposaurid *Apachesaurus* from North America (*Fortuny et al., Marcé-Nogué & Konietzko-Meier, 2017*). Overall it could be concluded that metoposaurids were well equippedadapted for survival under various conditions, yet not specialised as far as feeding strategies are concerned. This ability to acquire food independently of environmental conditions could be the key character to guarantee the very common occurrence of metoposaurids during the Late Triassic. However, the question remains why, in spite of their wide adaptive strategies, they disappeared, together with other

temnospondyl groups, at the end of Late Triassic. *Milner* (1993, 1994) documented the demise of capitosaurids, metoposaurids and laticopids at the Norian-Rhaetian boundary as a part of the end-Triassic extinction event (ETE), considered to rank amongst the 'Big Five' mass extinctions. Global changes in environmental and ecological conditions then were too much, even for may have surpassed the widely adaptive *Metoposaurus* capabilities for metoposaurids.

CONCLUSIONS

1. The histological analysis of skull microstructure and sutures morphology mostly confirm the models created by FEA with the exceptions of the vomer which is histological a low loaded bone, but in on the basis of FEA, there is a stress increase in the vomer during lateral biting (absent under bilateral biting). Also the significant change of microstructural conditions, and thus biomechanical properties, shows that the lateral line canals might be crucial structures for the biomechanical function of the skull; especially for metoposaurids with an extremely deep system of lateral canals and should be considered in the FEA modelling. The merging of histological studies and FEA confirm that the 'negativ' scenario (in this case unilateral biting) was correctly indicated by FEA. However, the limited amount of tested scenarios ~~may provide to under interpretations of wrongly interpret~~ 'positive' behaviours and may lead to serious simplifications.
2. *Metoposaurus* have been was an aquatic animal that could adapt to various environmental conditions and was low specialised unspecialised in the mode of feeding. It has may have used two foraging techniques in hunting; an ambush strategy using bilateral biting, as well as lateral strikes, and active hunting using lateral strikes of the head. The morphology
2. One of sutures clearly indicates that suction feeding did not occur in *Metoposaurus*.

3. The potential main factor that determines factors determining the mode of life probably may have been water level. During favourable water conditions metoposaurids may have been ambush and active predators capable of lateral strikes of the head. The dry season required a less active mode of life with particularly efficient bilateral biting, together with their characteristically anteropositioned orbits, optimal insured for an ambush strategy.

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Figure captions

Figure 1 Von Mises stress results (in MPa) of bilateral (A), lateral biting (B) and of skull raising system (C) in *Metoposaurus krasiejowensis* (UOPB 00124).

Figure 2 Skull of *Metoposaurus krasiejowensis* from the UpperLate Triassic of southwest Poland (UOPB 01029) used in the histological study (A and B) and schematic drawings (C and D) of the same with sectioning planes marked, in dorsal (A and C) and palatal (B) views (B and D). In (C) and (D), red lines indicate thin sections used in microstructural analysis; purple lines refer to thin sections used in both microstructural analysis and cranial suture study; green lines indicate thin sections used in cranial suture analysis.. Scale bar equals 10 cm.

Figure 2 Loading and boundary conditions used to simulate bilateral, unilateral and lateral biting, and the skull-raising system. ImageCredit: Journal of Anatomy/Wiley.

Figure 3 Sectioning planes of dermal bones of skull of *Metoposaurus krasiejowensis* (UOPB 01029) in dorsal (A) and palatal (B) views. Scale bar equals 10 cm. Abbreviations: ec, ectopterygoid; ex, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pl, palatinum; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; qj, quadratojugal; sq1, squamosal -1; sq2, squamosal -2; st, supratemporal; t, tabular; v, vomer.

Figure 4 Von Mises stress results (in MPa) of bilateral (A), unilateral biting (B), lateral (C) and of skull raising system (D) in *Metoposaurus krasiejowensis* (UOPB 00124) using a gape angle of 10°. ImageCredit: Journal of Anatomy/Wiley.

Figure Figure 3 5 General microstructure of skull bones of *Metoposaurus krasiejowensis* (UOPB 01029) from). All bones are in scale, whereas the Upper Triassic of southwest Poland. A, nasal; B, postorbital; C, jugal; D, lacrimal; E, prefrontal; F, parietal; G, postparietal; H,

postfrontal; I, supratemporal; J, frontal; K, squamosal 1; L, tabular; M, squamosal 2; N, quadratojugal; O, parasphenoid; P, pterygoid; Q, vomer. skull miniatures are included only to show the position of bones and are out of scale. Scale bar equals 10 mm.

Figure 46 Estimated biomechanical loading as reconstructed on the basis of microstructural characters of the skull of *Metoposaurus krasiejowensis* (UOPB 01029). Note that the estimated values (average bone thickness vs compactness), on sectioned regions of the skull of *Metoposaurus krasiejowensis* (UOPB 01029) from the Upper Triassic of southwest Poland. Note that the estimated values) are relative and show merely if loading on any given region was higher or lower (on the scale bar from red to blue, respectively). It is not possible to calculate the objective amount of stress in this case. Black bars inside colour ellipses indicate the sectioning places; the ellipses without bars are symmetric to section areas.

Figure 5 Microphotography and drawings illustrating the morphology of selected cranial sutures in the skull of *Metoposaurus krasiejowensis* (UOPB 01029) from supplementary thin sections between the postorbital - jugal (A), parietal - supratemporal (B), squamosal - jugal (C) and pterygoid - exoccipital (D). Scale bar equals 1 mm. Abbreviations: Ex, exoccipital; J, jugal; P, parietal; Po, postorbital; Pt, pterygoid; Sq, squamosal; St, supratemporal.

Figure 6 Inferred strain patterns in the skull of *Metoposaurus krasiejowensis* (UOPB 01029) from the Upper Triassic of southwest Poland, based on suture morphology.

Figure 7 Histological framework of maxilla-vomer cranial suture in the skull of *Metoposaurus krasiejowensis* (UOPB 01029) from the Upper Triassic of southwest Poland; image in plane polarised light. White arrows indicate Sharpey's fibres.

Figure 8 Von Mises stress results (in MPa) of bilateral (A), lateral biting (B) and of skull raising system (C) in *Metoposaurus krasiejowensis* (UOPB 124) using a gape angle of 10° merged with the model of biomechanical loading created on the basis of microstructural characters; skulls. Von Mises stress results represent unilateral (A), bilateral (B), lateral (C) biting and of skull raising system (D) in *Metoposaurus krasiejowensis* (UOPB 00124) using a gape angle of 10° . Model of biomechanical loading is created on the basis of microstructural characters for skull UOPB 01029. Skulls in the background show FEA results; the outcome of histological reconstructions is illustrated as oval forms, of different colours. Note that similar colours were used in FEA analysis and histological estimates in order to illustrate how the general stress distribution in FEA and histological analyses correlate; however, same colours do not signify the same stress values. In FEA, the colours refer to objective values, (compare with figure 4), while in histological models estimated values are relative and show merely if the loading on any given region is higher or lower within a single skull (on the scale bare from red to blue, what means from high to low loading, respectively). Black bars inside colour ellipses indicate the sectioning places; the ellipses without bars are symmetric to section areas. The black dotted lines shows the sutures, the red lines indicated the reconstructed borders.