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# To be or not to be heavier: The role of dermal bones in the buoyancy of the Late Triassic temnospondyl amphibian *Metoposaurus krasiejowensis*

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**Abstract**

Stereospondyli are a clade of large aquatic temnospondyls known to have evolved a large dermal pectoral girdle. Among the Stereospondyli, metoposaurids in particular possess large interclavicles and clavicles relative to the rest of the postcranial skeleton. Because of the large size of these dermal bones, it was first proposed that they served as ballast during hydrostatic buoyancy control which assisted metoposaurids to live a bottom-dwelling mode of life. However, a large bone need not necessarily be heavy, for which determining the bone compactness becomes crucial for understanding any such adaptation in these dermal bones. Previous studies on the evolution of bone adaptations to aquatic lifestyles such as osteosclerosis, pachyostosis, osteoporotic-like pattern and pachyosteosclerosis have been observed in the long bones of secondarily aquatic amniotes. However, there are no known studies on the analysis of bone compactness in the dermal pectoral girdle of non-amniote taxa including Temnospondyli. This study looks at evidence of changes in bone mass adaptations in the dermal bones of the pectoral girdle of two stereospondyls occurring in the Late Triassic Krasiejów locality (Southwestern Poland), namely: *Metoposaurus krasiejowensis* and *Cyclotosaurus intermedius*. However, because of lack of research on bone compactness of temnospondyls in general, there is no existent frame of reference to infer bone mass increase (BMI) in the *M. krasiejowensis* samples, and thus the bone compactness results of this taxon are compared with that of the samples of *C. intermedius*. Results of this study indicate that the interclavicles of *M. krasiejowensis* partially evolved BMI-like condition rendering these bones to be heavy enough to get selected as ballast during hydrostatic buoyancy control. Additionally, *M. krasiejowensis* shared its habitat with *C. intermedius*, however, the dermal pectoral girdle sample of the latter taxon does not display signs of BMI-like condition. Furthermore, the absence of variation in hydrostatic buoyancy control in the ontogenetic series of interclavicles of *M. krasiejowensis* could imply lack of ontogenetic niche shift along the water column.

**KEYWORDS**
bone mass increase (BMI), clavicle, interclavicle, Krasiejów, Stereospondyli

## 1 | INTRODUCTION

Temnospondyli (Zittel, 1888) are a diverse group of non-amniotes tetrapods that originated in the Paleozoic (Early Carboniferous, 330 Ma) and survived until 115 Ma in the Early Cretaceous in the Mesozoic (Milner, 1990; Schoch, 2013, 2014). Regardless of their amphibious origins, temnospondyls recolonized, and decolonized both aquatic and terrestrial habitats several times in their evolutionary history (Schoch, 2014). During the Late Triassic, a group of temnospondyls within the clade Stereospondyli, the Metoposauridae, started dispersing in different regions of Pangea as known based on the current global distribution of the fossil taxa (Brusatte et al., 2015; Chakravorti & Sengupta, 2019; Fortuny et al., 2019; Gee & Jasinski, 2021; Gee & Reisz, 2018; Sulej, 2007). Metoposaurids are characterized by their anteriorly located orbits in the parabolic-shaped skull and massive dermal bones of the pectoral girdle; which are the interclavicles and clavicles (Brusatte et al., 2015; Buffa et al., 2019; Dutuit, 1976; Gee & Jasinski, 2021; Sulej, 2007).

Temnospondyli in general present high variation in the ratio between the sizes of these dermal elements of the pectoral girdle to the rest of the postcranial skeleton (Schoch, 2014). Even more, such variation is strikingly distinguishable among different temnospondyl lineages with different eco-morphological adaptations. In large aquatic stereospondyls, the size difference between the humeri and the dermal elements of the pectoral is higher than that of the non-stereospondyls (Gee & Reisz, 2018; Holmes et al., 1998; Schoch, 2008, 2014; Sulej, 2007; Sulej & Majer, 2005; Witzmann & Brainerd, 2017; Witzmann & Schoch, 2006). In groups of small terrestrial Temnospondyli, such as *Cacops* (Williston, 1910) and *Dendrerpeton* (Owen, 1853) the ratio of total length of interclavicle to that of the humerus approximately equals to 1:1 (Gee & Reisz, 2018) and 4:3, respectively (Holmes et al., 1998). In comparison to these, large Stereospondyli taxa like the metoposaurids and capitosaurids have interclavicle lengths that are three to four times larger than the humeri, respectively (Sulej, 2007; Sulej & Majer, 2005). Similar convergence is seen in dvinosaurian temnospondyl *Trypanognathus remigiusbergensis* (Schoch & Voigt, 2019), with the interclavicle three times longer than the humerus (Schoch & Voigt, 2019). Taking into account the increasing size difference of these dermal elements of the pectoral girdle and the corresponding humerus in aquatic Temnospondyli, it is important to investigate if these dermal elements have any role in aquatic adaptation.

Bones in general show dynamic aquatic adaptations in several tetrapod lineages (Taylor, 2000) at both morphological (De Buffrénil et al., 1990, 2010; Gray et al., 2007; Taylor, 2000) and microanatomical levels (De Buffrénil et al., 1990, 2010; Gray et al., 2007; Houssaye, 2009, 2013, 2014a, 2015, 2016; Kolb et al., 2011; Kriloff et al., 2008; Laurin et al., 2011; Sanchez et al., 2010). Aquatic bone adaptations are broadly classified into three different types, namely—osteosclerosis (Houssaye, 2009, 2013), osteoporosis (Houssaye et al., 2014b), and pachyostosis (De Buffrénil & Rage, 1993; Houssaye, 2009). All these bone adaptations eventually affect the

bone mass leading to bone mass increase (BMI) or decrease (BMD) (Houssaye et al., 2016; Taylor, 2000) which assists in buoyancy control during aquatic locomotion (Houssaye et al., 2016). Any secondarily aquatic amniote or anamniote taxa have to outweigh the effects of positive buoyancy or flotation (due to air-filled lungs and body fat in animals with blubber) in order to submerge underwater or attain neutral to negative buoyancy (Taylor, 2000). Hydrostatic buoyancy control is related to attaining neutral (suspended stance) or negative (submersion) buoyancy by changing bone mass whereas during hydrodynamic locomotion, the locomotion speed usually assists in regulating the position in the water column (Taylor, 2000). During hydrostatic buoyancy control, bones exhibiting BMI act as ballast facilitating submersion (Taylor, 2000). Previous studies have described metoposaurids as sedentary bottom dwellers of their freshwater habitats (Dzik et al., 2000; Murry, 1989; Ochev, 1966) which could imply that metoposaurids could have evolved hydrostatic buoyancy control since their habitat was mostly a shallow water floodplain environment (Jewuła et al., 2019). Most importantly, Fraas (1913) first proposed that the massive dermal pectoral girdle bones of metoposaurids acted as a ballast. However, a thick and large bone does not necessarily have to be heavy. In order to be heavy, the mass of a bone is always affected by its compactness, hence, determining bone compactness is crucial for estimating BMI.

Until now, there are no known data on bone compactness of temnospondyl dermal pectoral girdle which might reveal a research bias on aquatic bone adaptations for these anamniotes. Most research on previously mentioned aquatic bone adaptations (osteosclerosis, osteoporotic-like pattern, BMI or BMD, pachyostosis, and pachyosteosclerosis) are based on the long bones of amniotes (Amson et al., 2014; Canoville & Laurin, 2010; Canoville et al., 2016; Cooper et al., 2012; De Buffrénil et al., 1990, 2010; Gray et al., 2007; Houssaye, 2009, 2013, 2014a, 2015, 2016; Hugi et al., 2011; Kolb et al., 2011; Kriloff et al., 2008; Quemeneur et al., 2013; Sanchez et al., 2010). Furthermore, only a few studies have been conducted on the aquatic bone adaptations in anamniote taxa at the microanatomical level (Canoville & Chinsamy, 2015; Lennie et al., 2021; Mukherjee et al., 2010; Sanchez et al., 2010; Steyer et al., 2004). Mukherjee et al. (2010) sheds light on the terrestrial lifestyle of trematosaurid temnospondyls from India, using description of local microanatomical variation. Other studies such as Sanchez et al. (2010) used novel microanatomical and histological parameters of the stylopod elements of manus and pes of various Temnospondyli to elucidate niche specializations. For example, several Stereospondyli taxa (*Gerrothorax* spp. Nilsson, 1934; *Benthosuchus sushikini* Efremov, 1929; *Wetlugasaurus angustifrons* Riabinin, 1930; *Mastodonsaurus giganteus* Von Jäger, 1828; *Dutuitosaurus ouazzoui* Dutuit, 1976) showed highly remodeled stylopod elements in comparison to *Eryops* (Cope, 1877) and other basal Stereospondyli which still preserved a predominantly compact cortex composed of primary bone. This suggests a more aquatic mode of life for the derived stereospondyls as microanatomical specializations became important to adapt to a watery habitat (Sanchez et al., 2010). Nevertheless, histological and microanatomical studies

performed on the dermal elements do exist for non-amniote tetrapods (Konietzko-Meier et al., 2018; Witzmann, 2009; Witzmann & Soler-Gijón, 2010; Witzmann et al., 2010). However, the focus of the study by Witzmann (2009) was a novel and comprehensive histological description rather than the microanatomy of the dermal bone samples of several non-amniotes. Furthermore, studies on the dermatocranium of *Metoposaurus krasiejowensis* (Gruntmejer et al., 2016, 2019; Konietzko-Meier et al., 2018) showed that the histology of the skull bones is strongly related to the local biomechanical loading and varies considerably in different regions of the skull roof. Hence, there is a lack of research on the role of dermal bones of the pectoral girdle of these taxa associated with aquatic lifestyle.

The aim of this study is to test if the dermal bones of pectoral girdle of the *Metoposaurus krasiejowensis* (Sulej, 2002) acted as a ballast during hydrostatic buoyancy control and if an ontogenetic niche shift existed among *M. krasiejowensis* individuals along the water column. It is noteworthy to enquire about the role of these dermal bones in the niche shift across ontogenetic stage because skeletal adaptations play an important role in shaping the lifestyle of ontogenetic stages in Temnospondyli (Schoch, 2014). Furthermore, to assess the bone compactness of the interclavicles and clavicles of *M. krasiejowensis*, it needs to be compared with the same bones from other closely related taxa in order to observe any BMI. The Late Triassic locality of Krasiejów yields two Stereospondyli taxa, *M. krasiejowensis* and *Cyclotosaurus intermedius* (Sulej & Majer, 2005), where both taxa could have occupied two different niches along the water column. Hence, the compactness results of these bones of a metoposaurid species have been compared to a capitosaurid temnospondyl.

## 2 | MATERIALS AND METHODS

### 2.1 | Data acquisition

The samples for this study originate from the Late Triassic locality of Krasiejów, Poland. In total three interclavicles and a fragmentary clavicle of *Metoposaurus krasiejowensis*, as well as a fragment of the interclavicle and clavicle from *Cyclotosaurus intermedius* were used (Table 1). *M. krasiejowensis* interclavicles were measured along the long axis

(cranio-caudal axis) and based on the partially articulated specimen—UOPB 00097 (Konietzko-Meier et al., 2020) the incomplete extremities of the interclavicles used for microanatomical analysis were estimated. The relative age of each dermal bone was estimated based on the age of the corresponding humerus and/or femur calculated from the skeletochronological data of *M. krasiejowensis* and *D. ouazzoui* from Teschner et al. (2018), Konietzko-Meier and Klein (2013) and Steyer et al. (2004). The ages of the interclavicles were used to categorize the microanatomical sample into an ontogenetic series of *M. krasiejowensis* individuals (Table 1). Age class estimation of microanatomical sample of interclavicles of *M. krasiejowensis* represent three broad age classes: early juvenile (3–5 years), late juvenile (6–8 years), and adult (10–12 years) as shown in Table 1. These age classes represent the ontogenetic series of interclavicles. No age class estimation of both the *C. intermedius* samples and the clavicle of *M. krasiejowensis* were performed due to low sample size and fragmentary nature.

All sampled bones were sectioned along the transverse axis to produce histological thin sections. Thin sections of the interclavicles of *M. krasiejowensis* were produced using the histological core drill method (Stein & Sander, 2009), and each interclavicle was core drilled at five different positions (Ae, anterior extreme; Ai, anterior intermediate; Co, center of ossification; Cr, center right; Po, posterior; Figure 1a). The sectioning location of the *C. intermedius* interclavicle (Figure 1b) corresponds to the position Co of the core drill location of *M. krasiejowensis* interclavicles (Figure 1a). The assigning of *C. intermedius* interclavicle fragment as posterior is deduced from the interclavicle shape of *C. intermedius* provided in Sulej and Majer (2005). Additionally, partial posterior ends of two clavicles, each belonging to *M. krasiejowensis* (Figure 2a) and *C. intermedius* (Figure 2c), respectively, were used for microanatomical analyses. For the *M. krasiejowensis* clavicle, histological thin sections along the transverse axis were directly used from the collection of University of Opole (Figure 2a). The shape of the clavicles- UOPB 00144 (Figure 2a) and UOBS 02807 (Figure 2c) are illustrated with a simplified figure of *M. krasiejowensis* clavicle (Figure 2b). The sectioning position of the *C. intermedius* clavicle approximately corresponds to section P4 (P, posterior) of *M. krasiejowensis* clavicle (Figure 2).

Post sectioning, thin sections were ground using silicon carbide of varying grit sizes (400–600). Furthermore, grinding was done until the birefringence of the different bone tissues were not clearly

**TABLE 1** List of samples used for this study and their estimated ontogenetic stages

| Catalog number | Taxa | Anatomical part | Estimated ontogenetic stage |
|---|---|---|---|
| UOBS 02486 | *Metoposaurus krasiejowensis* | Interclavicle | Early juvenile |
| UOBS 02485 | *M. krasiejowensis* | Interclavicle | Late juvenile |
| UOBS 02473 | *M. krasiejowensis* | Interclavicle | Adult |
| UOPB 00144 | *M. krasiejowensis* | Clavicle | Unknown |
| UOBS 02585 | *Cyclotosaurus intermedius* | Interclavicle | Unknown |
| UOBS 02807 | *C. intermedius* | Clavicle | Unknown |

Abbreviations: UOBS, University of Opole, Department of Biosystematics; UOPB, University of Opole, Institute of Biology.
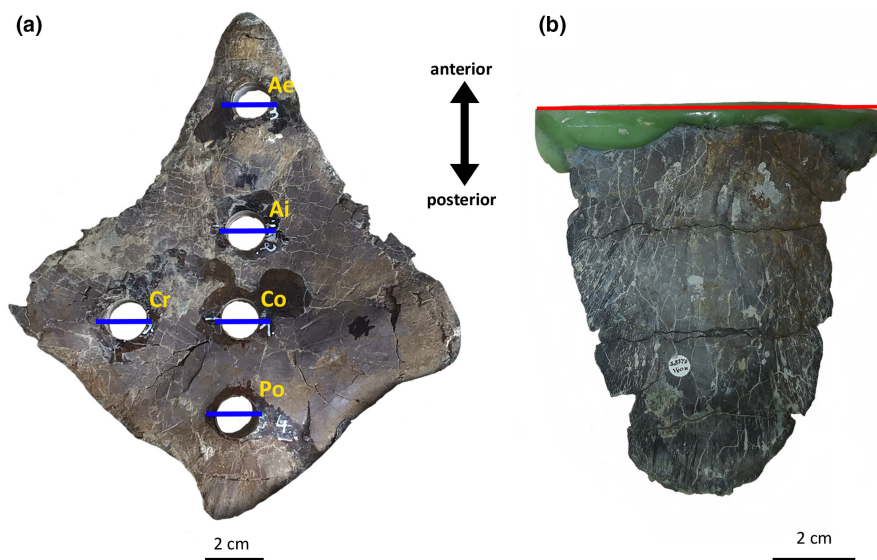
**FIGURE 1** Interclavicle samples of *Metoposaurus krasiejowensis* (a) and *Cyclotosaurus intermedius* (b) with sectioning plane and location. (a) UOBS 02486 (dorsal view) with core drill sites named; Ae, anterior extreme; Ai, anterior intermediate; Co, center of ossification; Cr, center right; Po, posterior. (b) UOBS 02585 (dorsal view). Blue lines show the plane of sectioning across extracted cores in (a) and red line shows sectioning plane and location in (b). Green material is the resin used to stabilize specimen (b) prior to sectioning

visible under the lambda filtered double-polarized view of a LEICA DM LP polarizing light microscope (© 2022 Leica Microsystems). The thicknesses of the thin section were measured along the dorsoventral axis using a Vernier's caliper (total length of the main scale: 150 mm, the accuracy of Vernier scale up to 0.02 mm). Since the dermal bone sections have ridges and valleys along the external cortex, the distance between six points along the external and internal cortex were chosen that marked the thicknesses in each section. These six points were placed by considering the straight-line distance between the highest point (tallest ridge), the lowest point (deepest valley), and an intermediate point (small ridge or shallow valley) from the external cortex to the corresponding points on the outer edge of internal cortex. The mean of these distances served as the thickness of each section. These thicknesses from thin sections and area of the interclavicles (Figure S1) were used to calculate the volume of the same (Supporting Information S1). Areas of other samples were not calculated due to their fragmentary nature. Thin sections were scanned with Epson Perfection 750 V PRO (© 2022 Seiko Epson) scanner. Further, the scanned images were imported to Autodesk Sketchbook (© Autodesk Inc.) and converted to binary (black and white) images using the pen and color filling tool. Prepared binary images were then converted into a jpeg file format and exported to a custom pixel counting software called BW-Counter (© Peter Göddertz, University of Bonn). This software measures the percentage of bone compactness and porosity from the binary images by calculating the percentage of only black and white pixels, respectively. Additionally, it does not consider pixels of any other color. For the binary thin sections of the clavicle of *M. krasiejowensis*, only the blade of the clavicle (excluding the dorsal process, anterior plate, and ascending crest) has been considered for microanatomical analysis. Additionally, the binary thin sections

of the clavicle blade have been divided into three regions (medial, middle, and lateral region) for compactness analysis.

## 2.2 | Data analysis

To test the significance of the linear correlation between bone thickness and bone compactness for each specimen across the ontogenetic series, linear regression models were performed from the compactness and thickness values using the Data Analysis function in Microsoft Excel 2007 (© 2006 Microsoft Corporation). The term effective compactness is defined as the changing compactness with respect to changing bone thickness, quantified as the ratio of compactness to thickness. Quantified effective compactness for every section of each bone was used to calculate the mean effective compactness of each bone. Since the software BW-counter already considers the area covered by black and white pixels to quantify mere compactness, the effective compactness further takes into account the effect of thickness in these compactness values obtained from this software. It is noteworthy to mention the importance of this relative comparison because the thickness varies significantly in each homologous region of all the interclavicles (Figure 3). This varying thickness occurs due to the different number of ridges and valleys along the external cortex for the homologous regions of the ventral surface of interclavicles. For example, if two sections from two interclavicles from the same region are compared only based on mere compactness, the analysis remains incomplete as one of them may lack additional ridges which could attribute to reduced compactness for the same. Furthermore, effective compactness is important to observe the variation of bone compactness along the ontogenetic series that is affected by the thickness of each section which is dependent on minor changes in the
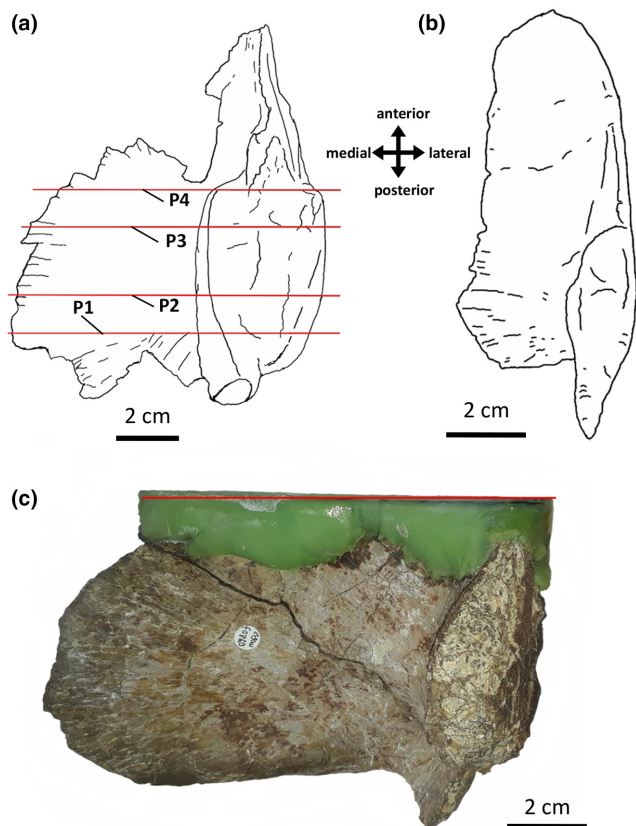
**(a)**

**(b)**

anterior

medial ←→ lateral

posterior

P4

P3

P1    P2

2 cm

2 cm

**(c)**

2 cm

**FIGURE 2** Clavicles of *Metoposaurus krasiejowensis* (a, b) and *Cyclotosaurus intermedius* (c). (a) Illustration of UOPB 00144 (dorsal view) with sectioning sites named; P1, P2, P3, P4; P, posterior. (b) Illustration of clavicle (dorsal view) of *M. krasiejowensis*. (c) UOBS 02807 (dorsal view). Red lines show the sectioning plane and location in (a) and (c). Green material is the resin used to stabilize specimen (c) prior to sectioning

ventral ornamentation. For the diagnosis of the normal distribution of effective compactness values, a Shapiro–Wilk normality test was conducted. To further observe the variation of effective compactness across the ontogenetic series, a Kruskal–Wallis rank sum test along with confirmatory permutation ANOVA would be used to observe any variation in effective compactness. All tests were performed using the software R (© RStudio Version 1.4.1103). For specific test packages and scripts see Supporting Information S2.

## 3 | RESULTS

### 3.1 | Qualitative microstructure variability across the samples

#### 3.1.1 | Interclavicles of *M. krasiejowensis* and *C. intermedius*

The interclavicle sections of *M. krasiejowensis* exhibit clear microanatomical variability inside one bone and between relative sectioning planes from different bones. The posterior-most position (position

Po; Figure 3) in all the interclavicles exhibit low compactness and high thickness. Similarly, a low variability in compactness is observed between the sections from the posterior region (position Co, Cr, and Po). The anterior region (position Ai and Ae) is thinner and exhibit high compactness (Figure 3). Additionally, position Co, being the ossification center of the interclavicle, has lower compactness than the anterior region (position Ai and Ae).

The relative compactness of the interclavicle section of *C. intermedius* (Figure 4a) is lower than the position Co (Figure 3) of all three interclavicles of *M. krasiejowensis*. Comparatively, the thickness of the *C. intermedius* section is higher than the section thickness at position Co of *M. krasiejowensis* interclavicle. Furthermore, the *C. intermedius* interclavicle (Figure 4a) has thinner external and inner cortices than *M. krasiejowensis* (Figure 3).

#### 3.1.2 | Clavicles of *M. krasiejowensis* and *C. intermedius*

There is no prominent visual difference in the porosity among the clavicle sections of *M. krasiejowensis* (Figure 5). Nevertheless, the medial region of all the clavicle sections depicts higher bone compactness in comparison to other regions, with the lateral region being the least compact (Figure 5). In comparison to the section P4 of the clavicle of *M. krasiejowensis* (Figure 5b), the *C. intermedius* clavicle section has higher porosity with thin cortices (Figure 4b). However, the medial region of the *C. intermedius* section is more compact (Figure 4b) than the medial region in section P4 (Figure 5b). Additionally, the *C. intermedius* section has organized porosity in both external and internal cortices with dorsoventrally compressed pores (Figure 4b). The vascularization in the *M. krasiejowensis* section is sparse in both external and inner cortices (Figure 5b) relative to *C. intermedius*. Moreover, in the *C. intermedius* clavicle, the middle region porosity is more extensive in the dorsoventral direction relative to the medio-lateral axis; with the medial region having the least amount of erosional porosity but with a significantly higher vascular porosity (Figure 4b). In contrast to this, all *M. krasiejowensis* sections have a higher extension of middle region porosity in the mediolateral axis than dorsoventral, leading to thick cortices with even the medial side having a prominent middle region (Figure 5).

### 3.2 | Quantitative compactness variability across the samples

#### 3.2.1 | Interclavicles of *M. krasiejowensis*

All interclavicle sections show a similar tendency of decrease in bone compactness with the increasing thickness (Figure 6) belonging to different age classes (Table 1). This observation is reinforced by the linear regression analysis (Table 2), which shows a significant
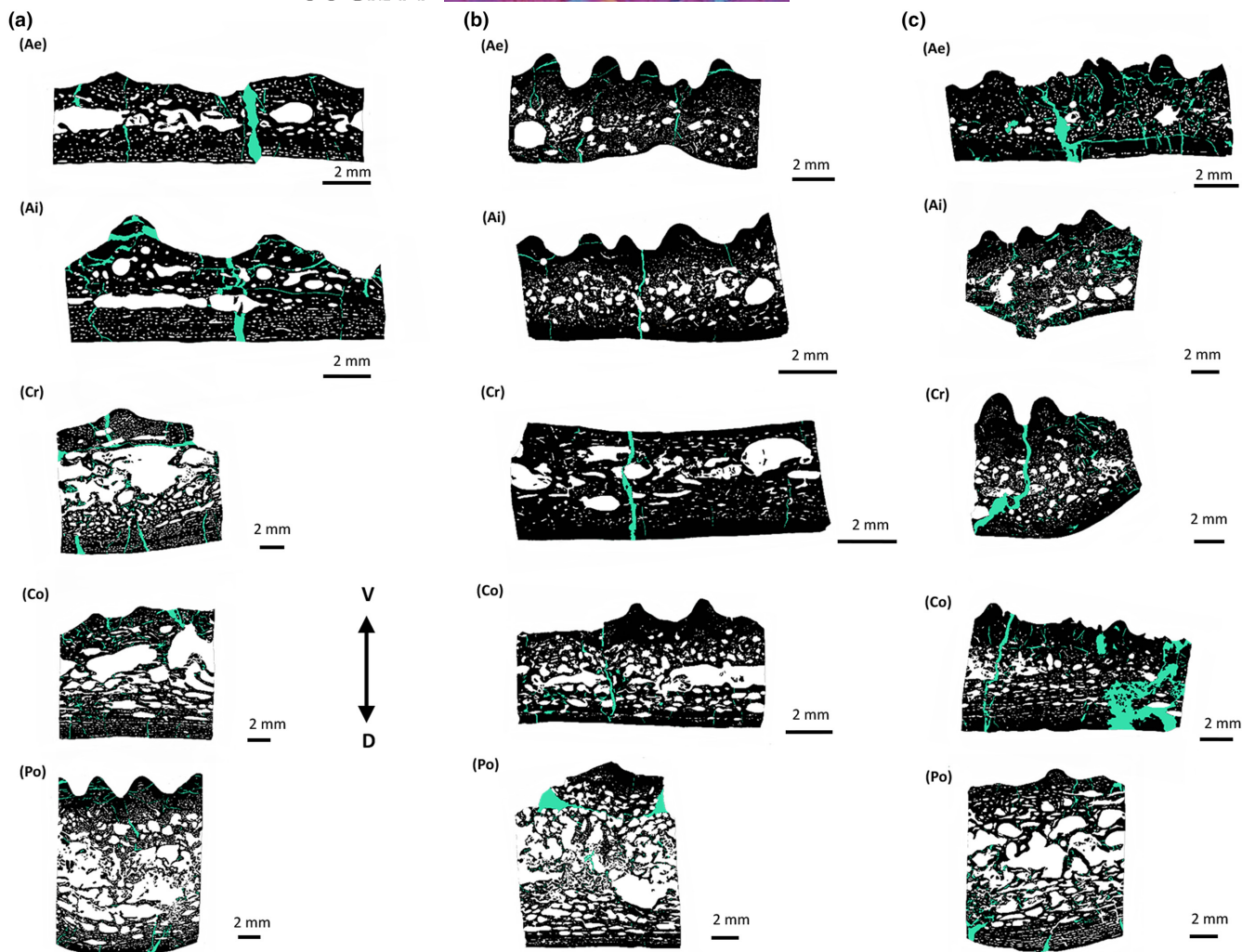
**FIGURE 3** Schematic binary transformed illustrations indicating microanatomical variability in the ontogenetic series of interclavicles of *Metoposaurus krasiejowensis*. Transverse core sections of (a) UOBS 02473 (adult), (b) UOBS 02485 (late juvenile), and (c) UOBS 02486 (early juvenile) with the corresponding core positions shown as; Ae, anterior extreme; Ai, anterior intermediate; Co, center of ossification; Cr, center right; Po, posterior. D, dorsal; V, ventral. Black colored region represents bone, white represents biological pore and cyan corresponds to taphonomic/artificial cracks and background

negative correlation ($p \leq 0.05$) between the thickness and compactness of each interclavicle. Positions Ai and Ae are the most compact and thinnest regions whereas position Po is the least compact but the thickest region. This implies that the anterior ends of the interclavicles are much more compact than the posterior ends (Figure 6) and is consistent with the qualitative evidence in the microstructure where a highly compact anterior region is observed relative to the posterior region (Figure 3). In the adult individual (Figure 6a), there is high compactness variability between anterior (positions Ai and Ae) and central regions (positions Co and Cr). Comparatively, in the juvenile specimens- UOBS 02485 (Figure 6b) and UOBS 02486 (Figure 6c), the anterior end does not have a higher compactness difference than the center.

Across the ontogenetic series, the middle region (positions Co and Cr) of interclavicles has the highest variability in effective compactness (Figure 6). Additionally, position Po despite being the least compact position has minimum compactness greater than 50% for all ontogenetic stages (Figure 6). The distribution of quantified effective compactness across the ontogenetic series was non-normal from the significant result ($p = 0.017$) of the Shapiro–Wilk normality test (Supporting Information S2). Additionally, the results of Kruskal–Wallis test ($p = 0.92$) and confirmatory permutation ANOVA ($p = 0.98$) show that variation in mean effective compactness across the ontogenetic series is not significant (Supporting Information S2). Moreover, there is a distinct negative correlation between the increasing volume of the interclavicles and their mean compactness (Figure 7a). This is reinforced by the significant ($p = 0.0075$) result of linear regression analysis for the volume versus compactness graph (Figure 7a). However, the lack of effective compactness is not well projected in the boxplot (Figure 7b) where the adult specimen shows high variation in the range of effective compactness. This can be attributed to the wide compactness distribution of compactness positions in the adult specimen (Figure 6a).
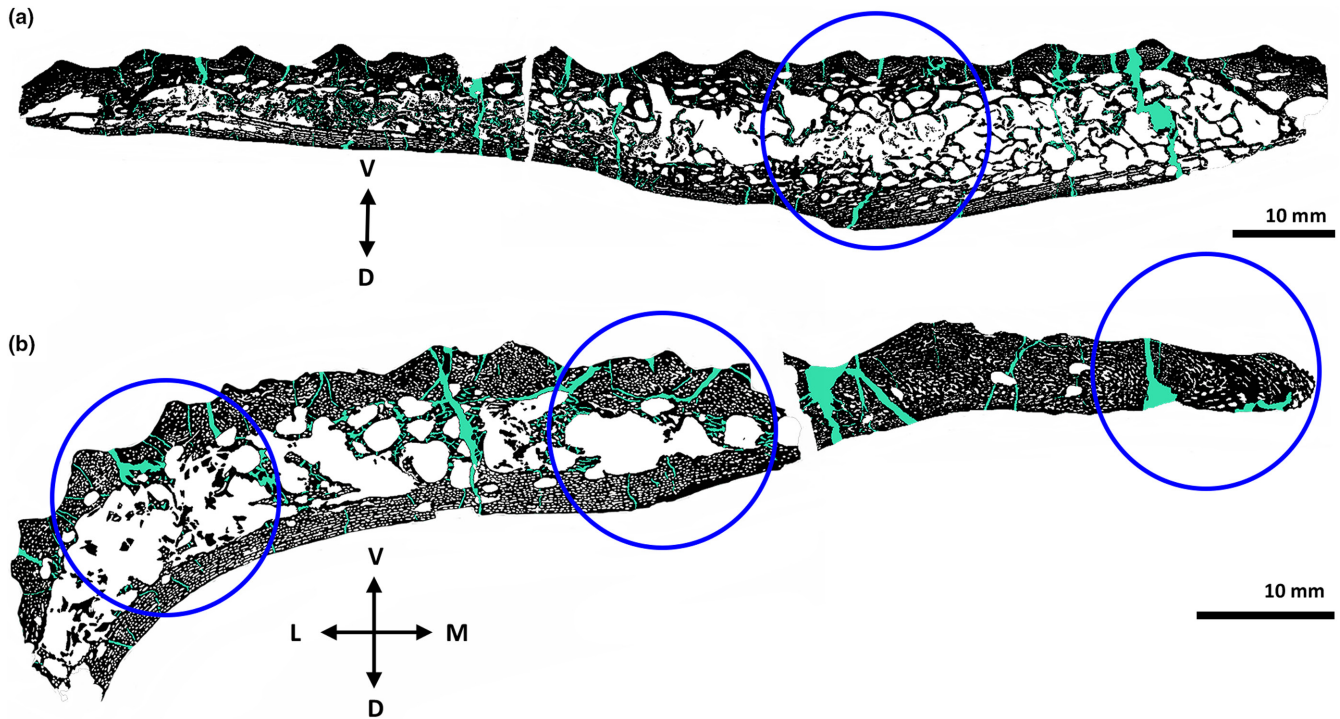
**FIGURE 4** Schematic binary transformed illustration indicating microanatomical variability in the transverse plane of interclavicle (a) and clavicle (b) of *Cyclotosaurus intermedius*. (a) interclavicle (UOBS 02585). (b) clavicle (UOBS 02807). Blue circles show the comparative position of *C. intermedius* samples with that of *Metoposaurus krasiejowensis*. D, dorsal; L, lateral; M, medial; V, ventral. Black colored region represents bone, white represents biological pore and cyan corresponds to taphonomic/artificial cracks and background
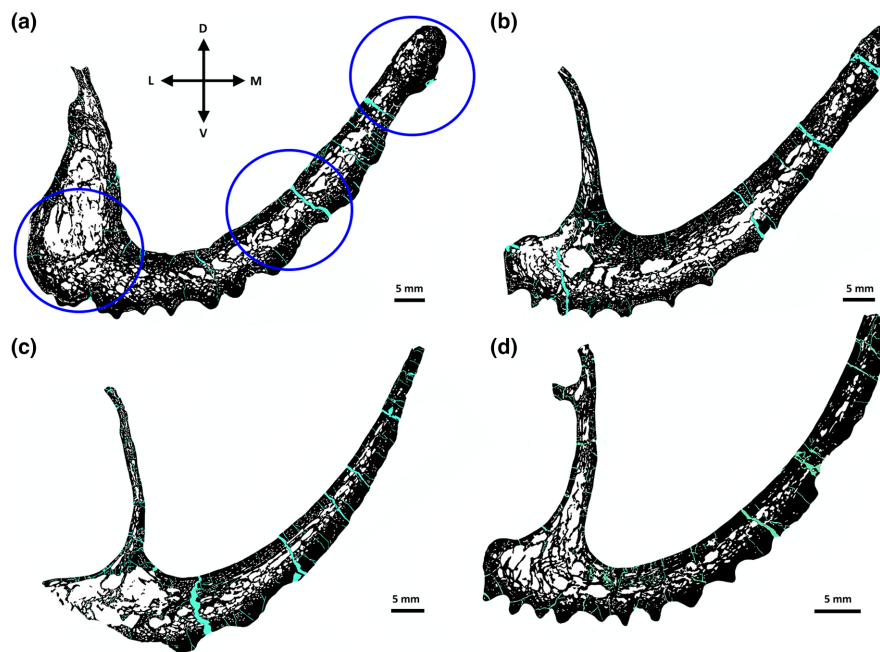


**FIGURE 5** Schematic binary transformed illustration indicating microanatomical variability in the transverse plane of the clavicle (UOPB 00144) of *Metoposaurus krasiejowensis*. (a) Section P1. (b) Section P2. (c) Section P3. (d) Section P4. Blue circles show the regions of the clavicle (medial, middle, and lateral) used for compactness quantification. D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Black colored region represents bone, white represents biological pore and cyan corresponds to taphonomic/artificial cracks and background
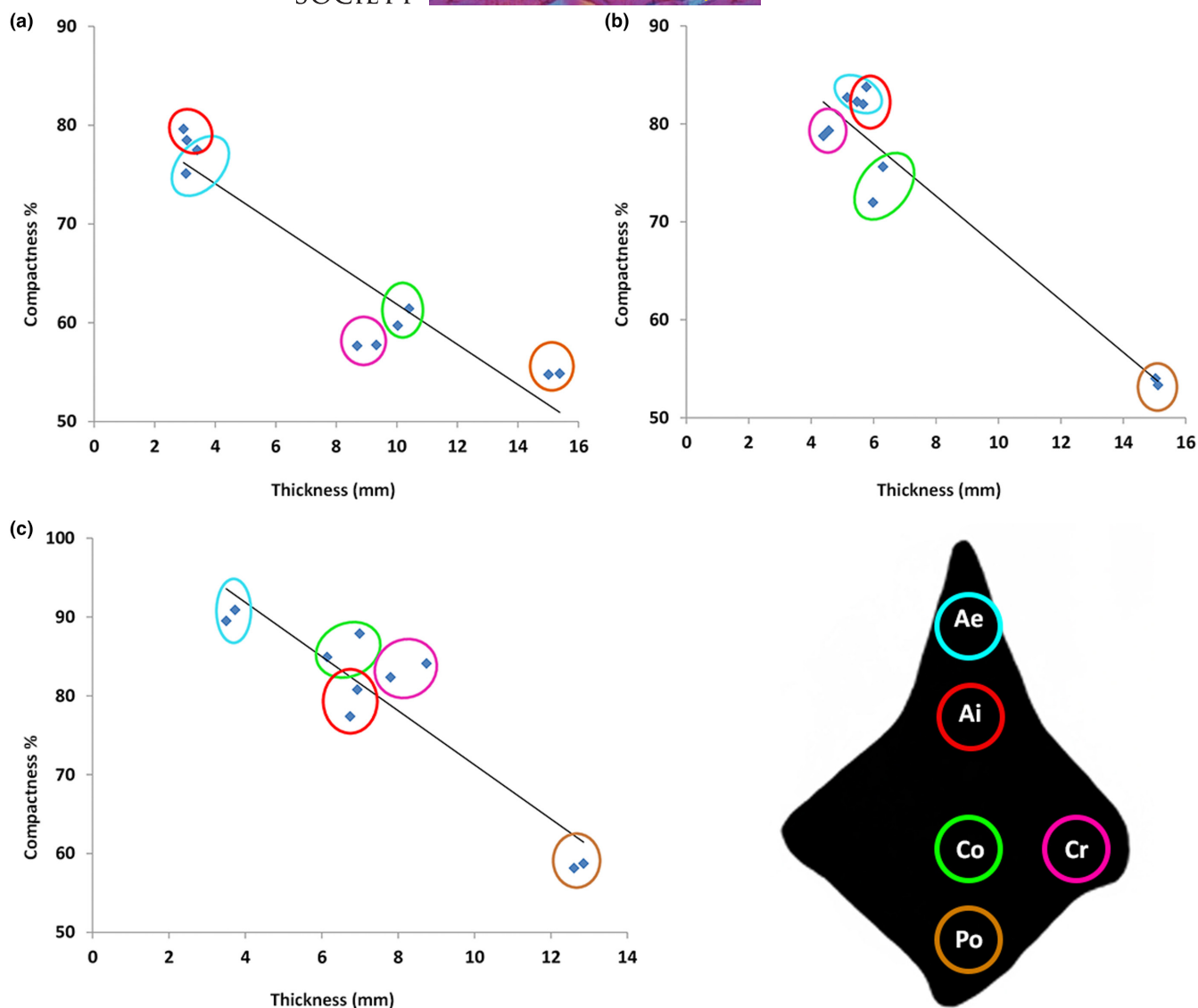
**FIGURE 6** Effective compactness in the sampled interclavicles of *Metoposaurus krasiejowensis* for microanatomical analysis. (a) UOBS 02473 (adult). (b) UOBS 02485 (late juvenile). (c) UOBS 02486 (early juvenile). Silhouette of *M. krasiejowensis* interclavicle with sectioning positions marked in colors that correspond to the colored circles in (a–c). Ae, anterior extreme; Ai, anterior intermediate; Co, center of ossification; Cr, center right; Po, posterior

**TABLE 2** Linear regression analysis of effective compactness for interclavicles of *Metoposaurus krasiejowensis*

| Ontogenetic age group | Interclavicle catalog number | $R^2$ | Slope | *p*-value |
| --- | --- | --- | --- | --- |
| Adult | UOBS 02473 | 0.87 | −2.03 | $8.24 \times 10^{-5}$ |
| Late juvenile | UOBS 02485 | 0.91 | −2.66 | $1.98 \times 10^{-5}$ |
| Early juvenile | UOBS 02486 | 0.84 | −3.44 | $17.75 \times 10^{-3}$ |

Abbreviation: UOBS, University of Opole, Department of Biosystematics.

### 3.2.2 | Clavicle of *M. krasiejowensis*

The clavicle (UOPB 00144) does not show a significant decrease ($p = 0.57$) in compactness with increasing thickness. Mean compactness of the sections of this specimen is 68.69%. No volumetric comparison to total compactness exists for this specimen as the compactness values are observed only from the preserved posterior end.

### 3.3 | Quantitative comparison to the microstructure of *C. intermedius*

The mean compactness at position Co of the interclavicles of *M. krasiejowensis* is between 60%–90% whereas the interclavicle of *C. intermedius* is in the range of 50%–65% in the comparative region (Figure 6; see Tables S2–S4 and S6 for absolute values of
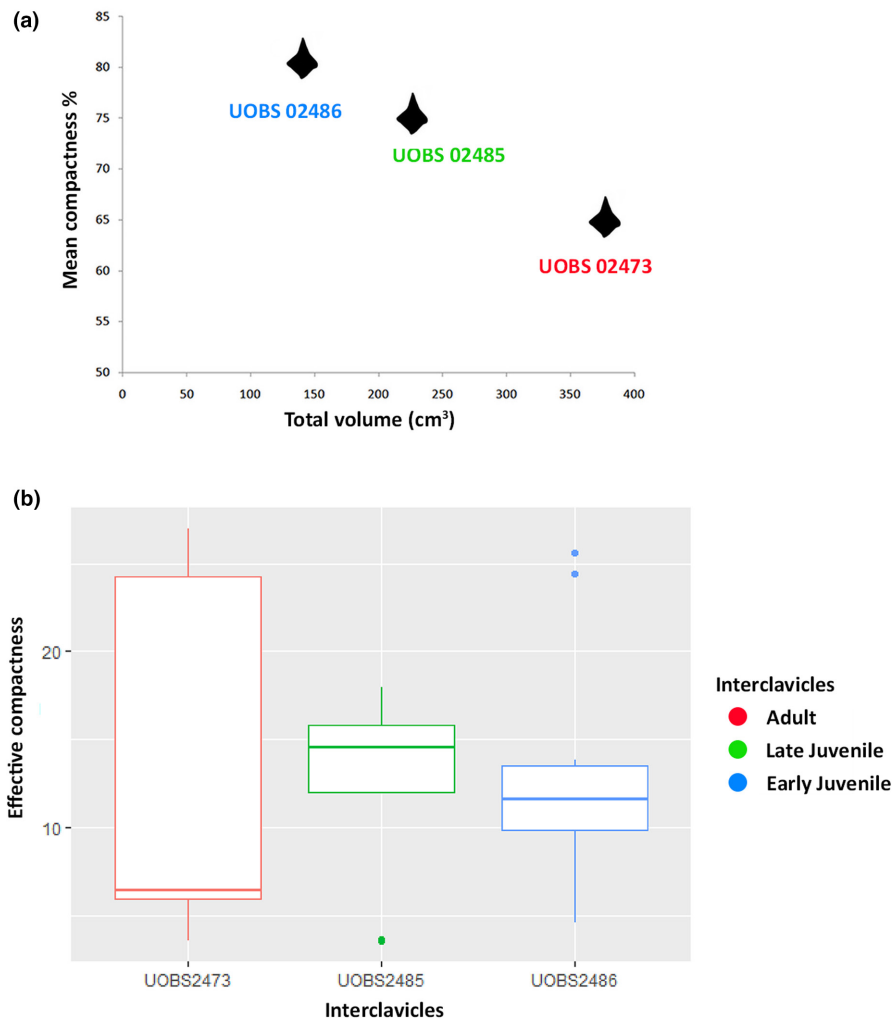
**FIGURE 7** Compactness variation across the ontogenetic series of interclavicles of *Metoposaurus krasiejowensis*. (a) Linear correlation between compactness and volume of the sampled interclavicles of *M. krasiejowensis*. (b) Variation of effective compactness in the interclavicles of *M. krasiejowensis*. Colored labels displaying interclavicle catalog numbers of *M. krasiejowensis* in (a) correspond to the plot legend in (b)

compactness). Additionally, the compactness of the position Co of the adult specimen (Figure 6a) has almost no noticeable difference from the compactness range of *C. intermedius* interclavicle. However, the compactness of the position Co in the juvenile specimens (Figure 6b,c) is comparatively much higher than the *C. intermedius* interclavicle. Additionally, the mean compactness of the clavicle section of *C. intermedius* is 62.5% relative to the position P4 of the *M. krasiejowensis* clavicle (Figure 5b) which is 68.7%.

## 4 | DISCUSSION

### 4.1 | Applying the compactness parameter for dermal bones

Several studies have used different types of compactness parameters to quantify bone compactness at various levels. Some parameters such as global compactness (De Buffrénil et al., 2010)

and compactness index (Houssaye et al., 2014a) measure the amount of bone present in the total area of the studied section. On the other hand, parameters like compactness profile conduct a relative quantification of compactness in the different regions of the same section; measuring compactness variability between periosteal and endosteal regions (De Buffrénil et al., 2010). The percentages of interclavicle compactness from this study are comparable to global compactness (De Buffrénil et al., 2010) or compactness index (Houssaye et al., 2014a) as all of them consider the area covered by bone relative to total area. However, as mentioned previously, the thickness in dermal bones is relevant as mere compactness values only provide a partial understanding of changing compactness so effective compactness is more relevant from the perspective of the chosen samples for this study. This renders effective compactness to remain valid for dermal bones only. In long bone sections, values of global compactness provide a clear overview of bone compactness as the area considers all the homologous regions if multiple samples from the same skeletal

element of the same taxon are involved (such as adductor crests of femur mid shafts). For dermal bones, however, the homology of individual ridges is not clear even if the overall pattern of ornamentation is similar throughout the external cortex, there could be several minor variations in the appearance of new ridges and valleys or discontinuity of ridges across the pattern. This may not play a big role in understanding the similarity of ornamentation in one taxon but for individual sections, it alters the thickness to a great amount. Hence, the magnitudes of effective compactness have no comparative importance to any parameters used for long bones. Instead, effective compactness is more important if comparisons are made between dermal bones belonging to the same or different taxa. Furthermore, it is important to mention that there can only be an empirical comparison of the compactness values of this study with compactness ranges of other parameters from other studies (De Buffrénil et al., 2010; Houssaye et al., 2014a). Anecdotal comparison with long bone observations could be superficial due to different developmental origins of dermal and endochondral bones.

## 4.2 | Relative BMI visible in interclavicles of *M. krasiejowensis*

The local microstructure variations of effective compactness in the interclavicles are similar to that of the local microanatomical variations observed in the skull roof of *M. krasiejowensis* (Konietzko-Meier et al., 2018). Additionally, despite the strong negative correlation between compactness and thickness (Table 2), all the sampled interclavicles have an upper limit of local compactness of nearly 80% (in the adult; Figure 6a) and higher (in the juveniles; Figure 6b,c). However, the major issue arises with the high negative correlation between thickness and compactness (Table 2). However, in spite of that there is high compactness in the anterior regions (in all ontogenetic stages; Figure 6) and high compactness in the middle regions of the juveniles (Figure 6b,c). Such a condition could have been caused due to increasing bone thickness resulting in reduced compactness in the middle region of the adult specimen (Figure 6a) and posterior regions of all specimens. Furthermore, this effect of growth leading to low mean compactness is evident from the increasing volume in the interclavicles (Figure 7a). However, in spite of this growth affect, the anterior region of the adult specimen exhibits a lower drop in compactness compared to the middle region (Figure 6a). In this case, the thickness of the anterior region in the adult did not increase at the same rate as the rest of the interclavicle, resulting in the retention of high compactness across the anterior end. This shows that the high bone compactness in the juvenile stages (Figure 6b,c) provided some adaptive advantage which could have led to slower growth of the anterior region relative to the rest of the bone eventually retaining high compactness till the individual attained the adult stage. Additionally, the anterior region does cover a significant portion of the area of the interclavicles (Figure 1a) which could reinforce the need for high bone compactness adaptation in this region

as a larger portion in a skeletal element serves more biomechanical purpose. According to De Buffrénil et al. (2010), specialized osteosclerotic patterns in bones exhibit a high global compactness range above 0.817. Sirenians, in particular, display a very high global compactness range of 0.96–1 which if converted to percentage is higher than 96% compactness (De Buffrénil et al., 2010). Comparatively the anterior regions in the juvenile interclavicles (Figure 6b,c) display a similar range of bone compactness, with the adult specimen almost being at the lower limit of the high compactness range of the juveniles (Figure 6). Furthermore, Houssaye et al. (2016) mentioned that BMI-like condition is attained through osteosclerosis, pachyostosis, and pachyosteosclerosis. The presence of pachyostotic or pachyosteosclerotic patterns is difficult to determine for the metoposaurid interclavicles because there is no consensus on what is a 'regular' interclavicle in Temnospondyli, without these specialized bone adaptations. So, from the perspective of current research limitation in this area, it is only safe to assume an osteosclerotic-like pattern partially occurring in the interclavicles. Additionally, BMI adaptation is more likely to be attained via osteosclerotic-like pattern, if not osteosclerosis sensu stricto (Houssaye et al., 2016). Furthermore, Houssaye et al. (2014a), observed high compactness index range of 80%–85% and low compactness index for a range of 50%–55% in several ichthyosaur limb bones (femora, epipodial, and humerus). In comparison, the compactness of the anterior end of the interclavicles does overlap the high compactness index range by Houssaye et al. (2014a). Therefore, an osteosclerotic-like pattern could have evolved in the anterior region of the interclavicles leading to a BMI-like condition in the same regions.

The comparison of the compactness of the posterior end of the interclavicle fragment of *C. intermedius* with that of the comparative region of *M. krasiejowensis* interclavicles does not yield any relevant insights. Since the compactness difference between the posterior interclavicle end of both species is quite low, based on this comparison, there is no informative interpretation that would reinforce the presence of relative BMI in the anterior end of the interclavicles of *M. krasiejowensis*. However, the interpretation of BMI-like condition in these anterior regions of metoposaurid interclavicles are based on a comparison to amniote taxa that exhibit definitive BMI such as Sirenians (De Buffrénil et al., 2010). Hence, it is relevant to mention the presence of a relative BMI-like pattern and not absolute BMI in the interclavicles. Nevertheless, it is noteworthy to mention that any comparison of the compactness of interclavicles with that of the long bone samples of amniotes (De Buffrénil et al., 2010; Houssaye et al., 2014a) is done to provide a relative viewpoint on whether these interclavicles of *M. krasiejowensis* are compact at all. Since there are no known studies on bone compactness of dermal bones, there is no existent frame of reference to analyze the extent of compactness in the dermal bone samples in this study. Future studies with more temnospondyl groups with diverse ecomorphological adaptations should shed some more light on the 'regular' bone compactness of the dermal pectoral girdle without any compactness specializations. Furthermore, such studies would also provide precise insights into the comparative ranges of the dermal pectoral girdle associated with the habitat type of the

concerned taxon and may indicate the upper limit of bone compactness that can be attained in the dermal pectoral girdle.

## 4.3 | Implications of BMI in the interclavicles

### 4.3.1 | Creating a ballast

The remains of *M. krasiejowensis* occur in a secondary deposit (Bodzioch & Kowal-Linka, 2012) because of which it is difficult to predict accurately the habitat of *M. krasiejowensis*. Nevertheless, the paleoenvironment of Late Triassic Krasiejów and its surroundings did have shallow water ecosystems (Jewuła et al., 2019). The occasional flooding events formed ephemeral ponds with shallow depths and even the depth range of the braided fluvial channels was shallow in the depth range of 2–10 m (Jewuła et al., 2019). According to Taylor (2000), BMI allows animals to have a hydrostatic lifestyle at shallow depths. Some groups of Late Cretaceous shallow marine squamates display pachyostotic and osteosclerotic patterns throughout the entire skeleton, whereas others display only osteosclerosis (Houssaye, 2013); both phenomena resulting in a BMI-like condition. However, BMI alone is not enough to predict the lifestyle of the taxa concerned. One example is the evolution of BMI in the ribs of *Basilosaurus* and *Pachycostasaurus*, despite these animals being highly aquatic and deep-diving taxa (Houssaye et al., 2016). BMI itself is a functional effect and can be altered depending on the type of underwater locomotion (Dumont et al., 2013) and the location of the skeletal part exhibiting BMI (Houssaye, 2009). Additionally, BMI in the anterior dorsal region of the skeleton allows hydrostatic buoyancy control (Houssaye, 2009). However according to Taylor (2000), the ventral position of a dense bone is also related to the stabilization of the body rendering the bone as ballast. Although the interclavicles are not placed dorsally, they are large (Dutuit, 1976; Sulej, 2007), heavy (presence of BMI), and are located anteriorly and ventrally (Dutuit, 1976; Sulej, 2007). Even though BMI is not exhibited in the entire interclavicle, the anterior regions display a relative BMI-like pattern as discussed previously. Furthermore, Konietzko-Meier et al. (2018) observed high compactness of skull roof bones (more than 75%), which reinforces the idea that *M. krasiejowensis* evolved relative BMI-like pattern in the skull. Altogether the placement of the interclavicle and its close proximity to the skull (Dutuit, 1976; Sulej, 2007) eventually shifts the center of mass anteriorly making metoposaurids thoraco-cranially heavy swimmers. However, for an animal that has evolved hydrostatic buoyancy control, the lower part of the body must be heavier to stabilize the body (Taylor, 2000). The anterior region of the interclavicles which form a significant part of this skeletal element may seem like only a local ballast. Nevertheless, it may not be the case as it is not only the anterior part of the interclavicle acting as a local ballast but local ballasts along with the other tissues contributes to the total density of the individual (Taylor, 2000), therefore, the entire interclavicle functioned as a ballast unless the posterior postcrania of *M. krasiejowensis* decreased the mass through osteoporotic-like

phenomenon. The latter is unlikely as there is no evidence of osteoporotic condition from any skeletal element of the hind limbs of *M. krasiejowensis* (Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013). Nonetheless, stabilization after submersion has greater relevance for hydrodynamic swimming taxa inhabiting open ocean niches (Taylor, 2000), having ample space and selective advantage for stabilization to avoid predation or chase prey. Since, *M. krasiejowensis* inhabited a shallow flood plain environment with depths up to 10 m and the average length of metoposaurids are within 1.5–2.5 m (Dutuit, 1976), there is no potential selective advantage of stabilization during submersion in these amphibians. The heavy anterior center of mass could have provided an effortless maneuverability toward the bottom of the waterbody after the metoposaurid individual would come to the surface for air. Considering these, there is a high possibility that these dense pectoral girdle bones got secondarily selected to function as ballast which is consistent with the first interpretation of the interclavicles acting as ballast in metoposaurids (Fraas, 1913).

### 4.3.2 | Cause and effect of hydrostatic buoyancy control

Amson et al. (2014) showed that extensive osteosclerosis in secondarily aquatic sloth *Thalassoconus* due to a passive hydrostatic lifestyle. Additionally, Gray et al. (2007) demonstrate that selection for hydrostatic buoyancy control in early archaeocetes was a result of attaining BMI via osteosclerosis, pachyostosis, and a combination of both. Despite the fact that *M. krasiejowensis* was thoraco-cranially heavy, the additional ballast acting anteriorly and dorsally (since the skull roof is situated dorsally) along with the ballast provided by the interclavicle ventrally, assisted in balancing the entire body without inclining anteriorly while swimming. This in fact implies a definite hydrostatic buoyancy control (Houssaye, 2009) in *M. krasiejowensis* where the ballasts itself assists in balancing without the expenditure of muscle energy. This is consistent with findings by Houssaye et al. (2016) where it is mentioned that incorporating BMI to attain negative and neutral buoyancy is energetically advantageous as the taxa need not spend muscle power to move along the water column. Furthermore, passive swimming taxa that rely on BMI for buoyancy control do not exhibit a plesiomorphic tubular microstructure in their long bones (Houssaye et al., 2016). Houssaye et al. (2016) also mention that load-bearing forces at the bone surface form distinct cortices which are indicative of active swimming taxa but not deep divers. Furthermore, tubular microstructure in the stylopod bones of crocodiles and marine iguanas are as a result of hydrodynamic swimming and robust terrestrial mobility despite the significantly high amount of time spent in their shallow water habitats (Houssaye et al., 2016). According to Watkins (1999), highly compact bones are more brittle and are not adapted for a terrestrial habitat. From the histology of the humeri in metoposaurids: *M. krasiejowensis* and *Panthasaurus maleriensis* show no distinct cortex and the tubular arrangement of the microstructure is essentially non-existent

(Teschner et al., 2018, 2020). Similar lack of tubular microstructure is also observed in the femora of *M. krasiejowensis* (Konietzko-Meier & Klein, 2013; Konietzko-Meier & Sander, 2013) and *P. maleriensis* (Teschner et al., 2020). Lack of distinct cortices in long bones implies load-bearing forces reverberating to the medullary core or minimal loading forces at the surface of the bone, where the latter could be the case for dermal and long bones of *M. krasiejowensis*. This suggests that in the course of attaining a primarily aquatic niche, the long bones eventually got adapted by losing their tubular microstructure. Additionally, the evolution of bone ballast is correlated with becoming more aquatic and less terrestrial (Taylor, 2000). If *M. krasiejowensis* populations became predominantly aquatic due to positive selection of relative BMI-like pattern in the interclavicles and eventually increasing the weight of these bones, it could indicate a potential loss of partial or total terrestrial maneuverability in terms of agility and speed. According to Bodzioch and Kowal-Linka (2012), the Late Triassic environment of Krasiejów did experience seasonal aridity and complete desiccation of small water bodies which would be flooded during heavy rainfall. Additionally, Konietzko-Meier and Sander (2013) provide insights from the highly vascularized zones in the femora of *M. krasiejowensis* indicating an aquatic habitat with prey abundance. However, at the same time, the presence of thick annuli in the outermost periosteal region indicates a lengthy dry season (Konietzko-Meier & Sander, 2013). Contrary to the claims of arid season in Late Triassic Krasiejów (Bodzioch & Kowal-Linka, 2012; Konietzko-Meier & Sander, 2013), recent histological studies on postcrania of aetosaurs and phytosaurs exhibit lack of deposition of Lines of Arrested Growth implying not so drastic dry season (Teschner et al., 2022). However, the interpretation of unfavorable seasonal conditions is better reflected in taxa that are more vulnerable to the resource crisis rather than in those that have a better chance of leaving for better foraging grounds. Hence, the presence of an arid season is better interpreted from *M. krasiejowensis* bones as it could have been relatively less mobile than aetosaurs and phytosaurs, rendering the latter better at migrating to resource-rich foraging areas than to wait out the time of crisis hibernating or aestivating. From the remains of *D. ouazzoui* that are preserved in situ (Dutuit, 1976), indicate death due to prolonged arid weather, rendering the individuals lethargic, and eventually succumbing due to the same. However, it is not yet known if there was any BMI-like pattern in the dermal pectoral girdle of *D. ouazzoui*, which points to the uncertainty that a heavy pectoral girdle restricted terrestrial mobility. Nevertheless, Steyer et al. (2004) observed high global compactness in femora samples of *D. ouazzai*, which could have been negatively selected whenever arid conditions would increase terrestrial locomotor demands. Future studies on the locomotor abilities of both girdles of *M. krasiejowensis* may shed some light on its ability to undertake terrestrial locomotion in the first place, and if the heavy girdle was anyway a suboptimal design for land maneuverability. Hence, it is possible that the lifestyle of *M. krasiejowensis* was predominantly aquatic with hydrostatic buoyancy control where the anterior skeleton acted as ballast allowing it to live as a bottom-dwelling predator as historically hypothesized (Fraas, 1913).

## 4.4 | Ontogenetic variation of BMI and its implications

Due to the lack of significant difference in effective compactness or relative BMI across the ontogenetic series for the interclavicles, it can be predicted that the extent of hydrostatic buoyancy control across the ontogenetic stages did not change significantly. This shows that there is no clear niche separation along the water column between early juveniles, late juveniles, and adult individuals. Because of this, there is a possibility that individuals who were at least 3 years old (Table 1), already attained a bottom-dwelling lifestyle which remained consistent after attaining adulthood. The mean compactness of the adult interclavicle specimen is lower than the juveniles as a result of its large size (Figure 7a). This may seem to exhibit a distinct compactness variation across the ontogenetic series nullifying the relevance of the lack of variation in effective compactness (Figure 7b). This may lead to the interpretation of the presence of potential ontogenetic niche shift along the water column. However, such a scenario is unlikely as it is not just the interclavicle that grows in size but also the surrounding soft tissue and other postcranial elements including the skull which already depicts a 75% compactness (Konietzko-Meier et al., 2018). This results in an overall increase in total body weight in larger specimens. Due to this, the buoyancy control provided by compact interclavicle is maintained by limiting the maximum attainable compactness rather than causing an increase in body weight to such an extent that surfacing for oxygen becomes difficult. Since it is not yet known if metoposaurids evolved cutaneous respiration, it is more relevant than they had to surface for air after a finite time of submersion. Moreover, the water depth in the floodplains of the Silesia region during the Late Triassic was about 7–10 m (Jewuła et al., 2019) which is still a significant depth where surfacing for air becomes necessary after a certain amount of time spent submerged. Ultsch et al. (2004) showed that occasional air breathing in aquatic amphibians and reptiles is important to avoid lung collapse due to prolonged submersion. Taking into consideration such possibilities for metoposaurids, if the mean compactness of the adult interclavicle would be 75% or above, it may increase the total body weight significantly rendering potential lung collapse because of prolonged submersion. Moreover, the shape of the metoposaurid torso from the flat interclavicle and very low curvature of the ribs is not like a barrel as in Sirenians, which may indicate low lung volume in metoposaurids. Additionally, there was no need for blubber in metoposaurids as the Late Triassic climate in Krasiejów was warm flood plain environment (Bodzioch & Kowal-Linka, 2012) and not cold oceanic waters. As a result of these, neither lungs nor any blubber could have assisted *M. krasiejowensis* individuals to attain positive buoyancy to surface for air. This leaves the metoposaurid individuals to rely on their underwater locomotor abilities to swim up to the water surface. Hence, the low mean compactness in the adult interclavicle could be a way of compensating for the negative physiological aspects of increasing total body weight but at the same time provide a role as ballast (along with the weight of the remaining postcranium and other soft tissue) and assist a bottom-dwelling mode of life. Thus, the lack of variation of effective compactness could actually mean a

lack of variation in the hydrostatic buoyancy control across the ontogenetic series of metoposaurid individuals leading to no potential ontogenetic niche shift along the water column. Furthermore, lack of ontogenetic niches in metoposaurids from the results of our study is consistent with previous observations of metoposaurid congregating in groups in freshwater habitats (Brusatte et al., 2015) suggesting that individuals of all sizes occupied a single niche.

According to Steyer et al. (2004), less vascularized femora of smaller individuals mean an amphibious lifestyle rather than a fully aquatic lifestyle inferred from thin sections of adult *D. ouazzoui*. However, for these results, the increase in relative skeletal weight due to skeletal growth of the specimens was not considered (Steyer et al., 2004). The incorporation of bone mass is significant because lack of ontogenetic niche shift in *M. krasiejowensis* individuals could be a result of attaining bone mass equilibrium through BMI. However, it is noteworthy that the absence of the ontogenetic niche shift could be a result of low sample size and conducting parametric tests with statistically significant samples might give consistent results with that of observations of ontogenetic niche existence observed in *D. ouazzoui* (Dutuit, 1976; Steyer et al., 2004). Nevertheless, temporal variation between the three interclavicles (adult, UOBS 02473; late juvenile, UOBS 02485; early juvenile, UOBS 02486) is high (Table 1). This implies that each of the interclavicles truly represents the particular ontogenetic stage. Hence, the absence of an ontogenetic niche shift along the water column could be an actual phenomenon. Any ontogenetic niche variation in *M. krasiejowensis* could only exist for very young individuals which were less than 3 years old.

## 4.5 | Comparison of ontogenetic niche partitioning with other metoposaurid species

Findings of ontogenetic niche shift in *D. ouazzoui* were based on in situ preservation which exhibits separation of larger and smaller individuals (Dutuit, 1976). According to a later study by Dutuit and Heyler (1983), this spatial organization in the skeletons along the ontogenetic series is due to mass mortality in a coastal fluvial ecosystem where juveniles being less aquatic, lived in relatively shallow water. Furthermore, other studies also claim ontogenetic niche partitioning in metoposaurids based on osteological evidence (Gee et al., 2017; Sulej, 2007). This ontogenetic niche partitioning could have been selective during taphonomy which does not preserve very young individuals (Brusatte et al., 2015; Dutuit, 1976; Sulej, 2007). However, interpretations from taphonomic bias in the preservation of osteological evidence has its limitations. It can predict niche partitioning but may not provide precise insights into niche accessibility. From the results of this study, the early juvenile individuals could have been able to access the niche of the adult individuals, if not shared the niche entirely. Additionally, lack of ontogenetic niche shift in the Polish metoposaurid species in comparison to other metoposaurids sheds some light on variation of life history strategies across closely related taxa. Another explanation for this lack of ontogenetic niche could concern only the lack of niche partitioning

along the water column for *M. krasiejowensis*. It is possible that ecological ontogenetic niche partitioning could exist in other areas of the benthic habitat with changing water parameters such as velocity and temperature. Such existence of ecological niche partitioning was observed in young metoposaurids whose remains (previously diagnosed into its own taxon *Apachesaurus*) occurred alongside articulated material and infrequent taxa such as *Revueltosaurus* indicating low energy habitat, which could have been inhabited by the former to avoid being preyed upon by large metoposaurid individuals (Gee & Parker, 2018).

## 4.6 | Selection of BMI independent of habitat type

Antczak and Bodzioch (2018) observed two ornamentation morphotypes of *M. krasiejowensis* based on the sculpturing on the skull roof and clavicles, where the T1 morphotype (irregular ornamentation) was representative of living in large water bodies whereas the T2 (coarse ornamentation) belonging to flowing water conditions. If the adult specimen used in this study belonged to a T2 ornamented morphotype that was a facultative neotenic adult (Antczak & Bodzioch, 2018) then it must have migrated between water systems of different fluid dynamics in terms of size and water current. Or it could also be a paedomorphic adult residing in the large lake habitat as the T1 ornamented morphotype (Antczak & Bodzioch, 2018). This is consistent with the bone ballast condition of dugongs as they are benthic shallow water grazers but are still affected by the current from the surf (Taylor, 2000), which implies that a true bottom-dwelling lifestyle may occur independently of the water current of the aquatic habitat. Regardless of either possibility of the adult residing in calmer or unstable water, the results of this study showing the lack of ontogenetic niche shift supports both as the functional requirement in both water conditions is essentially the same: to be heavy enough to stay submerged. Moreover, whether *M. krasiejowensis* was a sedentary bottom dweller or a bottom walker, BMI can convergently evolve in both scenarios (Taylor, 1994). This implies that lack of ontogenetic niche from bone compactness results are not adequate to precisely predict a sedentary or dynamic mode of life as BMI-like condition is a functional process as previously discussed. In that case, young or adult metoposaurids could have lived a benthic mode of life in flowing water or stagnant water conditions at different times in their life history stages but they still exhibit a BMI-like condition as observed from the results herein. Future studies on the biomechanics of the entire pectoral girdle and the pelvic girdle of *M. krasiejowensis* could shed more light on its underwater locomotor abilities.

## 4.7 | Interpretations for clavicle (UOPB 00144) of *M. krasiejowensis*

Since only the posterior region of UOPB 00144 is preserved, there is no microanatomical information from the anterior region,

introducing an interpretation bias. Furthermore, the compactness of the clavicle sample is not high enough to provide any insights into potential BMI-like condition. Nevertheless, only a larger sample of clavicles will clarify if it played a role in hydrostatic buoyancy control.

## 4.8 | Comparison with *C. intermedius*

Comparison of *C. intermedius* specimen with the adult interclavicle of *M. krasiejowensis* (Figure 6a) does not provide a relevant interpretation of differences in hydrostatic buoyancy control in either taxon. Even though there is a distinct compactness variation between juvenile metoposaurid interclavicles (Figure 6b,c) with that of *C. intermedius* specimen, this relative observation is superficial because the age of the latter is unknown. However, the thickness of the *C. intermedius* specimen is closer to the thickness values of position Co of the adult metoposaurid specimen (Supporting Information). Nevertheless, even though the *C. intermedius* specimen is considered an adult, the comparison with the adult metoposaurid interclavicle still does not yield any noticeable difference in bone compactness at the position Co. Considering these, it is unlikely that the results of *C. intermedius* interclavicle compactness provide any insights into the separation of niches along the water column in both taxa. Furthermore, it does not provide any evidence of the presence of BMI-like pattern in *C. intermedius*. Since the clavicles of both species do not display drastically different compactness values in comparative regions, it is possible that these skeletal elements in both species were not specially selected for hydrostatic buoyancy control due to additional biomechanical loading.

However, local microanatomical variation within the thin section of *C. intermedius* interclavicle (Figure 4a) indicates that this taxon did not need hydrostatic buoyancy control and was a more dynamic swimmer. The distinct cortices of the *C. intermedius* sections in comparison to that of *M. krasiejowensis* (Figure 3) indicate that forces during swimming were acting more in the cortices than the middle region of the former taxa (Houssaye et al., 2016). Nevertheless, lack of hydrostatic buoyancy control could imply a more hydrodynamic mode of life or at least no strongly benthic adaptation. Historically capitosaurids were considered as passive benthic predators (Watson, 1958) but later studies found that capitosaurids as more surface-dwelling taxa (Damiani, 2001; Defauw, 1989), which is consistent with the interclavicle microanatomy of *C. intermedius* studied herein.

## 4.9 | Niche partitioning between *M. krasiejowensis* and *C. intermedius*

Several fossil faunal assemblages that bore metoposaurid remains also include large aquatic predators such as phytosaurs (Milner & Schoch, 2004; Sengupta, 1988; Sulej, 2007; Sulej & Majer, 2005). In the Late Triassic Maleri Formation, metoposaurid *Panthasaurus maleriensis* shared its habitat with the phytosaur *Parasuchus*

(Sengupta, 1988; Teschner et al., 2020). But unlike the Late Triassic deposit in Krasiejów, there are no capitosaurid remains from the Maleri Formation. Additionally, it is unlikely that *P. maleriensis* shared its habitat with other larger chigutisaurid Temnospondyli from the upper horizons (Sengupta, 1988). Nevertheless, even the habitat in Maleri Formation shows coexistence of metoposaurids with other large aquatic predators (Sengupta, 1988). Other evidence of metoposaurids coexisting with large predators comes from the Schilfsandstein layer, which is a deposition of sandstones by a braided river system that indicates temporal or spatial coexistence of four temnospondyl species (Milner & Schoch, 2004), all being predatory in nature. However, *Metoposaurus diagnosticus* rarely occurred alongside *Cyclotosaurus* remains during the Early Carnian but did occur alongside phytosaurs in the Late Carnian (Milner & Schoch, 2004). Additionally, *M. diagnosticus* remains from the Stubensandstein layer (Norian) were found alongside *Cyclotosaurus*, phytosaurs *Mystriosuchus*, and *Nicrosaurus* (Milner & Schoch, 2004). The Krasiejów locality also harbored *Parasuchus*, which could act as a potential predator/competitor in the pelagic habitat for *M. krasiejowensis* individuals (Bodzioch & Kowal-Linka, 2012). Hence, it is clear that metoposaurids evolved to coexist with other aquatic predators in their shared habitat.

If multiple predatory taxa coexisted then their presence close by could create ecological pressures such as competition between the species or one species preying on the other. These ecological pressures could have led to *M. krasiejowensis* occupying a benthic niche since early ontogenetic stage due to resource competition with *C. intermedius* and *Parasuchus* or the latter taxa preying on the young ontogenetic stages of the former. Exploiting the benthic zone to avoid competition or predation is also observed for the extant coelacanth *Latimeria*, which resides in the depths of oceans (Fricke & Hissmann, 2000). Although the case for *M. krasiejowensis* cannot be directly compared to *Latimeria*, nevertheless it is a useful strategy for species survival through niche separation (Fricke & Hissmann, 2000).

## 4.10 | Limitations to the microanatomical approach to determine lifestyle

Laurin et al. (2011) extensively studied microanatomical variations in the long bones of aquatic, amphibious, and terrestrial tetrapod taxa. Despite an exhaustive and elaborate observation of microstructural adaptations to habitat type, there is a certain degree of convergence. In species of extant terrestrial chelonians, the humeral microstructure is osteosclerotic in nature (Laurin et al., 2011). Therefore, in order to precisely predict the lifestyle of an extinct taxa, a comprehensive morphological, histological, and microanatomical analysis of multiple bones should be carried out. One such example is the study by Konietzko-Meier and Schmitt (2013), which observed a highly porous *Plagiosuchus* femur, an aquatic stereospondyl amphibian, and in spite of that, assigned it as a bottom dweller based on its massive osteoderms with thick cortex which would increase the total skeletal mass,

outweighing the BMD of the femora. Additionally, the sectioning positions inside a bone are of paramount importance to observe any changes in the microstructure to maintain consistency of homologous comparison. Witzmann (2009) conducted a detailed histological study of dermal bones of several non-amniote taxa but the data from his work cannot be used for comparative microanatomical analysis due to differences in sectioning locations within samples. Furthermore, the local microanatomical variation in the interclavicles and clavicle sample used in this study cannot be explained exclusively with quantitative compactness parameters. In order to explain why local microstructural variations, exist, the knowledge of ossification patterns of these bones is of importance. This implies that, in order to precisely understand variable relative allometry in the thickness and compactness across these bones, understanding biomechanical interpretations are necessary with regard to the variations in load-bearing capacity across the bones.

## 4.11 | Summary

*Metoposaurus krasiejowensis* is particularly known for its large and thick dermal pectoral girdle. However, the weight of a bone cannot be determined by only the thickness; but also, the compactness of the bone. Fraas (1913) first proposed the role of these bones as weights for attaining negative buoyancy. This study tested this hypothesis proposed by Fraas (1913) using BMI as a criterion. Since no comparative frame of reference exists for bone compactness in Temnospondyli, bone compactness results of the dermal pectoral girdle samples of *M. krasiejowensis* were compared with that of *Cyclotosaurus intermedius* to confirm evidence of BMI and check if the former taxa lived a bottom-dwelling mode of life as previously understood (Dzik et al., 2000; Murry, 1989; Ochev, 1966). Dimensions of interclavicles and clavicles were compared to dimensions and skeletochronological data of limb bones to determine ontogenetic age class. Samples were used for microanatomical analysis where core drills and sawed sections were extracted, scanned, and scans converted to binary illustrations which were further analyzed with a pixel counting software to quantify compactness. The relationship between thickness and compactness values was used to calculate effective compactness which is compactness variability with changing thickness and quantified compactness: thickness. Results show that the anterior region of *M. krasiejowensis* interclavicles have a compactness range of 70%–95% indicating a partial BMI-like condition when compared to several amniote taxa exhibiting high compactness range. Thus, the compact anterior end of the interclavicles along with the heavy skull (Gruntmejer et al., 2019; Konietzko-Meier et al., 2018) could have acted as ballast for hydrostatic buoyancy control by shifting the center of mass anteriorly. Additionally, the adult interclavicle specimen used in this study seems to have an upper limit of maximum attainable compactness which could be due to the avoidance of negative physiological effects of being extremely heavy. Also, lack of significant difference in the effective compactness across ontogenetic series of *M. krasiejowensis* infers to lack of variation in the relative BMI-like condition across the ontogenetic series, potentially implying that there was no variation in hydrostatic buoyancy control in the ontogeny of *M. krasiejowensis* individuals, potentially indicating no niche separation along the water column. There is no noticeable compactness difference between the samples of *C. intermedius* and *M. krasiejowensis*, as a result of which the *C. intermedius* sample herein does not serve as a good frame of reference due to its fragmentary nature. This demands a need for comprehensive comparative bone compactness studies that includes several temnospondyls and other anamniote taxa to shed light on bone compactness adaptation and if there is an upper limit to maximum compactness in the dermal pectoral girdle. Furthermore, the bone compactness results from the clavicles of both species are not comparable due to low sample size and fragmentary nature of the sampled material. Further studies on the aquatic locomotor abilities of both taxa may elaborate on the mode of life, niche delimitation, and accessibility.

## DATA AVAILABILITY STATEMENT
The data that supports the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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