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

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A useful method for understanding form and function is 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. 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 local stress and these results can be combined with 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. 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 Triassic of southwest Poland were tested accordingly and microscopical observations of dermal bone microstructure and suture morphology in 39 thin sections were added. For the first time, three independent models were merged in a revision of the feeding strategy of *Metoposaurus*. *Metoposaurus* appears to have been an aquatic animal that was little specialised concerning feeding behaviour. This taxon may have used two foraging

techniques in hunting; an ambush strategy, using bilateral biting, or active hunting, using lateral strikes of the head. However, microscopic data suggest that lateral biting was commoner than can be observed in Finite Element Analysis only. The main factor that determined its mode of life probably was water levels. During optimum water conditions, metoposaurids were active ambush predators capable of lateral strikes of the head. The dry season required a less active mode of life with particularly efficient bilateral biting and, combined with their characteristically anteriorly positioned orbits, optimal for ambush strategy. This ability for food acquisition, independent of environmental conditions, could be the key to explain the very common occurrence of metoposaurids during the Late Triassic

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ABSTRACT

A useful method for understanding form and function ~~is 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. 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~~ local stress and these results can be combined with the Finite Element models. To test this scenario, the early tetrapod group of Temnospondyli is an excellent case-study. This clade ranks among~~st~~ 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. 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 Triassic of southwest Poland were tested accordingly and microscopical observations of dermal bone microstructure and suture morphology in 39 thin sections were added. For the first time, three independent models were merged in a revision of the feeding strategy of *Metoposaurus*. *Metoposaurus* appears to have been an aquatic animal that was little specialised concerning feeding behaviour. This taxon may have used two foraging techniques in hunting; an ambush strategy, using bilateral biting, or active hunting, using lateral strikes of the head.

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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 modern world~~. 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*., 2014*a, b*; *Cheng et al*., 2014; *Chun Li et al*., 2011, 2013, 2016; *Klein et al*., 2015*a*,*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 evolutional 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).

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 ~~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 capitosaurs, 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).

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 fill 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

Another approach to ensure reliable results and problem solving is the use of bone histology. The bony framework is a product of biological optimisation and the bone structure is created to meet local mechanical conditions. 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 (i.e., *Martin*, 1991; *Currey*, 2003, 2006, 2012; *Currey, Pitchford & Baxter*, 2007; *Zioupos, 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 the long term, as an evolutionary adaptation. The mechanical properties of bone are a 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 the same biological safety factors 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 level, 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).

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 & Mohuiddin*, 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 (*Jasinoski, 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*, 2007*a,b*). *Markey and Marshall* (2007*a*) 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*, 2007*b*). 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*, 2007*b*). This suggests that even the fully aquatic *Acanthostega* was adapted to feeding by biting (*Markey and Marshall*, 2007*b*).

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). 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 capitosaurs (*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

297 and posterior rami of the pterygoids (Fig. 1C). Lower, but still measurable, stress is indicated in
298 the anterior rami of the pterygoid, ectopterygoid and in the vomer (Fig. 1C).

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

307 However, ~~how it~~ was mentioned above the FEA analysis has a limitation concerning the
308 amount of tested scenario. The results confirm the presence of direct lateral and bilateral biting,
309 but not exclude other combinations, except of unilateral biting, simple because of lack of models.
310

311 **Microscopic studies -** Cranial suture morphology and its predicted function for
312 *Metoposaurus* have been studied histologically in preliminary fashion (*Gruntmejer*, 2012). Most
313 of the sutures were defined as complex interdigitated which served a compression-resistant
314 purpose. Moreover, a shallowly interdigitated suture (prefrontal-lacrimal) has been observed,
315 which resisted tensile strains and two samples of probably overlapping sutures (maxilla-nasal
316 and frontal-postfrontal), which counter variable strains forces, have also be noted (*Gruntmejer*,
317 2012). Based on these facts, a predominant feeding mode of direct biting was concluded for
318 *Metoposaurus*. However, because of the presence of overlapping sutures in the anterior part of
319 the skull, capture of prey by suction could not be ruled out (*Gruntmejer*, 2012).

320

321 ## MATERIAL AND METHODS

322

323 ### Material

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

330

331 ### Methods

332 **Thin-sections -** The histological study of skull bones of *Metoposaurus krasiejowensis*
333 Skull UOPB 01029 has indicated a relatively stable collagen fibre pattern with parallel-fibred
334 bone constructing the grooves and inner cortex and lamellar bone present in the troughs/grooves
335 of the skull (*Gruntmejer et al*., 2016). In contrast, microstructural characters (thickness and
336 compactness) change very clearly (*Gruntmejer et al*., 2016), and thus may be used as a proxy to
337 estimate the mechanical loading. However, the detailed studies were not performed to analyse
338 the relations between the thicknesses, compactness and estimated biomechanical loading. It may
339 be assumed then that these characters influence the results of estimation significantly. This is
340 why these two features, based on the same thin-sections collection (Fig. 2) as published by
341 *Gruntmejer et al.* (2016) are ~~widely~~ analysed here and only these two were taken into account in

342 biomechanical simulation. Additionally, the thin-sections from the various border regions were
343 prepared to test the morphology of sutures (Fig. 2).
344 UOPB 01029 was sectioned in 39 places, inclusive of 19 flat dermal bones (Fig. 2),
345 according to standard petrographic procedures (*Chinsamy & Raath*, 1992). Non-dermal bones
346 such as exoccipital and quadratojugal were not analysed, because of their endochondral origin
347 and different shape. Cross-sectional shape morphology of cranial sutures was conducted on 26
348 thin sections (Table 1; green and purple lines in Fig. 2).The bone microstructure was studied in
349 16 thin sections (Table 2; red and purple lines in Fig. 2). Subsequently, the thin sections were
350 studied under a LEICA DMLP light microscope in normal and polarised light. Additionally,
351 cranial sutures were qualitatively analysed ~~in~~ Scanning Electron Microscope (SEM) to assess
352 their morphology.
353 In the thin sections, the average thickness of the entire bone was estimated, expressed as
354 an arithmetical average from three measurements of the thickness of the entire bone. The average
355 thickness of the bone was measured three times over the distance between the ventral side of the
356 bone and the bottom of troughs/grooves, and three times as the distance to the top of ridges. The
357 mathematical average was calculated from these measurements.
358 To estimate bone porosity the thin sections were scanned ~~by~~ Epson Scanner and
359 transformed into black and white images (Fig. 3). The analysis of compactness was done ~~by~~
360 Bone Profiler (*Girondot & Laurin*, 2003).
361 In the prefrontal, squamosal 2 and parasphenoid, on account of the strongly variable bone
362 thickness, the significantly thinner parts of these bones (labelled in Figures 3 and 4 and in the
363 text as *b*, as opposed to the thicker part named *a*), were calculated separately (Fig. 3I,M and O).
364

365 **Finite Elements Analysis -** Skull UOPB 00124 (290 mm in length) was CT scanned for
366 3D-Finite Element Analysis. A Structural Static Analysis to evaluate the biomechanical
367 behaviour during biting and skull raising was performed using the Finite Element Package
368 ANSYS 14.5 in a Dell Precision™ Workstation T7600 with 32 GB (4X8GB) and 1600 MHz.
369 The detailed methodology was published by *Fortuny et al*. (2017). In this study the generated
370 models (*Fortuny et al*., 2017; for summary see also chapter III) were reformulated in order to get
371 information about sutures function.
372
373 **RESULTS**
374
375 **Biomechanical loading approach from thin-section analysis**
376
377 **Bone microstructure -** The average thickness of dermal bones varies from 2 to 10 mm
378 (Table 2, Figs 3 and 4). In the posterior part of skull bones are the thickest (postparietal and
379 tabular), up to 10 mm ~~with~~ a compactness varying between 80 and 82%. The microstructural
380 characters indicate a very high biomechanical loading on this part of the skull (Table 2; Fig. 4).
381 The postorbital and jugal represent a similar average thickness (close to 7 mm), but the
382 compactness varies from 83% to 88%, respectively. These bones show a lower loading,
383 compared to the posterior part of skull, but still have high stress level. Further decrease of the
384 strength is observed for the lacrimal, quadratojugal, frontal and pterygoid bones, in which the
385 thickness oscillates around 6 mm and the compactness varies from 73 to 80% (Table 2; Figs 3
386 and 4). The postfrontal, squamosal 1, posterior part of squamosal 2, parietal and
387 supratemporal(a) present thicknesses of around four mm, with the compactness changing from

88 to 95% (Table 2; Figs 3 and 4). The nasal, prefrontal and parasphenoid(a) with a relatively limited thickness and compactness received low biomechanical loads (Table 2; Figs. 3 and 4). The vomer is extremely porous, with a compactness of only about 55%, accompanied by limited thickness and possibly free of stress (Table 2, Figs 3 and 4). Markedly thinner are also medial parts of the supratemporal and parasphenoid (Fig. 3 I and O). In these bones the thinnest fragments are about 2 mm thick, contrary to the remaining part with an average thickness of about 4 mm (Table 2, Figs 3 and 4). In squamosal 2 the decrease in bone thickness is more gradual (Fig. 3M). In ~~all~~ these three bones the compactness increases along with thickness decreasing, reaching more than 90% in the thinnest region. Despite the high compactness these portions of bones are very weak, in view of their extreme thinness (Table 2, Figs 3 and 4).

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, with a tendency to decrease in the otic notches region and postorbital area (Fig. 4). A slight increase of biomechanical loading is present only next to the posterior margin of the orbits (Fig. 4). The anterior part of squamosal 2 and the deep trough/groove in the supratemporal 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. 3I). The squamosal 2 shows a gradual decrease in mechanical resistance in an anterior direction, indicating low loading on the lateroposterior part of the skull. The postfrontal, squamosal 1, posterior part of squamosal 2, parietal and supratemporal(a) are thinner, but significantly more compact than the lacrimal, quadratojugal and frontal and thus represent only a slight decrease of final biomechanical strength.

The bones from the palatal side represent moderate or low stress levels. Extremely weak are the vomer and the medial part of the parasphenoid (Fig. 4), 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

433 **Bone histology *vs* computational biomechanics – how does bone structure correlate**
434 **with Finite Element Analysis? -** Values of equivalent Von Mises stresses and their distribution
435 were recorded in order to compare their behaviour under the effect of loads and constraints in the
436 bilateral and lateral cases. The Von Mises criterion is the most accurate for predicting fracture
437 location when isotropic material properties are used in cortical bone (*Doblaré, García & Gomez*,
438 2004). As stated previously, the von Mises stress patterns of the models could be used
439 indifferently with strain patterns, allowing to compare qualitatively these results with the
440 compactness obtained from histological thin sections.
441 The histological framework confirms mostly the stress distribution pattern obtained
442 during FE analyses. The histological characters support that the nasal and prefrontal are
443 relatively weak bones; thus, the biomechanical loading in these regions was relatively low. In
444 both simulations (bilateral and lateral) the same tendency is observed, with a slight increase of
445 stress level in the prefrontal (Fig. 8A and B), which is also thinner (Fig. 4). In the frontal region,
446 under a bilateral case, the estimated stress level exceeds that in the prefrontal and nasal (Fig.
447 8A). Histologically, the frontal is a relatively massive bone in comparison to the nasal and
448 prefrontal. This indicates that loading on the frontal region was high. The postfrontal, squamosal
449 2(a), parietal and squamosal 1 are thinner than the frontal, but more compact and thus the loading
450 could be the same or only slightly lower as on the frontal (Figs 3A-B and 4). The same tendency
451 is observed in bilateral and lateral FEA cases (Fig. 8A-B). Squamosal 2 is of special interest as
452 the FE models suggest a change of stress value from the posterior to the anterior part of this
453 element, receiving high to low levels, respectively (Fig. 8). Interestingly, the histological results
454 also reveal this change in the thickness of the cortex as well as in the porosity across the bone
455 (Fig. 4). Squamosal 2(b) in both FEA cases (bilateral and lateral) show barely any stress

anteriorly (Fig. 8A-B); 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 entirety, the supratemporal is adapted to moderate loading (Fig. 4), which is visible also in bilateral and lateral FEA cases (Fig. 8). 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. 4). 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*., 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 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. 8B), 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~~ 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 and 8). Additionally, the histological framework suggests that the parasphenoid was loaded ~~more next~~ 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*., 2016) it cannot be ruled out that the anterior part of this bone is highly metaplastic. This, along with large 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. 8C), but this stress pattern is not supported by the histological framework. The vomer is the weakest bone of the entire skull (Fig. 4).

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 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*., 2016). However, in

both bones very strong Sharpey's fibres are present (*Gruntmejer et al*., 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 parasphanoid-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

Merging three different approaches (Finite Element Analysis, bone histology and cranial suture morphology) provides data from different perspectives on skull biomechanics that, when correlated yield, a ~~clear~~ image of the feeding behaviour of *Metoposaurus*. *Metoposaurus* appears to have been an aquatic animal that could adapt to various environmental conditions and was less specialised in the 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 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).

548 However, microscopic data that indicate significantly high loading on the lateral margins
549 of the skull, suggest a ~~commoner~~ occurrence of lateral biting than is concluded from the Finite
550 Element Analysis only (Fig. 8). The main biting forces are connected with long rows of teeth
551 along the skull margin. These rows act actively with the tooth row in the dentary, which is
552 supported by the presence of sharp cutting edges on the tooth margin in dentary teeth (*Konietzko-*
553 *Meier & Wawro*, 2007). Important also is the role of the vomer tusk. As histology reveals, the
554 vomer is a very weak bone; on the basis of FEA, there was stress increase in the vomer during
555 lateral biting (absent under bilateral biting). At first view, this is contradictory. However, it may
556 indicate that the vomer tusks only played an active role in bilateral biting, but not in lateral biting
557 because it could easily have snapped.
558 The main factor that determines the mode of life probably is water level. The two-season
559 climate during the Late Triassic, with high and low water levels in local lakes and periodic rivers
560 (*Bodzioch & Kowal-Linka*, 2012) requires ecological strategies in order to survive the
561 unfavourable part (i.e., dry season) of the year. Among amphibians, the common strategy to wait
562 out the dry or cold season is aestivation/hibernation. However, the growth pattern preserved in
563 long bones (revealed by histology) of *Metoposaurus* does not show distinct, seasonal Lines of
564 Arrested Growth (LAGs) at all, but only zones and unusually thick annuli, which point to a
565 reduced growth rate for a certain period (*Konietzko-Meier & Klein*, 2013; Konietzko-Meier &
566 Sander, 2013). The numerous lines present in annulus indicate that animals reduced their activity
567 for several shorter periods but did not aestivate for the entire unfavourable time (*Konietzko-*
568 *Meier & Klein*, 2013; *Konietzko-Meier & Sander*, 2013). Growth, even slow, requires a regular
569 access to energy. Because of seasonally variable high and low water levels, also the feeding
570 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 ~~in~~ ambush strategy.

Interestingly, the same feeding strategies were suggested for the small metoposaurid *Apachesaurus* from North America (*Fortuny et al*., 2017). Overall it could be concluded that metoposaurids were well equipped 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 latiscopids 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 the widely adaptive *Metoposaurus*.

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 extremely deep system of lateral canals and should be considered in the FEA modelling.

2. *Metoposaurus* ~~have been~~ an aquatic animal that could adapt to various environmental conditions and was ~~low specialised~~ in the mode of feeding. It has used two foraging techniques in hunting; an ambush strategy using bilateral biting and active hunting using lateral strikes of the head. The morphology of sutures clearly indicates that suction feeding did not occur in *Metoposaurus*.
3. The main factor that determines the mode of life probably ~~is~~ 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 ~~in~~ ambush strategy.

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REFERENCES

Achrai B & Wagner HD. 2013. Micro-structure and mechanical properties of the turtle carapace as a biological composite shield. *Acta Biomaterialia* **9**:5890–5902.

Anderson PSL, Bright JA, Gill PG & Rayfield EJ. 2012. Models in palaeontological functional analysis. *Biology Letters* **8**:119–122.

Benton M J. 2010. Studying function and behavior in the fossil record. *PLoS Biology* **8**: e1000321.

Biewener AA. 1993. Safety factors in bone strength. *Calcified Tissue International and Musculoskeletal Research* **53**: 68–74.

Bodzioch A & Kowal-Linka M. 2012. Unraveling the origin of the Late Triassic multitaxic bone accumulation at Krasiejów (S Poland) by diagenetic analysis. *Palaeogeography Palaeoclimatology Palaecology* **346/347**: 25–36.

Bright J A & Rayfield EJ. 2011. Sensitivity and ex vivo validation of finite element models of the domestic pig cranium. *Journal of Anatomy* **219**: 456–471.

Carrier D & Leon LR. 1990. Skeletal growth and function in the California gull (*Larus californicus*). *Journal of Zoology* **222**: 375–389.

Carroll RL & Holmes R. 1980. The skull and jaw musculature as guides to the ancestry salamanders. *Zoological Journal of the Linnean Society* **68**: 1–40.

639 Chen X-H, Motani R, Cheng L, Jiang D-Y & Rieppel O. 2014a. The Enigmatic Marine Reptile
640 *Nanchangosaurus* from the Lower Triassic of Hubei, China and the Phylogenetic
641 Affinities of Hupehsuchia. *PLoS ONE* **9**: e102361.
642 Chen X-H, Motani R, Cheng L, Jiang D-Y & Rieppel O. 2014b. A Carapace-Like Bony 'Body
643 Tube' in an Early Triassic Marine Reptile and the Onset of Marine Tetrapod Predation.
644 *PLoS ONE* **9**: e94396.
645 Cheng L, Chen X-H, Shang Q-H & Wu X-C. 2014. A new marine reptile from the Triassic of
646 China, with a highly specialized feeding adaptation. *Naturwissenschaften* **101**: 251–259.
647 Chernin S & Cruickshank ARI. 1978. The myth of the bottom-dwelling capitosaur amphibians.
648 *South African Journal of Science* **74**: 111–112.
649 Chinsamy A & Raath MA. 1992. Preparation of fossil bone for histological examination.
650 *Palaeontologia Africana* **29**: 39–44.
651 Cox PG, Fagan MJ, Rayfield EJ & Jeffery N. 2011. Finite element modelling of squirrel, guinea
652 pig and rat skulls: using geometric morphometrics to assess sensitivity. *Journal of*
653 *Anatomy* **219**: 696–709.
654 Chun L, Rieppel O, Long C, & Fraser NC. 2016. The earliest herbivorous marine reptile and its
655 remarkable jaw apparatus. *Science Advances* **2**: e1501659.
656 Currey JD. 2003. The many adaptations of bone. *Journal of Biomechanics* **36**: 1487–1495.
657 Currey JD. 2006. *Bones: Structure and Mechanics*. Princeton University Press, Princeton.
658 Currey JD. 2012. The structure and mechanics of bone. *Journal of Materials Science* **47**: 41–54.
659 Currey JD, Pitchford J W & Baxter PD. 2007. Variability of the mechanical properties of bone,
660 and its evolutionary consequences. *Journal of the Royal Society Interface* **4**: 127–135.

661 Damiani R, Schoch RR, Hellrung H, Werneburg R & Gastou S. 2009. The plagiosaurid
662 temnospondyl *Plagiosuchus pustuliferus* (Amphibia: Temnospondyli) from the Middle
663 Triassic of Germany: Anatomy and functional morphology of the skull. *Zoological*
664 *Journal of the Linnean Society* **155**: 348–373.
665 Doblaré M, García JM & Gomez MJ. 2004. Modelling bone tissue fracture and healing: A
666 review. *Engineering Fracture Mechanics* **71**: 1809–1840.
667 Dzik J & Sulej T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland.
668 *Palaeontologia Polonica* **64**: 3–27.
669 Erickson GM. 2005. Assessing dinosaur growth patterns: A microscopic revolution. *Trends in*
670 *Ecology & Evolution* **20**: 677–684.
671 Fitton LC, Shi JF, Fagan MJ & O'Higgins P. 2012. Masticatory loadings and cranial deformation
672 in *Macaca fascicularis* a finite element analysis sensitivity study. *Journal of Anatomy*
673 **221**: 55–68.
674 Fortuny J, Marcé-Nogué J, de Esteban-Trivigno S, Gil L & Galobart Á. 2011. Temnospondyli
675 bite club: ecomorphological patterns of the most diverse group of early tetrapods. *Journal*
676 *of Evolutionary Biology* **24**: 2040–2054.
677 Fortuny J, Marcé-Nogué J, Gil L & Galobart Á. 2012. Skull mechanics and the evolutionary
678 patterns of the otic notch closure in Capitosaurs (Amphibia: Temnospondyli). *The*
679 *Anatomical Record* **295**: 1134–1146.
680 Fortuny J, Marcé-Nogué J, Heiss E, Sanchez M, Gil L & Galobart À. 2015. 3D Bite modeling
681 and feeding mechanics of the largest living amphibian, the chinese giant
682 salamander *Andrias davidianus* (Amphibia:Urodela). *PlosOne* **10**: e0121885.

683 Fortuny J, Marcè-Noguè J & Konietzko-Meier D. 2017. Feeding biomechanics of Late Triassic
684 metoposaurids (Amphibia: Temnospondyli): a 3D finite element analysis approach.
685 *Journal of Anatomy* **230**: 752–765.
686 Fortuny J, Marcè-Noguè J, Steyer JS, De Esteban-Trivigno S, Mujal E & Gil L. 2016.
687 Comparative 3D analyses and palaeoecology of giant early amphibians (Temnospondyli:
688 Stereospondyli). *Scientific Reports* **6**: 30387.
689 Girondot M & Laurin M. 2003. Bone Profiler: a tool to quantify, model, and statistically
690 compare bone-section compactness profiles. *Journal of Vertebrate Paleontology* **23**: 458–
691 461.
692 Gruntmejer K. 2012. Morphology and function of cranial sutures of the Triassic amphibian
693 *Metoposaurus diagnosticus* (Temnospondyli) from southwest Poland. In: *Krasiejów –*
694 *palaeontological inspirations* (eds E. Jagt-Yazykova , J. Jagt J, A. Bodzioch and D.
695 Konietzko-Meier), pp. 34–54. ZPW Plik, Bytom.
696 Gruntmejer K, Konietzko-Meier D & Bodzioch A. 2016. Cranial bone histology of
697 *Metoposaurus krasiejowensis* (Amphibia, Temnospondyli) from the Late Triassic of
698 Poland. *PeerJ* **4**: e2685.
699 Haines RW & Mohiuddin A. 1968. Metaplastic bone. *Journal of Anatomy* **103**: 527–538.
700 Holmes RB & Carroll RL. 1977. A temnospondyl amphibian from the Mississippian of Scotland.
701 *Bulletin of the Museum of Comparative Zoology* **147**: 489–511.
702 Houssaye A, Sander PM & Klein N. 2016. Adaptive Patterns in Aquatic Amniote Bone
703 Microanatomy—More Complex than Previously Thought. *Integrative and Comparative*
704 *Biology* **56**: 1349–1369.

Howie AA. 1970. A new capitosaurid labyrinthodont from East Africa. *Palaeontology* **13**: 210–253.

Hunt AP. 1993. Revision of the Metoposauridae (Amphibia, Temnospondyli) and description of a new genus from western North America. In: *Aspects of Mesozoic Geology and Paleontology of the Colorado Plateau* (ed M. Morales), pp. 67–97. *Museum of Northern Arizona Bulletin* **59**.

Jasinoski SC, Rayfield EJ & Chinsamy A. 2010. Functional implications of dicynodont cranial suture morphology. *Journal of Morphology* **271**: 705–728.

Jasinoski SC & Reddy BD. 2012. Mechanics of cranial sutures during simulated cyclic loading. *Journal of Biomechanics* **45**: 2050–2054.

Jäger GF. 1824. *De Ichthyosauri sive Proteosauri, Fossils, Speciminibus, in Agro Bollensi in Wurtembergia Repertis*. Cotta, Stuttgart.

Jäger GF. 1828. *Über die fossile Reptilien, welche in Württembergaufgefunden worden sind*. J.B. Metzler, Stuttgart.

Klein N, Houssaye A, Neenan JM & Scheyer TM. 2015a. Long bone histology and microanatomy of Placodontia (Diapsida: Sauropterygia). *Contributions to Zoology* **84**: 59–84.

Klein N, Voeten DFAE, Lankamp J, Jankamp J, Bleeker R, Sichelschmidt OJ, Liebrand M, Nieweg DC & Sander PM. 2015b. Postcranial material of *Nothosaurus marchicus* from the Lower Muschelkalk (Anisian) of Winterswijk, The Netherlands, with remarks on swimming styles and taphonomy. *Paläontologische Zeitschrift* **89**: 961–981.

726 Klein N, Sander PM, Krahl A, Scheyer TM & Houssaye A. 2016 Diverse aquatic adaptations in
727 *Nothosaurus* spp. (Sauropterygia)—inferences from humeral histology and
728 microanatomy. *PLoS ONE* **11:** e0158448.
729 Konietzko-Meier D, Bodzioch A & Sander PM. 2013. Histological characteristics of the
730 vertebral intercentra of *Metoposaurus diagnosticus* (Temnospondyli) from the Upper
731 Triassic of Krasiejów (Upper Silesia, Poland). *Earth and Environmental Science*
732 *Transactions of the Royal Society of Edinburgh* **103**: 1–14.
733 Konietzko-Meier D & Klein N. 2013. Unique growth pattern of *Metoposaurus diagnosticus*
734 *krasiejowensis* (Amphibia, Temnospondyli) from the Upper Triassic of Krasiejów,
735 Poland. *Palaeogeography Palaeoclimatology Palaeoecology* **370**: 145–157.
736 Konietzko-Meier D & Sander PM. 2013. Long bone histology of *Metaposaurus diagnosticus*
737 (Temnospondyli) from the Late Triassic of Krasiejów (Poland) and its paleobiological
738 implications. *Journal of Vertebrate Paleontology* **35**: 1–16.
739 Konietzko-Meier D & Wawro K. 2007. Mandibular dentition in the Late Triassic temnospondyl
740 amphibian *Metoposaurus*. *Acta Palaeontologia Polonica* **52**: 213–215.
741 Kupczik K, Dobson CA, Fagan MJ, Crompton RH, Oxnard CE & O'Higgins P. 2007. Assessing
742 mechanical function of the zygomatic region in macaques: validation and sensitivity
743 testing of finite element models. *Journal of Anatomy* **210**: 41–53.
744 Lautenschlager S, Witzmann F & Werneburg I. 2016. Palate anatomy and morphofunctional
745 aspects of interpterygoid vacuities in temnospondyl cranial evolution. *The Science of*
746 *Nature* **103**: 79.

747 Li C, Jiang D-Y, Cheng L, Wu X-C & Rieppel O. 2013. A new species of *Largocephalosaurus*
748 (Diapsida: Saurosphargidae), with implications for the morphological diversity and
749 phylogeny of the group. *Geological Magazine* **151**: 100–120.
750 Li C, Rieppel O, Wu X-C, Zhao L-J, & Wang L-T. 2011. A new Triassic marine reptile from
751 southwestern China. *Journal of Vertebrate Paleontology* **31**: 303–312.
752 Maganuco S, Steyer JS, Pasini G, Boulay M, Lorrain S & Bénéteau A. 2009. An exquisite
753 specimen of *Edingerella madagascarensis* (Temnospondyli) from the Lower Triassic of
754 NW Madagascar; cranial anatomy, phylogeny, and restorations. *Memorie della Societáa*
755 *italiana di scienze naturali Milano* **36**: 1–72.
756 Marcé-Nogué J, Fortuny J, De Esteban-Trivigno S, Sánchez M, Gil L & Galobart À. 2015. 3D
757 Computational mechanics elucidate the evolutionary implications of orbit position and
758 size diversity of early amphibians. *PlosOne* **10**: e0131320.
759 Margerie E, Robin JP, Verrier D, Cubo J, Groscolas R & Castanet J. 2004. Assessing a
760 relationship between bone microstructure and growth rate: a fluorescent labelling study in
761 the king penguin chick (*Aptenodytes patagonicus*). *Journal of Experimental Biology* **207**:
762 869–879.
763 Markey MJ, Main RP & Marshall CR. 2006. *In vivo* cranial suture function and suture
764 morphology in the extant fish *Polypterus*: implications for inferring skull function in
765 living and fossil fish. *Journal of Experimental Biology* **209**: 2085–2102.
766 Markey MJ & Marshall CR. 2007a. Linking form and function of the fibrous joints in the skull: a
767 new quantification scheme for cranial sutures using the extant fish *Polypterus endlicherii*.
768 *Journal of Morphology* **268**: 89–102.

769 Markey MJ & Marshall CR. 2007b. Terrestrial-style feeding in a very early aquatic tetrapod is
770 supported by evidence from experimental analysis of suture morphology. *Proceedings of*
771 *the National Academy of Sciences of the United States of America* 1**04**: 7134–7138.
772 Martin RB. 1991. Determinants of the mechanical properties of bones. *Journal of Biomechanics*
773 **24**: 79–88.
774 Maxwell WD & Benton MJ. 1990. Historical tests of the absolute completeness of the fossil
775 record of tetrapods. *Paleobiology* **16**: 322–335.
776 McCurry MR, Evans AR & McHenry CR. 2015. The sensitivity of biological finite element
777 models to the resolution of surface geometry: a case study of crocodilian crania. *PeerJ* **3**:
778 e988.
779 Milner AR. 1990. The radiations of temnospondyl amphibians. In: *Major Evolutionary*
780 *Radiations* (eds P. D. Taylor and G.P Larwood), pp. 321–34. Clarendon Press, Oxford.
781 Milner AR. 1993. Biogeography of Palaeozoic tetrapods. In: *Palaeozoic Vertebrate*
782 *Biostratigraphy and Biogeography* (eds J. A. Long), pp. 324–353. Belhaven Press,
783 London.
784 Milner AR. 1994. Late Triassic and Jurassic amphibians: fossil record and phylogeny. In: *The*
785 *Shadow of the Dinosaurs: Early Mesozoic Tetrapods* (eds N. C. Fraser and H. D. Sues),
786 pp. 5–22. Cambridge University Press, Cambridge.
787 Milner AR & Sequeira SEK. 1998. A cochleosaurid temnospondyl amphibian from the Middle
788 Pennsylvanian of Linton, Ohio, U.S.A. *Zoological Journal of the Linnean Society* **122**:
789 261–290.
790 Mishra S. 2009. Biomechanical aspects of bone microstructure in vertebrates: potential approach
791 to palaeontological investigations. *Journal of Biosciences* **34**: 799–809.

792 Murry PA. 1989. Geology and paleontology of the Dockum Formation (Upper Triassic), west
793 Texas and eastern New Mexico. In: *Dawn of the age of dinosaurs in the American*
794 *Southwest* (eds S. G. Lucas and A. P. Hunt), pp. 102–144. Museum of Natural History,
795 Albuquerque, New Mexico.
796 Ochev VG. 1966. *Systematics and Phylogeny of Capitosauroid Labyrinthodonts*. Saratov State
797 University Press, Saratov. [in Russian].
798 Racki G, Szulc J. 2015. The bone-bearing Upper Triassic of Upper Silesia, southern Poland:
799 integrated stratigraphy, facies and events – introductory remarks. *Annales Societatis*
800 *Geologorum Poloniae* **85**: 553–555.
801 Rafferty KL & Herring SW. 1999. Craniofacial sutures: morphology, growth, and *in vivo*
802 masticatory strains. *Journal of Morphology* **242**: 167–179.
803 Rayfield EJ. 2007. Finite Element Analysis and Understanding the Biomechanics and Evolution
804 of Living and Fossil Organisms. *Annual Review of Earth and Planetary Sciences* **35**:
805 541–576.
806 Rhee H, Horstemeyer MF, Hwang Y, Lim H, Kadiri HE & Trim W. 2009. A study on the
807 structure and mechanical behavior of the Terrapene Carolina carapace: a pathway to
808 design bioinspired synthetic composites. *Materials Science and Engineering*, C **29**:
809 2333–2339.
810 Rinehart LF & Lucas SG. 2013. The functional morphology of dermal bone ornamentation in
811 temnospondyl amphibian. In: *The Triassic System* (eds L. H. Tanner, J.A. Spielmann and
812 S.G. Lucas), pp., 524–532. *New Mexico Museum of Natural History and Science, Bulletin*
813 **61**.

814 Ross CF, Patel BA, Slice DE, Strait DS, Dechow PC, Richmond BG. & Spencer MA. 2005.
815 Modeling masticatory muscle force in finite element analysis: sensitivity analysis using
816 principal coordinates analysis. *The Anatomical Record Part A Discoveries in Molecular*
817 *Cellular and Evolutionary Biology* **283A**: 288–299.
818 Sanchez S, Germain D, Ricqlès A de, Abourachid A, Goussard F, Tafforeau P. 2010. Limb–bone
819 histology of temnospondyls: implications for understanding the diversification of
820 palaeoecologies and patterns of locomotion of Permo–Triassic tetrapods. *Journal of*
821 *Evolutionary Biology* **3**: 2076–90.
822 Sander PM, Christian A, Clauss M, Fechner R, Gee C, Griebeler E-M, Gunga H-C, Hummel J,
823 Mallison H, Perry S, Preuschoft H, Rauhut O, Remes K, Tütken T, Wings O & Witzel U.
824 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews*
825 *of the Cambridge Philosophical Society* **86**: 117–155.
826 Schoch RR. 2013. The evolution of major temnospondyl clades: an inclusive phylogenetic
827 analysis. *Journal of Systematic Palaeontology* **11**: 673–705.
828 Stayton CT & Ruta M. 2006. Geometric morphometrics of the skull roof of stereospondyls
829 (Amphibia: Temnospondyli). *Palaeontology* **49**: 307–337.
830 Steyer JS, Damiani R, Sidor CA, O'Keefe, FR, Larsson HCE, Maga A & Oumarou I. 2006. The
831 vertebrate fauna of the Upper Permian of Niger. IV. *Nigerpeton ricqlesi* (Temnospondyli:
832 Cochleosauridae), and the Edopoid colonization of Gondwana. *Journal of Vertebrate*
833 *Paleontolgy* **26**: 18–28.
834 Strait DS, Wang Q, Dechow PC, Ross CF, Richmond BG, Spencer MA & Patel BA. 2005.
835 Modeling elastic properties in finite-element analysis: How much precision is needed to
836 produce an accurate model? *The Anatomical Record* **283A**: 275–287.

837 Sulej T. 2002. Species discrimination of the Late Triassic temnospondyl amphibian
838 *Metoposaurus diagnosticus*. *Acta Palaeontologica Polonica* **47**: 535–546.
839 Sulej T. 2007. Osteology, variability, and evolution of Metoposaurus, a temnospondyl from the
840 Late Triassic of Poland. *Palaeontologia Polonica* **64**: 29–139.
841 Szulc J, Racki G & Jewuła K. 2015. Key aspects of the stratigraphy of the Upper Silesian middle
842 Keuper, southern Poland. *Annales Societatis Geologorum Poloniae* **85**: 557–586.
843 Szulc J, Racki G, Jewuła K & Środoń A. 2015. How many Upper Triassic bone-bearing levels
844 are there in Upper Silesia (Southern Poland)? A critical overview of stratigraphy and
845 facies. *Annales Societatis Geologorum Poloniae* **85**: 587–626.
846 Timoshenko S. 1976. *Strength of Materials*. Van Nostrand, New York.
847 Walmsley CW, McCurry MR, Clausen PD & McHenry CR. 2013. Beware the black box:
848 investigating the sensitivity of FEA simulations to modelling factors in comparative
849 biomechanics. *PeerJ* **1**: e204.
850 Wang Q, Smith AL, Strait DS, Wright BW, Richmond BG, Grosse IR, Byron CD & Zapata U.
851 2010. The global impact of sutures assessed in a finite element model of a macaque
852 cranium. *The Anatomical Record* **293**: 1477–1491.
853 Wang Q, Wood SA, Grosse IR, Ross CF, Zapata U, Byron CD, Wright BW & Strait DS. 2012.
854 The role of sutures in biomechanical dynamic simulation of a macaque cranial finite
855 element model: implications for the evolution of craniofacial form. *The Anatomical*
856 *Record* **295**: 278–288.
857 Warren AA. 2000. Secondarily aquatic temnospondyls of the Upper Permian and Mesozoic. In:
858 *Volume 4* (eds H. Heatwole and R. L. Carroll), pp. 1121–1149. Beatty & Sons, Chipping
859 Norton.

860 Warren A, Rich T & Vickers-Rich PV. 1997 The last labyrinthodonts? *Palaeontographica*
861 *Abteilung* A **247**: 1–24.
862 Witmer LM. 1995. The Extant Phylogenetic Bracket and the importance of reconstructing soft
863 tissues in fossils. In: *Functional Morphology in Vertebrate Paleontology* (ed J. J.
864 Thomason), pp. 19 – 33. Cambridge University Press, Cambridge.
865 Witzel U, Mannhardt J, Goessling R, Micheli de P & Preuschoft H. 2011. Finite Element
866 Analyses and virtual syntheses of biological structures and their application to Sauropod
867 skulls. In: *Biology of Sauropod Dinosaurus. Understanding the Life of Giants* (eds N.
868 Klein, K. Remes, C. T. Gee and P. M. Sander), pp.171–196. Indiana University Press,
869 Bloomington and Indianapolis.
870 Witzmann F. 2006. Cranial morphology and ontogeny of the Permo-Carboniferous
871 temnospondyl *Archegosaurus decheni* Goldfuss, 1847 from the Saar–Nahe Basin,
872 Germany. *Earth and Environmental Science Transactions of the Royal Society of*
873 *Edinburgh* **96**: 131–162.
874 Witzmann F. 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the
875 implications for the soft tissue dermis. *Palaeodiversity* **2**: 233–270.
876 Witzmann F. & Schoch RR. 2013. Reconstruction of cranial and hyobranchial muscles in the
877 Triassic temnospondyl Gerrothorax provides evidence for akinetic suction feeding.
878 *Journal of Morphology*, **274**: 525–542.
879 Wood SA, Strait DS, Dumont ER, Ross CF & Grosse IR. 2011. The effect of modeling
880 simplifications on craniofacial finite element models: the alveoli (tooth sockets) and
881 periodontal ligaments. *Journal of Biomechanics* **44**: 1831–1838.

882 Zioupos P, Hansen U & Currey JD. 2008. Microcracking damage and the fracture process in
883 relation to strain rate in human cortical bone tensile failure. *Journal of Biomechanics* **41**:
884 2932–2939.

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906 **Figure captions**

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908 **Figure 1** Von Mises stress results (in MPa) of bilateral (A), lateral biting (B) and of skull raising
909 system (C) in *Metoposaurus krasiejowensis* (UOPB 00124). Image Credit: Journal of
910 Anatomy/Wiley.

911

912 **Figure 2** Skull of *Metoposaurus krasiejowensis* from the Upper Triassic of southwest Poland
913 (UOPB 01029) used in the histological study (A and B) and schematic drawings (C and D) of the
914 same with sectioning planes marked, in dorsal (A and C) and palatal views (B and D). In (C) and
915 (D), red lines indicate thin sections used in microstructural analysis; purple lines refer to thin
916 sections used in both microstructural analysis and cranial suture study; green lines indicate thin
917 sections used in cranial suture analysis. Scale bar equals 10 cm. Abbreviations: ec,
918 ectopterygoid; ex, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf,
919 postfrontal; pl, palatinum; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt,
920 pterygoid; qj, quadratojugal; sq1, squamosal 1; sq2, squamosal 2; st, supratemporal; t, tabular; v,
921 vomer.

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923 **Figure 3** General microstructure of skull bones of *Metoposaurus krasiejowensis* (UOPB 01029)
924 from the Upper Triassic of southwest Poland. A, nasal; B, postorbital; C, jugal; D, lacrimal; E,
925 prefrontal; F, parietal; G, postparietal; H, postfrontal; I, supratemporal; J, frontal; K, squamosal
926 1; L, tabular; M, squamosal 2; N, quadratojugal; O, parasphenoid; P, pterygoid; Q, vomer. Scale
927 bar equals 10 mm.

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929 **Figure 4** Estimated biomechanical loading as reconstructed on the basis of microstructural
930 characters (average bone thickness *vs* compactness), on sectioned regions of the skull of
931 *Metoposaurus krasiejowensis* (UOPB 01029) from the Upper Triassic of southwest Poland. Note
932 that the estimated values are relative and show merely if loading on any given region was higher
933 or lower (on the scale bar from red to blue, respectively). It is not possible to calculate the
934 objective amount of stress in this case. Black bars inside colour ellipses indicate the sectioning
935 places; the ellipses without bars are symmetric to section areas.

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

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

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

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950 **Figure 8** Von Mises stress results (in MPa) of bilateral (A), lateral biting (B) and of skull raising
951 system (C) in *Metoposaurus krasiejowensis* (UOPB 124) using a gape angle of 10 ° merged with
952 the model of biomechanical loading created on the basis of microstructural characters; skulls in
953 the background show FEA results; the outcome of histological reconstructions is illustrated as
954 oval forms, of different colours. Note that similar colours were used in FEA analysis and
955 histological estimates in order to illustrate how the general stress distribution in FEA and
956 histological analyses correlate; however, same colours do not signify the same stress values. In
957 FEA, the colours refer to objective values, while in histological models estimated values are
958 relative and show merely if the loading on any given region is higher or lower within a single
959 skull (on the scale bare from red to blue, respectively). Black bars inside colour ellipses indicate
960 the sectioning places; the ellipses without bars are symmetric to section areas. Image Credit for
961 FEA figure: Journal of Anatomy/Wiley.
962

Table 1(on next page)

The cranial sutures analyzed in the skull of *Metoposaurus krasiejowensis* from Late Triassic of Poland.

Table 1. The cranial sutures analyzed in the skull of *Metoposaurus krasiejowensis* from Late Triassic of Poland.

cranial sutures[1]	**number of samples**
maxilla-nasal	1
maxilla-lacrimal	2
maxilla-palatine	1
maxilla-vomer	1
vomer-palatine	2
interfrontal	2
frontal-postfrontal	1
jugal-postorbital	3
prefrontal-lacrimal	1
parietal-supratemporal	2
supratemporal-squamosal	1
squamosal-jugal	1
interpostparietal	2
jugal-ectopterygoid	1
pterygoid-ectopterygoid	2
pterygoid-parasphenoid	2
pterygoid-exoccipital	2

[1]For the detailed localization of the sections see Fig. 1 – green and purple lines.

Table 2(on next page)

The thickness and compactness of the dermal skull bones of *Metoposaurus krasiejowensis* from Late Triassic of Poland.

[1]The average thickness of entire bone was estimated in thin sections, expressed as an arithmetical average from three measurements of the thickness of a bone taken on the bottom of valleys and the top of ridges; [2]Compactness was estimated using the software Bone Profiler (Girondot and Laurin, 2003).

Table 2. The thickness and compactness of the dermal skull bones of *Metoposaurus krasiejowensis* from Late Triassic of Poland.

bone	average thickness (µm)[1]	compactness (%)[2]
nasal	4758	77.4
prefrontal	4256	78.5
lacrimal	5940	79.2
frontal	5549	76.3
postfrontal	3960	94.5
jugal	6940	87.8
postorbital	6940	82.6
parietal	3840	92.2
supratemporal (a)	4800	92.5
supratemporal (b)	2050	98.6
squamosal1	3915	89.1
squamosal2 (a)	4000	94.0
squamosal2 (b)	1600	98.7
quadratojugal	5610	78.6
postparietal	8670	80.7
tabular	10000	82.5
vomer	2925	54.7
parasphenoid (a)	4050	77.7
parasphenoid (b)	2100	91.0
pterygoid	5460	73.1

[1]The average thickness of entire bone was estimated in thin sections, expressed as an arithmetical average from three measurements of the thickness of a bone taken on the bottom of valleys and the top of ridges; [2]Compactness was estimated using the software Bone Profiler (Girondot and Laurin, 2003).

Figure 1(on next page)

Von Mises stress results (in MPa) of bilateral (A), lateral biting (B) and of skull raising system (C) in *Metoposaurus krasiejowensis* (UOPB 00124). ImageCredit: Journal of Anatomy/Wiley.

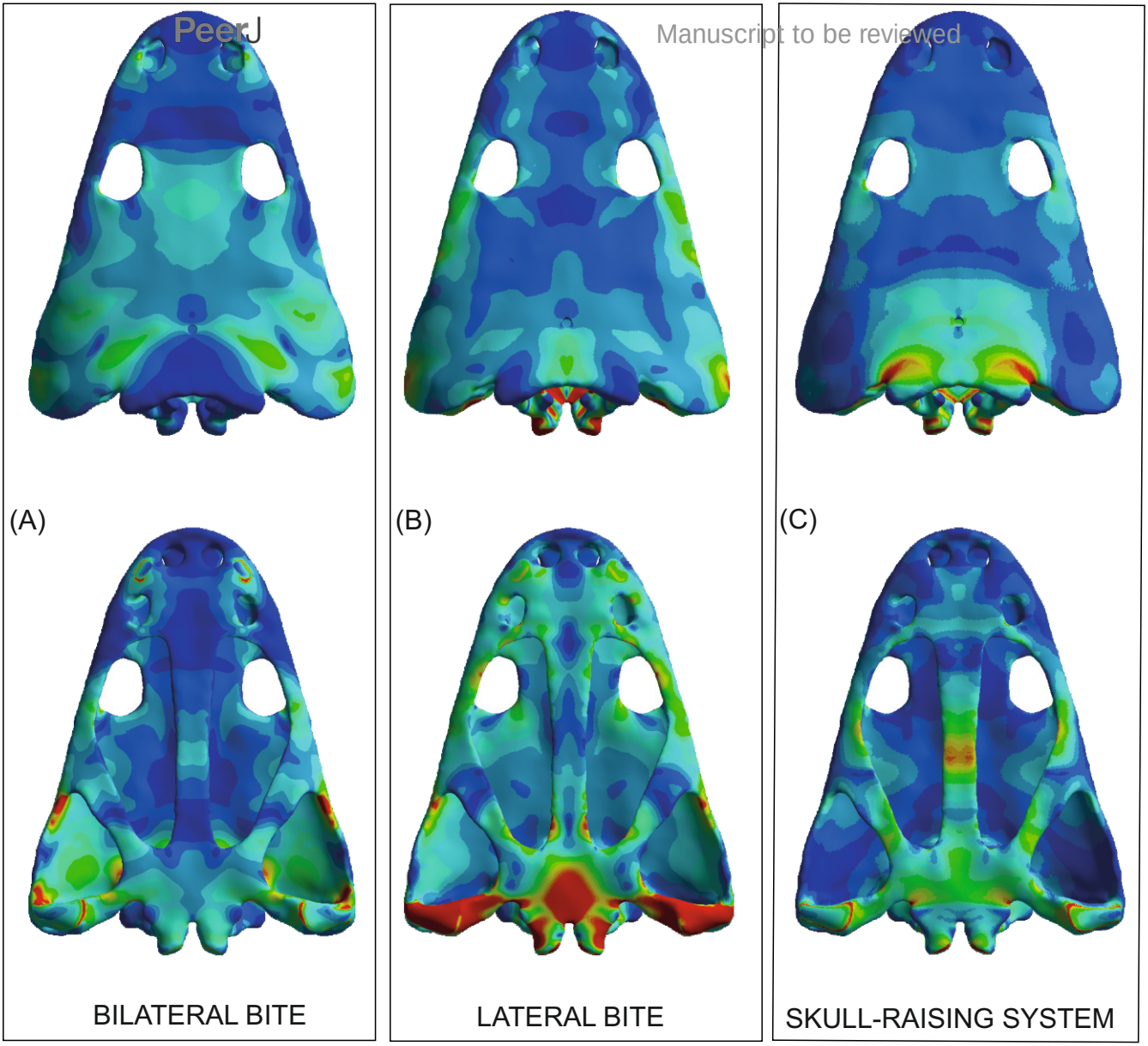


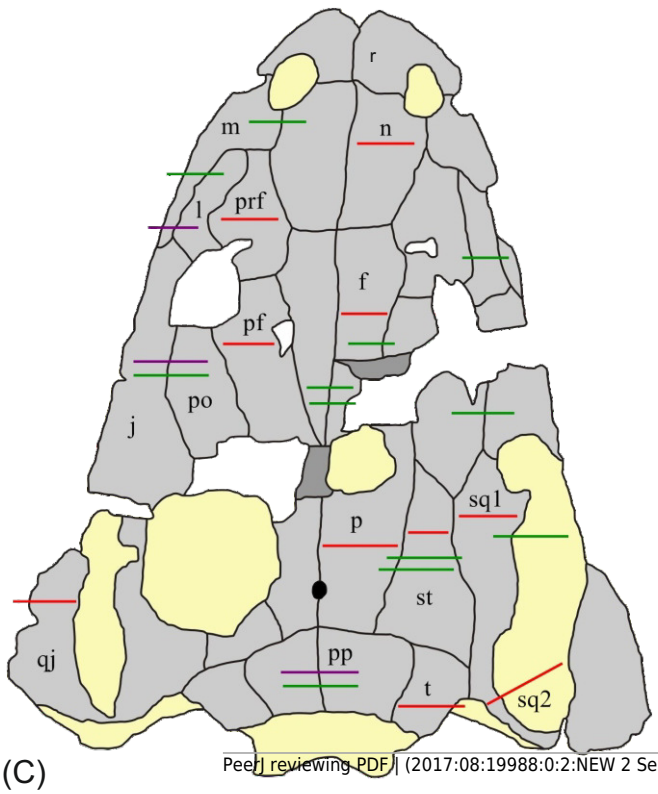
Figure 2(on next page)

Skull of *Metoposaurus krasiejowensis* from the Upper Triassic of southwest Poland (UOPB 01029) used in the histological study.

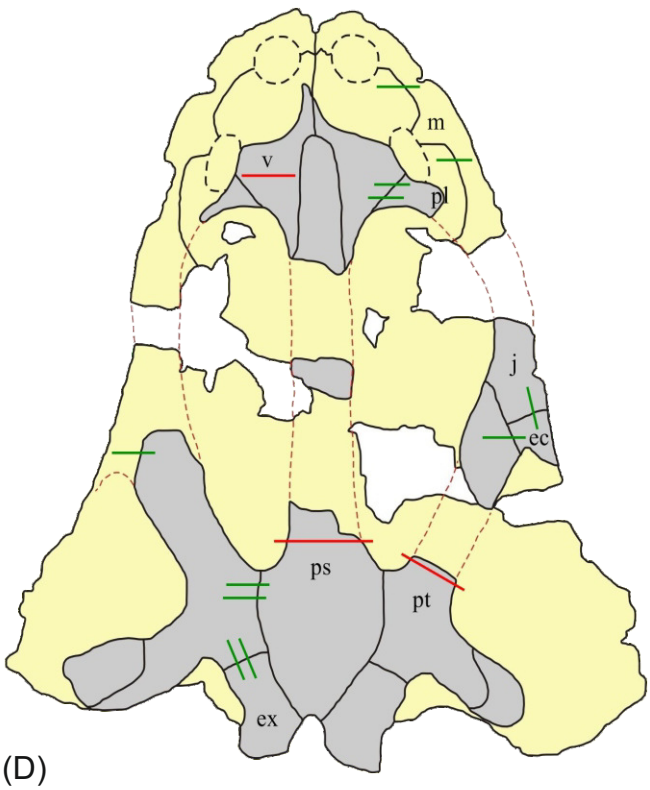
Skull of *Metoposaurus krasiejowensis* from the Upper Triassic of southwest Poland (UOPB 01029) used in the histological study (A and B) and schematic drawings (C and D) of the same with sectioning planes marked, in dorsal (A and C) and palatal views (B and D). In (C) and (D), red lines indicate thin 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. 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

(A)

(B)



(C)



(D)

Figure 3(on next page)

General microstructure of skull bones of *Metoposaurus krasiejowensis* (UOPB 01029) from 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. Scale bar equals 10 mm.

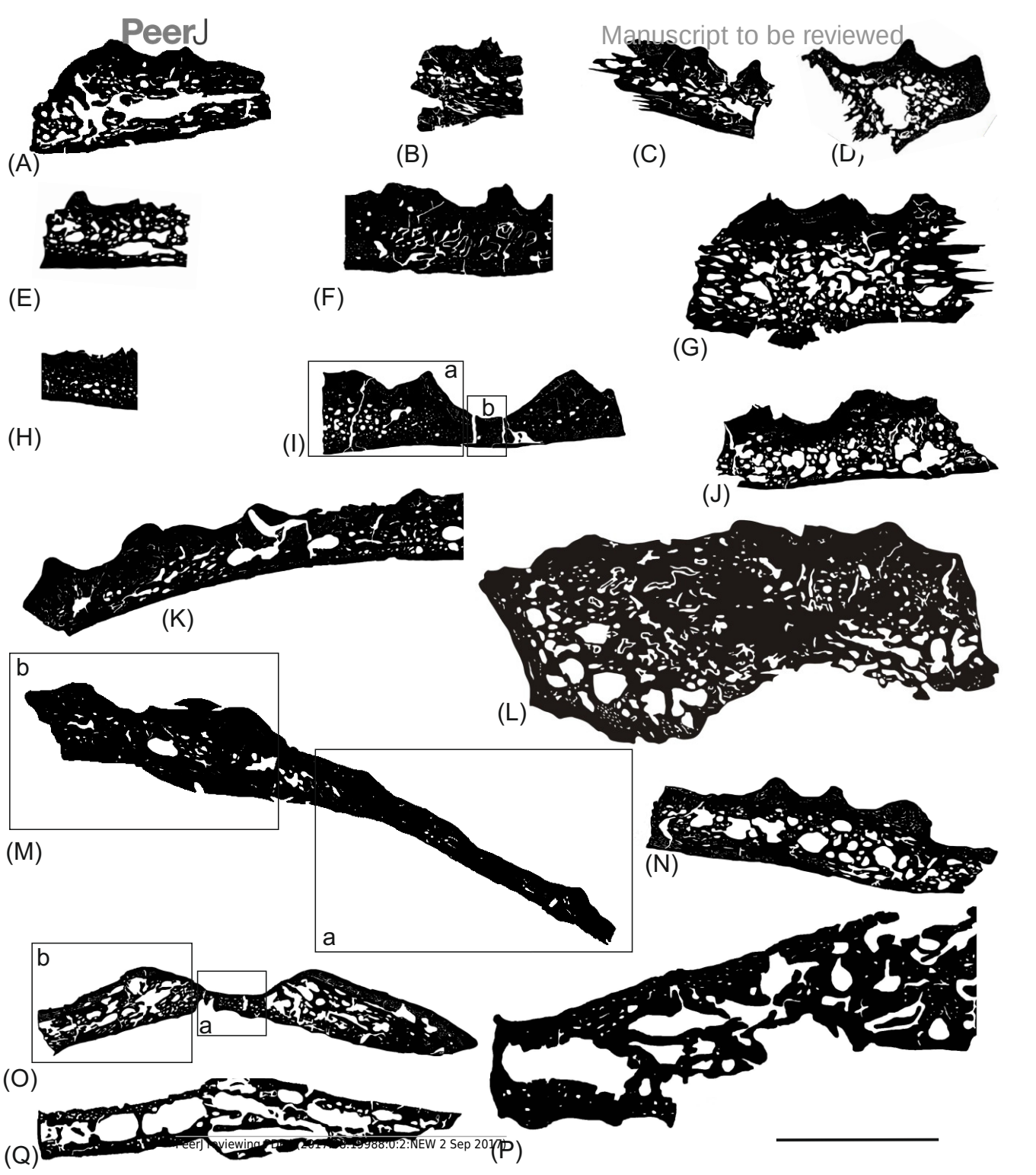
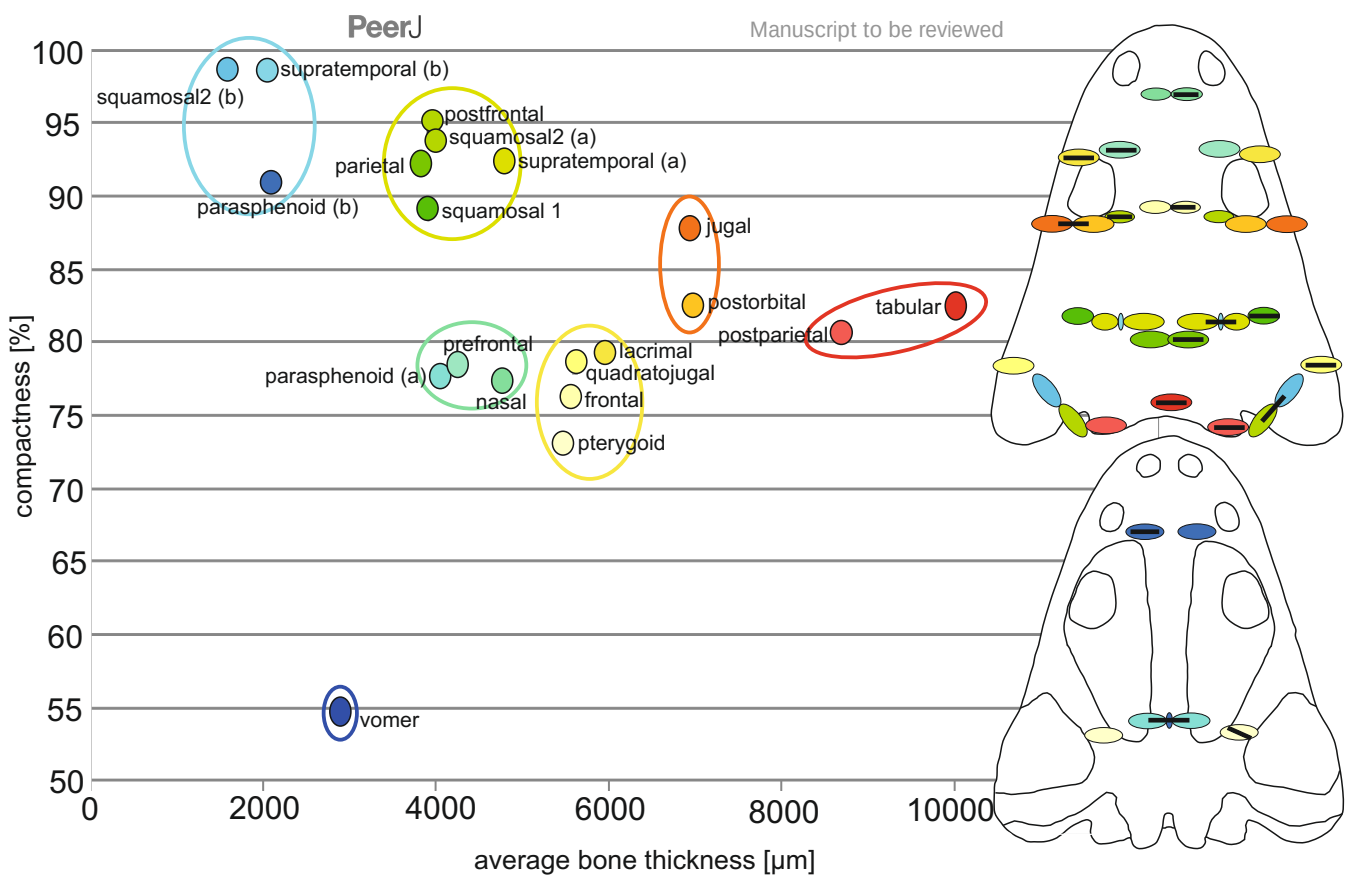


Figure 4(on next page)

Estimated biomechanical loading as reconstructed on the basis of microstructural characters (average bone thickness *vs* compactness), on sectioned regions of the skull of *Metoposaurus krasiejowensis*.

Estimated biomechanical loading as reconstructed on the basis of microstructural characters (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.


compactness [%]
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95
90
85
80
75
70
65
60
55
50
0
2000
4000
6000
8000
10000
average bone thickness [µm]
supratemporal (b)
squamosal2 (b)
parasphenoid (b)
postfrontal
squamosal2 (a)
parietal
supratemporal (a)
squamosal 1
jugal
postorbital
tabular
postparietal
prefrontal
parasphenoid (a)
nasal
lacrimal
quadratojugal
frontal
pterygoid
vomer
low
high
stress level as reconstructed from bone microanatomy

Figure 5(on next page)

Microphotography and drawings illustrating the morphology of selected cranial sutures in the skull of *Metoposaurus krasiejowensis.*

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.

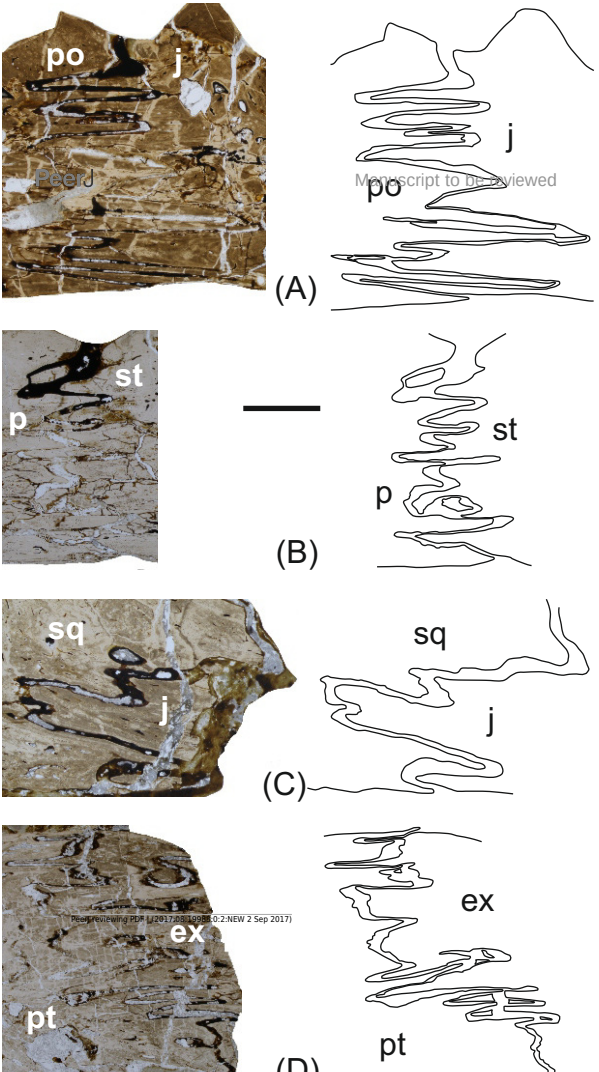
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Figure 6(on next page)

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

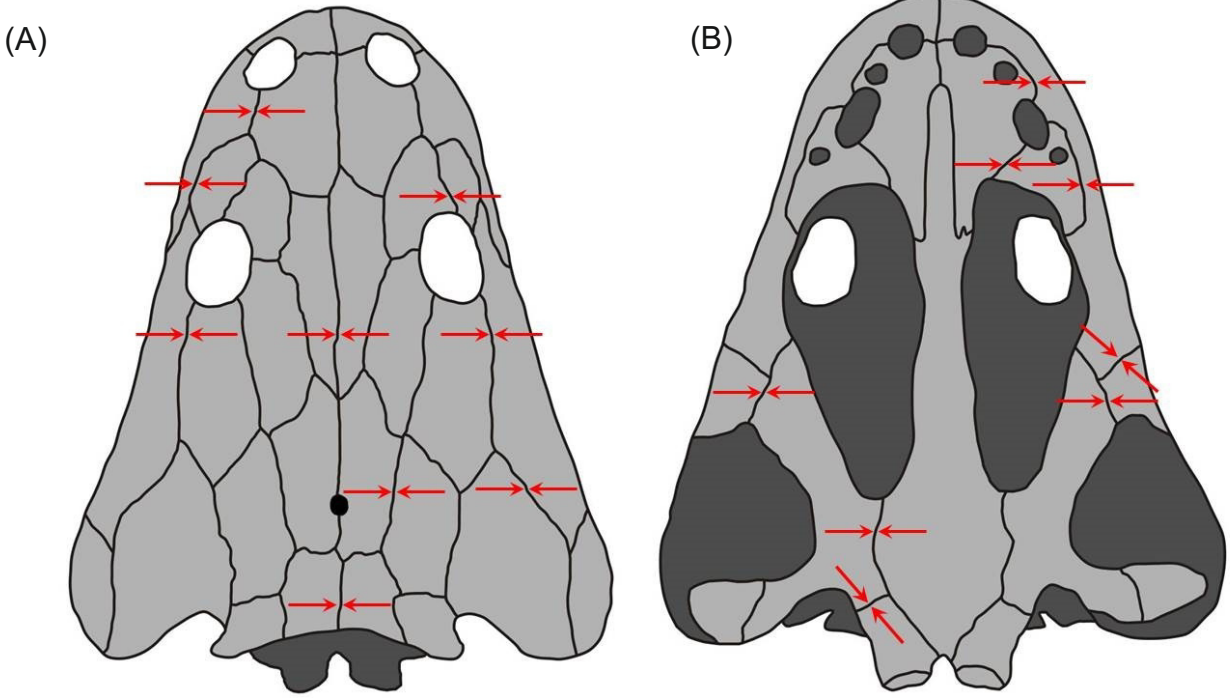
(A)
(B)

Figure 7 (on next page)

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.

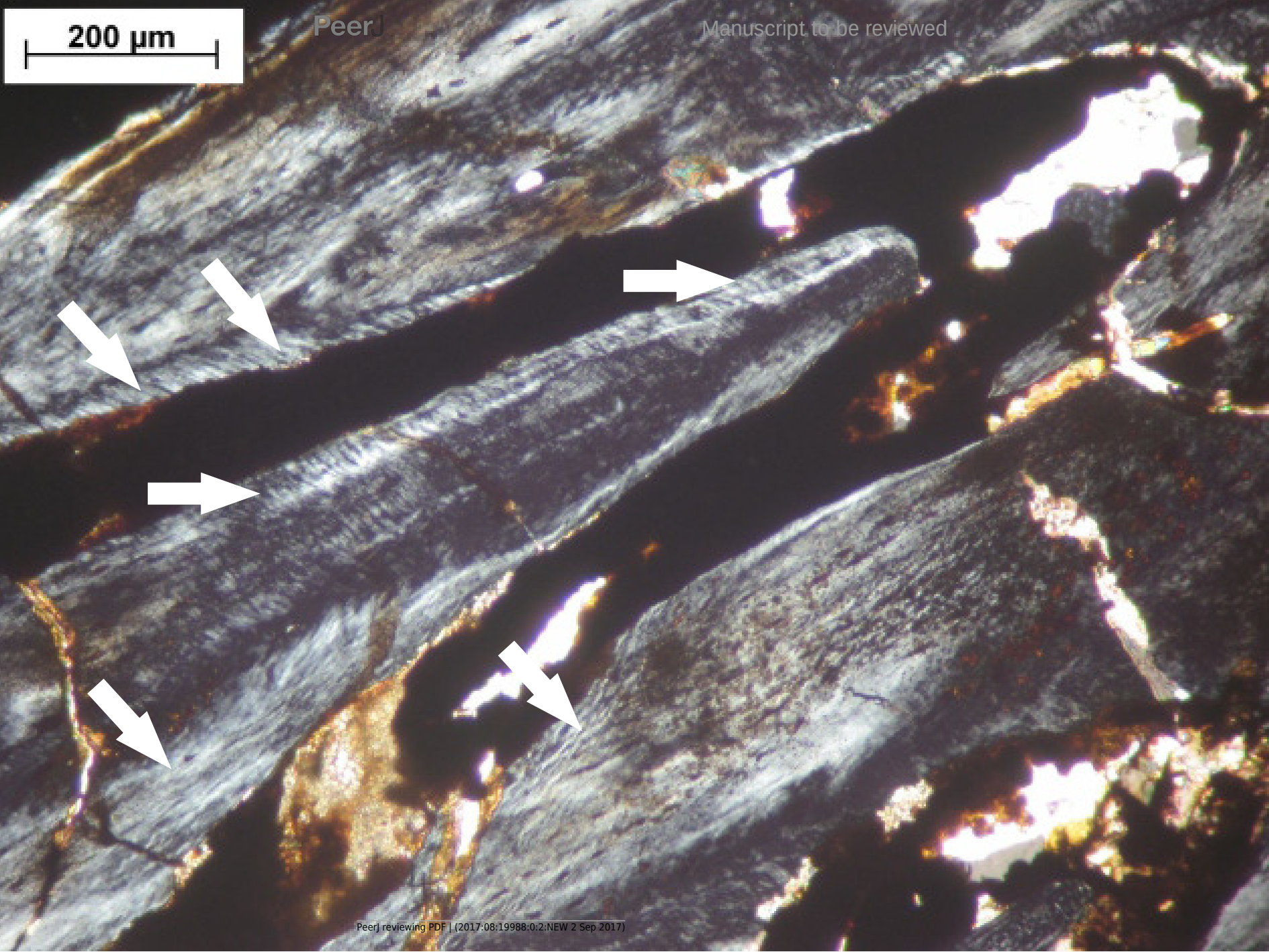

Figure 8(on next page)

Merging FEA with histology.

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 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, 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, respectively). Black bars inside colour ellipses indicate the sectioning places; the ellipses without bars are symmetric to section areas.