

# Pentadactyl manus of the *Metoposaurus krasiejowensis* from the Late Triassic of Poland, the first record of pentadactyly among Temnospondyli

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## Abstract

Temnospondyli are commonly believed to have possessed four digits in the manus and five in the pes. However, actual finds of articulated autopodia are extremely rare. Therefore, an articulated, slightly incomplete forelimb skeleton with preserved manus of *Metoposaurus krasiejowensis* from the Late Triassic of Poland is important in providing new details about the structure and ossification sequence in the temnospondyl limb. The most important observation is the presence of five metacarpals in this specimen. This allows reconstructing the manus as pentadactyl. The number of phalanges and the distribution of distal articulation facets allow reconstruction of the digit formula as (2?)-3-3-(3?)-(2?). The well-developed fifth digit suggests that the *Metoposaurus* manus shows a unique ossification sequence: the reduction or late ossification of the first digit conforms to the amniote-frog pattern, and the early development of the second and third digit makes *Metoposaurus* similar to salamanders. Based on the distribution of pentadactyly vs. tetradactyly in the temnospondyl manus, the number of digits was not phylogenetically constrained in temnospondyls, similar to today's amphibians.

## KEYWORDS

digits, manus, *Metoposaurus*, ossification, Temnospondyli

## 1 | INTRODUCTION

In contrast to crown tetrapods that rarely have more than five digits, basal tetrapod groups possessed more digits, such as *Acanthostega gunnari* Jarvik, 1952 which had eight in the forelimb (Coates and Clack, 1990) and *Ichthyostega Säve-Söderbergh*, 1932 with seven digits in the hindlimb (Säve-Söderbergh, 1932; Jarvik, 1996). This fact indicates that polydactyly is the plesiomorphic condition for the tetrapod autopodium (Laurin *et al.*, 2000). The

first known record of a pentadactyl hand belongs to the Early Carboniferous stegocephalian *Casineria kiddi* (Paton *et al.*, 1999). However, reconstruction of the evolution of digit reduction of the most basal and post-Devonian stegocephalians is not possible because of the lack of informative fossils. It is known that reductions in the number of digits have occurred frequently during tetrapod evolution, but it is still not known exactly when or even how many times the number of digits was reduced to five or less (Laurin *et al.*, 2000).

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Of all tetrapod groups, modern Lissamphibia show the greatest variation in digit number. The most extreme example is the cave-dwelling salamander *Proteus anguinus*, in which only digits I and II remain in its hindfeet (Saxena *et al.*, 2016). The four-digit manus and five-digit pes (Ruta *et al.*, 2003; Ruta and Coates, 2007) are considered as a synapomorphy for Amphibia (*sensu* Temnospondyli + Lissamphibia). This condition is also known for some Paleozoic lepospondyls (microsaurs, nectridians) and the Carboniferous colosteid stem-tetrapods.

Shared patterns of limb ossification in living lissamphibian species correlate closely with phylogenetic patterns of digit reduction and loss. In tetrapod limb development, two main patterns of ossification are known. Both patterns share that the stylopodium first gives rise to the two zeugopodial elements, establishing preaxial (radius/tibia) and postaxial (ulna/fibula) domains. In the postaxial ossification pattern, elements of the postaxial domain of the zeugopodium generally develop earlier than elements of the preaxial domain. Furthermore, during the numerous events of condensation that establish the carpal and tarsal bones, the proximal elements ossify first. Digits are formed starting with a postaxial digit, specifically the fourth one in a pentadactyl autopodium. In the preaxial pattern, the opposite process is observed, with the preaxial elements developing earlier than the postaxial ones. Another difference from the postaxial pattern is the *basale commune*, a preaxial structure typical only for salamanders. The *basale commune* is an aggregation of distal carpal/tarsal one and two. Finally, in the preaxial pattern, digits form in a postaxial direction with a dominance of digit II (Fröbisch and Shubin, 2011, and references therein).

The majority of tetrapods, including anurans and all amniotes, display postaxial dominance in limb development, explaining patterns of evolution. Thus, frogs evolutionarily lost manual digit I and severely reduced the phalangeal elements of digits II and V while maintaining normal morphology of the central digits (see Fröbisch, 2008, and references therein). As noted above, salamanders are the only known living exception to the conserved tetrapod pattern of postaxial dominance of condensation and chondrification in limb skeletal formation (Shubin and Alberch, 1986; Shubin and Wake, 2003; Fröbisch *et al.*, 2007). Instead, salamanders show preaxial dominance as described above with the primary loss of digit V and subsequently reduced digits from posterior to anterior (Shubin and Alberch, 1986; Shubin and Wake, 2003; Fröbisch *et al.*, 2007).

Among Paleozoic and Mesozoic Temnospondyli, ossification sequences are known for only a few taxa with preserved extensive ontogenetic series (e.g., *Micromelerpeton credneri* Bulman and Whittard, 1926; Witzmann and Pfretzschner, 2003; *Archegosaurus decheni* Goldfuss, 1847; Witzmann, 2006; and *Sclerocephalus hauseri* Goldfuss, 1847; Schoch, 2003). Among fossilized amphibians, only *Apateon pedestris* von Meyer, 1844 preserves a clear picture of the ossification patterns of the limbs throughout ontogeny (Fröbisch *et al.*, 2007; Fröbisch and Shubin, 2011). Most striking is the preaxial dominance, exhibited in the ossification of the zeugopodial elements and the early ossification of digit II with the reduction of digit V in the manus, which is a shared feature of salamanders and *Apateon*

(Fröbisch *et al.*, 2007; Fröbisch and Shubin, 2011). The presence of a *basale commune* is not confirmed for *Apateon*, because the carpals and tarsals remained unossified. However, a *basale commune* is known for a close relative of *Apateon*, the amphibamid *Gerobatrachus* from the Early Permian of Texas (Anderson *et al.*, 2008). Both taxa, *Apateon* and *Gerobatrachus*, belong to an important temnospondyl clade, the Dissorophoidea. Dissorophoids include the monophyletic clade of modern amphibians according to the most widely accepted hypothesis of lissamphibian origins and interrelationships (Bolt, 1969; Milner, 1993; Ruta *et al.*, 2003; Schoch and Milner, 2004; Ruta and Coates, 2007; Sigurdson and Bolt, 2010; Schoch, 2013). The fossil record and developmental data suggest that preaxial dominance in limb development has evolved twice: once in salamanders and once in dissorophoids. Alternatively, preaxial dominance is plesiomorphic for temnospondyls including Lissamphibia, and there was a reversal to postaxial dominance in frogs (Fröbisch and Shubin, 2011, and references therein).

However, it is important to keep in mind that, although the Temnospondyli form one of the main clades of Palaeozoic and Mesozoic Stegocephali Cope, 1868, well-grounded knowledge about many details of their postcranial skeletal architecture is scant. Most temnospondyls, especially the large-sized ones, are known only from their more massive bones like the well-ossified skulls, clavicles, and interclavicles whereas the knowledge about manus and pes architecture and its development is poor (i.e. and Fraas, 1889; Hunt, 1993; Schoch and Milner, 2000; Fröbisch *et al.*, 2007; Fröbisch, 2008; Fröbisch and Shubin, 2011; Schoch, 2013, 2014). The very few examples of Temnospondyli specimens preserved with an associated forelimb seem to confirm the inference of a four-digit manus and five-digit pes pattern (see Pawley, 2006), and all known deviations from this pattern have been considered to result from either preservational artifacts or pathological processes (Fröbisch *et al.*, 2014).

The first publication on the forelimb of *Eryops megacephalus* by Cope (1877) described five digits in the manus based on well preserved material. In 1923, Gregory and colleagues questioned this interpretation and postulated a phalangeal formula of 2-2-3-2, with the fifth digit in this view being a prepollex (Gregory *et al.*, 1923; Pawley and Warren, 2006). The latest revision of the carpus of *Eryops* not only confirms the presence of only four digits, but refutes even evidence for a prepollex (Dilkes, 2015). The supposed contact surface for prepollex on centrale 1 is reinterpreted as part of the articulation for metacarpal 1 that includes distal carpal (Dilkes, 2015). The pentadactyl state observed in the forelimbs of three specimens of *Micromelerpeton credneri* was recently explained by irregular regenerative activity in a normal four-digit manus (Fröbisch *et al.*, 2014). The holotype and only specimen of the Middle Triassic *Paracyclotus davidi* Watson, 1958 was described by Watson (1958) to have five digits based on the preserved five metacarpals. Watson (1958) reconstructed the phalangeal formula as 2-2-3-3-2. The specimen is an articulated skeleton in a siderite concretion. It was found in an Australian clay pit in 1910 and is kept in the Natural History Museum, London, UK (NHM). A mount currently on display in the public galleries at the

NHM shows only four manual digits, but an apparently older (black and white) image of the same mount on the NHM collections web page shows five digits (<https://www.nhm.ac.uk/our-science/collections/palaeontology-collections/fossil-amphibian-collection.html>, accessed March 31, 2020). Seemingly, this change in the number of digits reflects the current view that all temnospondyls were tetradactyl.

In addition to direct osteological evidence, trackways may be a good source of information about the anatomy of pes and manus. Based on pentadactyl manus-pes trackways from the Lower Triassic Moenkopi Formation, the capitosaurid *Wellesaurus peabodyi* (Peabody, 1948; Welles and Cosgriff, 1965) from the same stratigraphic level was reported to have five digits on the manus. Another pentadactyl ichnotaxon, *Capitosauroides*, initially attributed to temnospondyl producers (Haubold, 1971), is known from the Buntsandstein of Germany (Haubold, 1971) and from the Upper Permian of Italy (Marchetti *et al.*, 2018). Tracks questionably referred to *Capitosauroides* are also known from the Lower Triassic of Poland (Klein and Niedźwiedzki, 2012). However, the revisions of *Capitosauroides* by Marchetti *et al.* (2019a, 2019b) now suggest the rapsids as probable trackmakers.

In the case of temnospondyl amphibians, a direct identification of trackmakers is ambiguous as temnospondyl tracks are extremely scarce in the fossil record (Peabody, 1948; Klein and Lucas, 2010a, 2010b; Marsicano *et al.*, 2014; Mujal and Schoch, 2020). Because of the lack of osteological data and the widespread notion that no temnospondyl ever had a five-digit manus (Marsicano *et al.*, 2014; Mujal and Schoch, 2020), Temnospondyli were automatically excluded from consideration as producers of trackways showing five-digit manus inprints.

Among metoposaurid temnospondyls, articulated skeletons are known only for *Dutuitosaurus ouazzoui* (Dutuit, 1976), including some with preserved forelimbs. Dutuit (1976) described only four metacarpals for each specimen in his material and postulated a phalangeal formula of 2-3-3-2. *Dutuitosaurus ouazzoui* was accordingly taken as the model for other closely related Temnospondyli, like *Metoposaurus krasiejowensis* (Sulej, 2002) and *Panthisaurus malericensis* (Roychowdhury, 1965). Based on the available disarticulated material, these taxa were similarly reconstructed with four digits in the manus (Roychowdhury, 1965; Sulej, 2007; Chakravorti and Sengupta, 2019).

In the Late Triassic locality of Krasiejów (for more details see: Dzik *et al.*, 2000; Dzik and Sulej, 2007; Bodzioch and Kowal-Linka, 2012), numerous individuals of *Metoposaurus krasiejowensis* were discovered, although most of them in a completely disarticulated state. The rare exception is an articulated partial skeleton of this taxon which includes the atlas, interclavicle, clavicle, scapula, cleithrum, humerus, radius, ulna, bones of the manus, and a few ribs of the left body side (Figure 1). The most interesting part is the manus, which shows the unequivocal presence of five metacarpals. In this paper, we focus on the description of the articulated forelimb of this specimen and offer a new interpretation of the *Metoposaurus* manus and its ossification sequence.

## 2 | MATERIAL AND METHODS

### 2.1 | Material

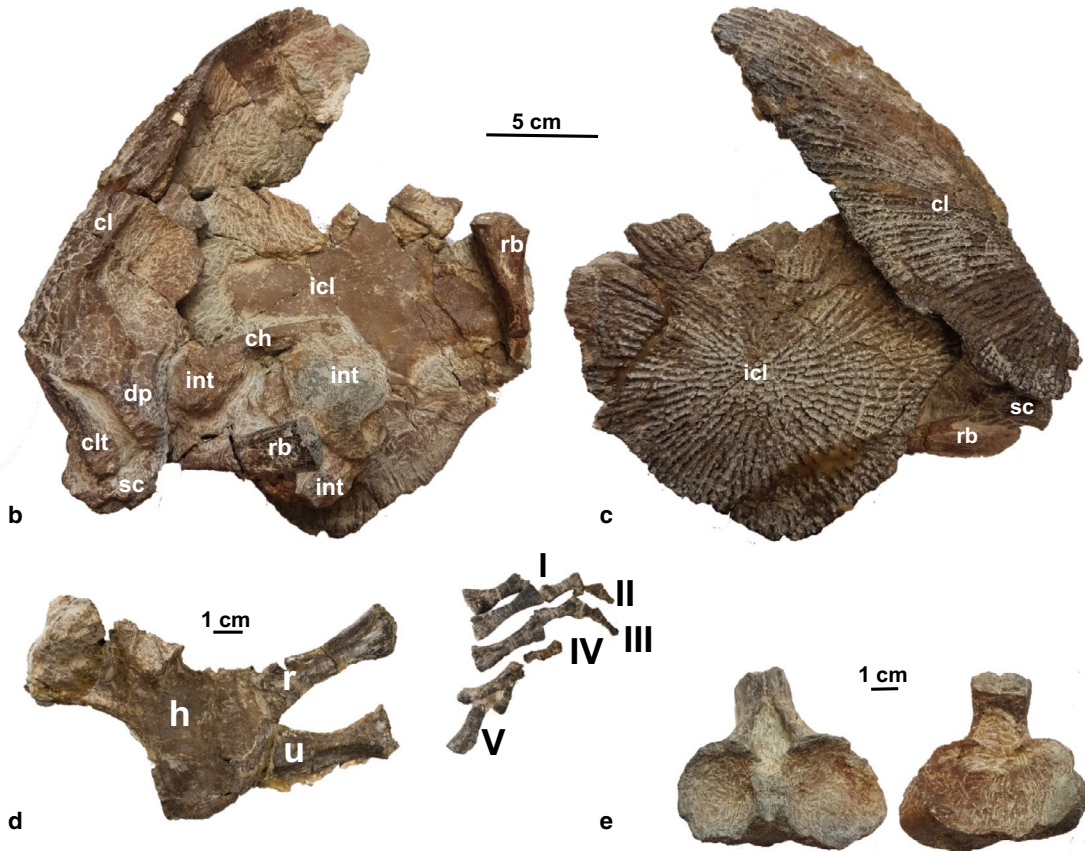
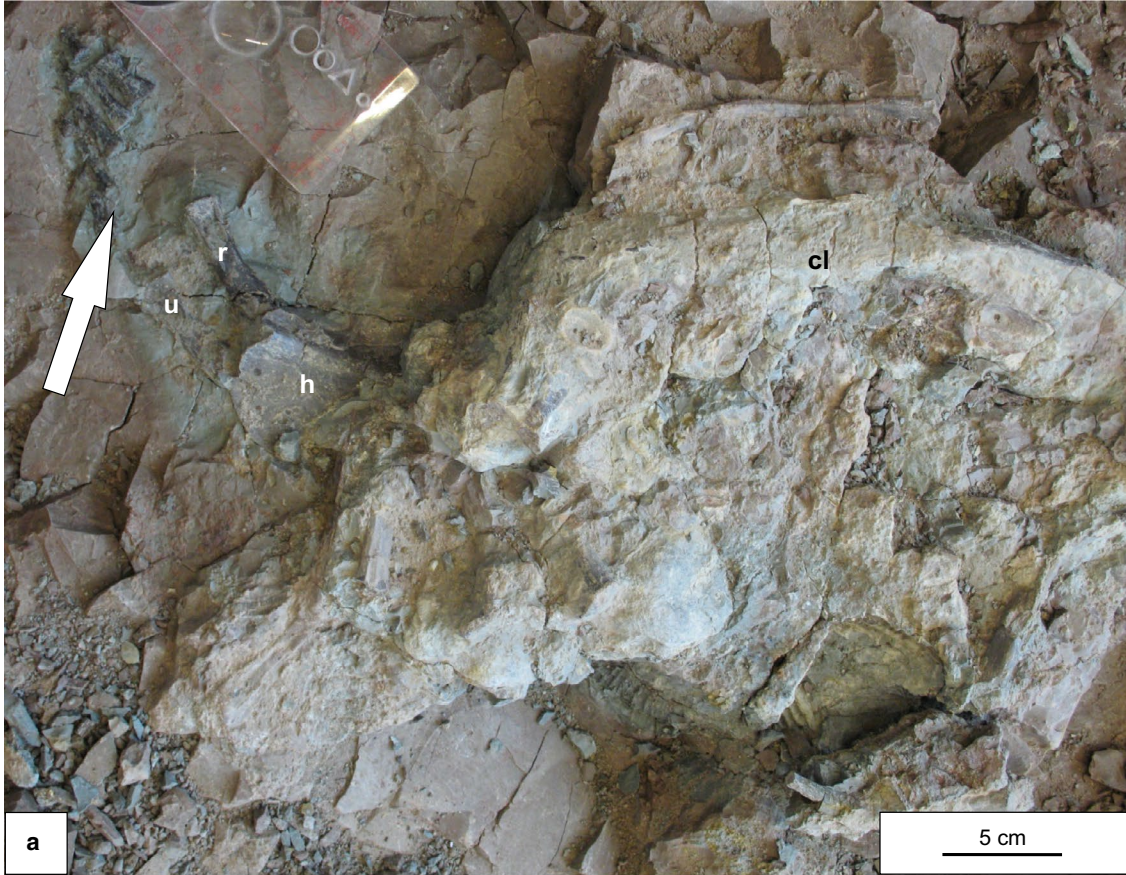
The current study is based on a completely articulated left forelimb (UOPB 00097/10-25) of *Metoposaurus krasiejowensis*, including the humerus, radius, ulna, and the bones of the manus (Figure 1; Figure S1). The specimen was discovered and prepared out of the matrix by the first author. No further phalanges were found in the surrounding sediment during excavation in the field (Figure 1a) nor during preparation in the laboratory, suggesting that the forelimb is completely preserved without taphonomic loss of elements. The material is stored at the Institute of Biology, University of Opole, Opole, Poland, collections acronym UOPB.

### 2.2 | Methods

**Photogrammetry**—For digitization of the manus, the method of computer-based photogrammetry was used (De Reu *et al.*, 2013; Mallison and Wings, 2014). The 3D model of the manus was constructed using the software *Agisoft PhotoScan Professional*. The 3D model of the manus is available in Appendix S1 (Figure S1).

**Ancestral State Reconstruction**—For the reconstruction of the distribution of the character of the number of manual digits (four vs. five) on the phylogenetic tree, the method of ancestral state reconstruction (ASR) was used. ASR is implemented in Mesquite v. 3.02, which offers two optimality criteria, maximum parsimony and maximum likelihood. The phylogenetic tree is based on Schoch (2013). Note that in the Schoch (2013) matrix, *Metoposaurus* was already coded with five fingers based on a personal communication by DK-M to Schoch about the specimen described here in detail.

The number of terminal ingroup taxa was 17, and *Greererpeton* was chosen as outgroup because it is the taxon closest to the ingroup for which manus architecture is known. *Greererpeton* has five digits in the manus (state 0) (Godfrey, 1989). To test the effect of discovery of five fingers in *Metoposaurus* described in the current paper, two trees were entered into Mesquite which differed in the coding of some ingroup taxa. The first tree reflected the accepted concept of a four-fingered manus (state 1) in all taxa with known forelimb structure. *Metoposaurus* was coded as unknown. The second tree included the new data presented here, and accordingly five fingers were coded for *Metoposaurus*. The pentadactyl state of *Paracyclotus davidi* based on the original description by Watson (1958) was also included in this second tree by coding five fingers for Capitosauria, to which the taxon belongs. With the second tree, we tested whether a more common occurrence of the five-fingered manus among temnospondyli would change the evolution of the character in the tree. Using the command series “Trace All Characters -> Stored Matrices -> Parsimony Ancestral States/Likelihood Ancestral States” in the menu “Analysis:Tree,” ASR was run under both optimality criteria which yielded similar results. However, we restrict the discussion to the maximum parsimony



**FIGURE 1** General overview of the entire accumulation of the bones of *Metoposaurus krasiejowensis* UOPB 00097. (a) Field photograph, the arrow indicates the left forelimb; the elements of the shoulder girdle were still covered by sediment at the time the picture was taken. All elements were preserved in correct anatomical position (dorsal view). (b) The shoulder girdle elements with associated bones after preparation, dorsal view (as in a). (c) The same specimen seen from the ventral side. (d) Articulated forelimb after the preparation, ventral view. (e) Atlas associated with the accumulation in anterior and posterior views. ch; chevron; cl, clavicle; clt; cleithrum; dp, dorsal process; h, humerus; icl, interclavicle; int; intercentrum; r, radius; rb, rib; sc, scapula; u, ulna

**FIGURE 2** Detailed illustration of the left forelimb of *Metoposaurus krasiejowensis* UOPB 00097. (a) The humerus, radius, ulna, and manus elements in ventral view. (b) Enlargement of the manus, ventral view. d, digit; h, humerus; m, manus; mt, metacarpal; ph, phalange; r, radius; u, ulna. Roman numerals indicate the identity of the phalanges (ph) and digits (d)



ASRs for the sake of simplicity since the maximum likelihood ASRs did not offer additional insights.

Its position is not parallel to the other metacarpals (Figure 1, Figure S1).

### 3 | RESULTS

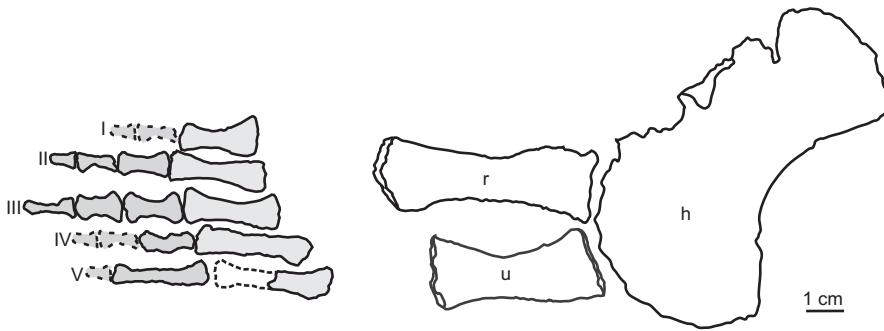
#### 3.1 | General preservation state

The bones of the forelimb of UOPB 00097/10-25 were dorsoventrally compressed during fossilization. The humerus is located posteromedially to the articulation surface of the scapula. Because of the dorsoventral compression of the radius and ulna, the articulation surfaces are deformed. The proximal head of the radius rests on the distal head of the humerus (Figure 1). Metacarpals IV and V are fractured, metacarpal IV is distorted and bent, and only the proximal half of metacarpal V is preserved.

#### 3.2 | Detailed description

**Humerus (UOPB 00097/10)**—A detailed description of the morphology of the *Metoposaurus* humerus is presented by Sulej (2007). Similar to most basal tetrapods, it is a short tetrahedron with a wide distal head, short shaft and a narrower but thicker proximal head. In UOPB 00097/10, the torsion of the shaft measures about 45°. The total length of the humerus is 82 mm, the proximal articulation surface is 42 mm wide, and the distal one is 57 mm wide (Figures 1d and 2a).

**Radius (UOPB 00097/12)**—The radius is dorsoventrally flattened, but nevertheless the shape of the proximal and distal



**FIGURE 3** Reconstruction of the manus of *Metoposaurus krasiejowensis* based on specimen UOPB 00097. Dashed lines indicate reconstructed elements. h, humerus; r, radius; u, ulna. Numbers indicate the identity of the digits

articulation surfaces is visible. The proximal head is rounded and anteromedially flattened, and the distal head still shows the triangular shape. On the medial side, a prominent groove runs along the radius from proximal to distal (Figures 1d and 2a). The total length of the bone is 51 mm, the proximal width is 17 mm, and the distal width is 18 mm.

**Ulna** (UOPB 00097/11)—The ulna is flattened dorsoventrally. However, it is difficult to determine the original shape of its heads. Generally, the proximal head seems to be more rounded and thicker than the distal one. In medial view, a sharp ridge is visible along the shaft (Figures 1d and 2a). The total length of the ulna is 41 mm, the width is 18 mm proximally and 19 mm distally.

**Carpals**—Carpals are not preserved. The relatively large empty space between the distal end of the zeugopodial bones and the metacarpals (Figures 1d and 2a) suggests that in the living animal cartilaginous carpals probably were present.

**Metacarpals**—The first metacarpal (mt I, UOPB 00097/18) is dumbbell-shaped. The proximal and distal articulation surfaces are broad, and thus the midshaft shows a pronounced diaphysis. The bone is 21 mm long. The second metacarpal (mt II, UOPB 00097/17) has a total length of 26 mm, with the proximal and distal heads not as broad as in mt I. The third metacarpal (mt III, UOPB 00097/16) has the same shape as mt I. Mt III measures 26 mm in length. The anteroventral insertion is clearly visible and has a triangular shape with sharp rims. The fourth metacarpal (mt IV, UOPB 00097/15) differs in shape from the others. Its heads are not broadened but are rectangular in shape. There is a groove on the bone's proximal part. Furthermore, the bone is ventrally convex and slightly distorted. Metacarpal IV is 24 mm long. The 6 mm-long fragment of mt V is broadened proximally, as in mt I.

**Digits**—In digit I (Figure 2b), there are no phalanges preserved, and the total length remains unknown. However, metacarpal I (mt I) possesses a distal articulation surface, which means that there was at least one phalange following distally.

The second digit measures 29 mm in length, with three phalanges preserved (Figure 2b). The first phalange (ph I/d II; UOPB 00097/21) is short and slightly dumbbell-shaped, however, not as

prominently as mt I. On the proximal head, a weak indentation is visible, whereas the distal head is round. The second phalange (ph II/d II; UOPB 00097/23) is shorter and thinner than the first one. There are no indentations, and both heads are round. The third phalange (ph III/d II; UOPB 00097/25) is the most distal preserved phalange and shows a triangular shape due to the broadened proximal head. It is the shortest bone of the entire manus. Because of the triangular shape, this phalange seems to be the terminal one; however its distal head is damaged, thus the potential presence of an articulation surface cannot be ascertained.

In digit III, there are three phalanges preserved (Figure 2b). The entire preserved digit is 33 mm in total length. The general shape of the bones is dumbbell-like. The second phalange (ph II/d III; UOPB 00097/22) is shorter than the first one (ph I/d III; UOPB 00097/20), whereas the third one (ph III/d III; UOPB 00097/24) is long and narrow.

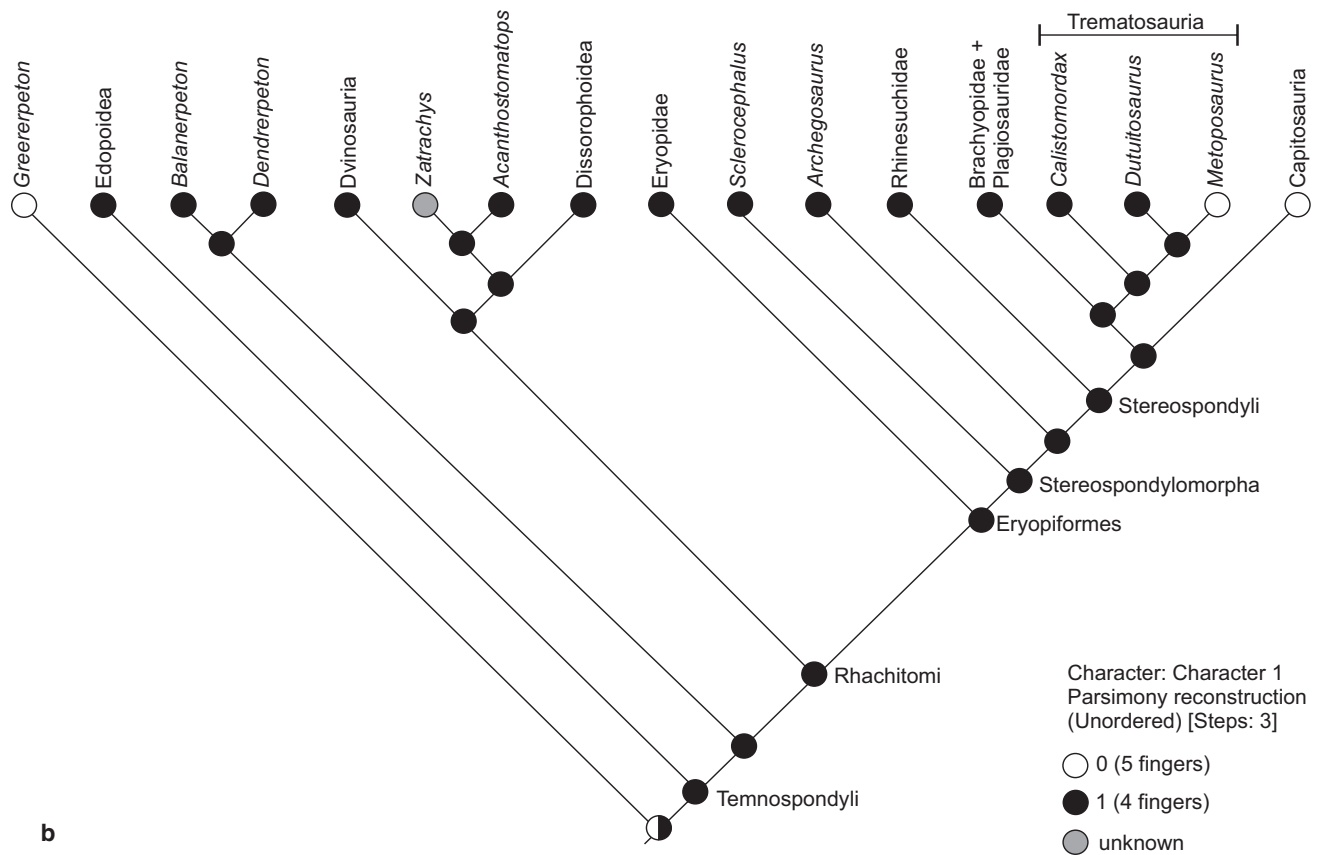
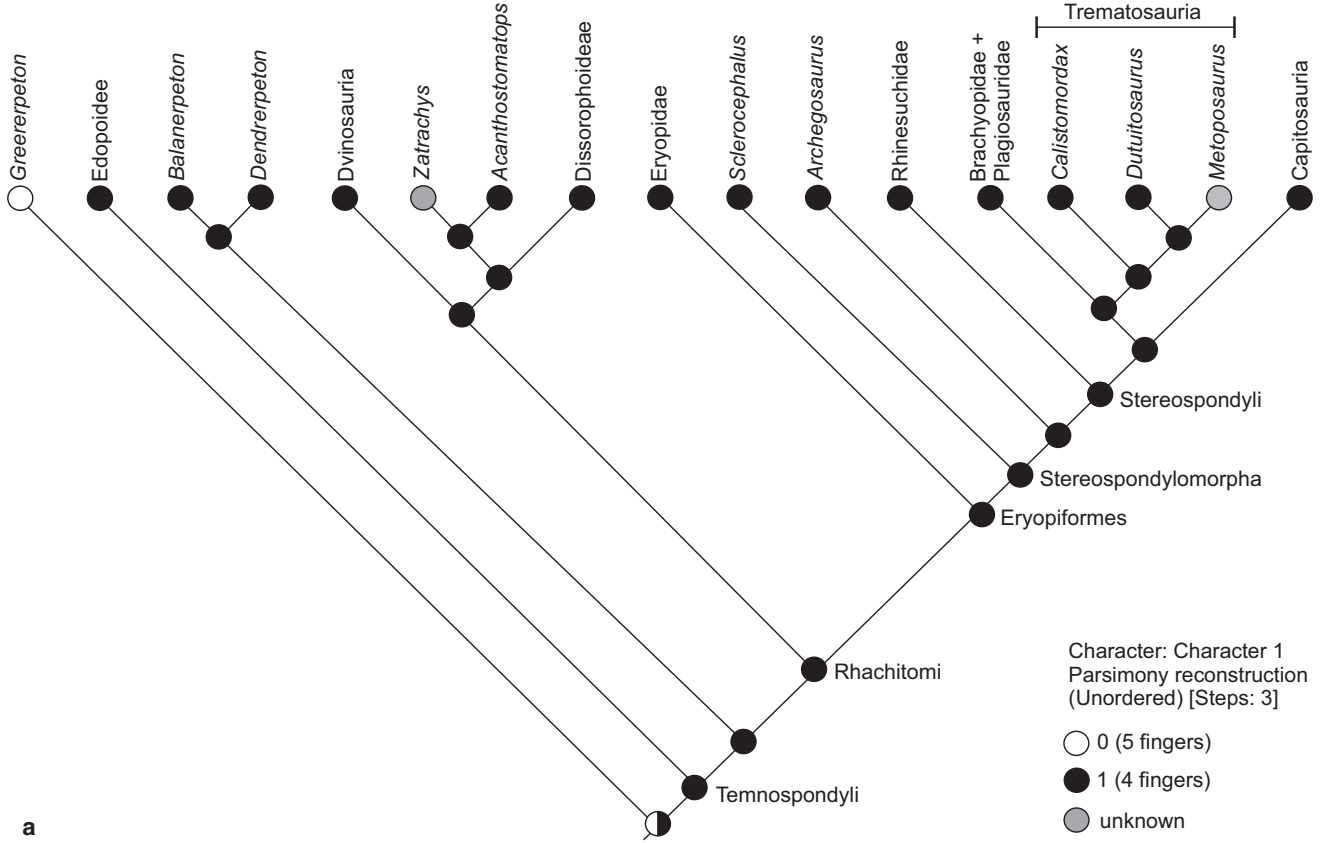
Only one 13 mm-long phalange (ph I/d IV; UOPB 00097/19) is preserved in digit IV (Figure 2b). It differs slightly in shape from the other phalanges. The proximal articulation surface is also flattened, but the distal head is subround. In contrast to the other bones of the manus, the diaphysis of this bone is hardly developed.

Digit V possesses one 19 mm-long phalange (ph I/d V; UOPB 00097/14). The bone is long and thin (Figure 2b). Its proximal head is round in contrast to the flattened distal head. The preservation of the articulation surfaces on the distal ends of the last preserved phalanges of UOPB 00097 suggests that in each digit, except for the second and third, some phalanges are lacking. Based on the fossil evidence, the phalangeal formula for *Metoposaurus krasiejowensis* thus is reconstructed as (2?)-3-3-(3?)-(2?) (Figure 3).

### 3.3 | Ancestral state reconstruction

ASR using maximum parsimony for both trees, the conventional one (Figure 4a) and the one based on the new evidence (Figure 4b), show that the last common ancestor of Temnospondyli

**FIGURE 4** Ancestral state reconstruction (ASR) using maximum parsimony of the number of digits in the manus among Temnospondyli. The phylogenetic tree is based on Schoch (2013). *Greererpeton* was chosen as the outgroup. (a) Tree reflecting the accepted concept of a four-fingered manus (state 1) in all taxa with known forelimb structure. *Metoposaurus* was coded as unknown. (b) Tree including *Metoposaurus* and *Paracyclotosaurus davidi* (Watson, 1958) as five-fingered taxa. Note that the inclusion of new data does not change the characters state reconstruction of any taxa except for those that were recoded according to the new evidence (*Metoposaurus* and *Capitosauria*)



and *Greerpeton* had either four or five fingers. The ASR of both trees shows the four-fingered manus to be plesiomorphic for Temnospondyli. Inclusion of the new data of five-fingered *Metoposaurus*, and coding of *Paracyclotosaurus* as pentadactyl did not have an effect on characters state reconstruction (Figure 4b) of any taxa except for those that were recoded, that is, *Metoposaurus* and *Capitosauria* (as represented by *Paracyclotosaurus*). ASR thus suggests the independent reversal from a four-fingered to a five-fingered hand in these two taxa.

## 4 | DISCUSSION

### 4.1 | Preservation and reconstruction of the manus

The newly described specimen and its five-fingered manus may be spurious and not representative for the taxon. However, parsimony suggests that the single known specimen represents the most common state in the taxon, and we thus take the five fingers we observed as representative for the species. In other words, we are much more likely to find the normal anatomy in the fossil record than an aberrant, possibly pathologic specimen. We thus argue that the new specimen is representative and informative. We also argue that the manus is completely preserved, and that the lack of phalanges in some digits indicates incomplete ossification and did not result from post-mortem loss (see Methods section above and Figure 1).

Our preferred reconstruction results in a peculiarity in relative phalangeal size, that is, that the first phalange of digit V is the longest phalange in the entire manus, considerably longer than the first phalanges of digits IV and III. Alternatively, the long phalange in question could represent a dislocated first phalange of digit IV that was displaced taphonomically. The current location of the two bones, just distal to metacarpals, argues against this view, however. This raises the question of the meaning of this elongated first phalange of digits V. It may represent a special adaptation of the species or possibly a pathology, but only further specimens will be able to provide an answer.

### 4.2 | Ossification sequences in comparison

With the exception of the specimen described here and possibly *Paracyclotosaurus*, all known and accepted articulated examples of the temnospondyl manus show only four fingers (Figure 4a). This raises the question of which finger was reduced from the plesiomorphic pentadactyl pattern in these taxa. The only temnospondyl for which the ossification sequence of the manus is known, is *Apateon* (Fröbisch *et al.*, 2007; Fröbisch and Shubin, 2011). Fröbisch *et al.* (2007) stated that *Apateon* underwent the salamander-like pattern of ossification of the manus, with the digital ossification sequence being II-I-III-IV, and a failure of digit V to develop. If all Temnospondyli followed the same ossification pattern, the logical

conclusion thus is that the missing digit in the four-fingered manus is finger V.

The new *Metoposaurus* specimen from Krasiejów (UOPB 00097) shows that digit V is well ossified, with a minimum of one phalange (Figure 2b). Digit I lacks phalanges, with only the metacarpal being preserved (Figure 2b). The best-developed digits are digits II and III, both with three preserved phalanges each. The detailed architecture of digits IV and V is uncertain because of poor preservation of the distal end of the phalanges (Figure 2b).

However, under the assumption of complete preservation of the manus, we reconstruct the sequence of ossification of the digits in the specimen as digit II-III first, then digit IV-V, and finally I. This reconstruction is based on the observation (reviewed in Fröbisch *et al.*, 2007) that ossification of the phalanges in the manus of Anura and Urodela starts from the most proximal phalange in the fourth digit (Anura) or second digit (Urodela) and then proceeds distally. Thus, the proximal phalanges are the oldest whereas the terminal ones are the youngest (Fröbisch *et al.*, 2014, and references therein). In our *Metoposaurus* specimen, digits II and III show complete ossification with three phalanges each, including the terminal ones, and thus these digits can be inferred to have ossified first. Digits IV and V both have one phalange, and digit V has none. Following the same principle, the start of ossification of these two digits was later in ontogeny, and that of digit V last. However, we cannot exclude the possibility that finger IV had more ossified phalanges and that these are not preserved. Potentially, the last ossifying elements are the phalanges of digit I, which are not seen in our specimen. However, the distal articulation surface visible on the metacarpal I suggests that there would have been at least one phalange on this digit, which possible had not yet ossified in this specimen at the time of its death.

The ontogenetic age of specimen UOPB 00097 can be inferred from histological studies of growth series of humeri of *Metoposaurus* (Teschner *et al.*, 2018). The length of the humerus (UOPB 00097/10) described here is 76% of the length of the largest humerus known for *Metoposaurus krasiejowensis* (Barycka, 2007; ZPAL III 830 – 107.5 mm). The estimated ontogenetic age for similar-sized humeri of *Metoposaurus krasiejowensis* is maximally 4 years (Teschner *et al.*, 2018). Histologically, neither humeri (Teschner *et al.*, 2018) nor femora (Konietzko-Meier and Sander, 2013; Konietzko-Meier and Klein, 2013) of this size show any signs of a permanent decrease of bone growth rate. This, besides other histological characters implying young age, suggests that 4-year-old *Metoposaurus* were still actively growing animals. This might explain the incomplete ossification of the phalanges in UOPB 00097.

The reconstructed pattern of digital ossification of *Metoposaurus* places this taxon between the two main patterns known so far for tetrapods (Fröbisch, 2008). *Metoposaurus* shares with the amniote-frog pattern the reduction of the first digit, but on the other hand shows a salamander-like pattern (also seen in *Apateon*) in the early development of the second and third digit. Although it is problematic to discuss details of manus ossification based on only one



specimen, it is clear that among Temnospondyli, there was variation in the development of the manus at low taxonomic levels, for example, in the clade Trematosauroida (which includes Metoposauridae) and Capitosauria, or even only in Metoposauridae and Capitosauria (Figure 4).

### 4.3 | Phylogenetic and comparative view

Based on embryological data (e.g., Fröbisch and Shubin, 2011, and references therein), the pentadactyl manus is considered as a primitive character of extant salamanders and frogs. If we assume that the four-digit Temnospondyli are also descended from pentadactyl ancestors, as indicated by ASR (Figure 4), the question arises why pentadactyly re-occurs in derived groups such as in some metoposaurids (but not others) and probably in capitosaurids.

In Metoposauridae, both conditions are represented: *Dutuitosaurus ouazzoui* has four digits (Dutuit, 1976) while *Metoposaurus krasiejowensis* is pentadactyl. As noted above, the only other articulated metoposaurid forelimb material is that of *Dutuitosaurus ouazzoui* (Dutuit, 1976). It clearly shows only four metacarpals with a digital formula of 2-3-3-2 (specimen AZA XIII/18/66, Dutuit, 1976 and pers. obs. DK-M). Moreover, the Middle Triassic *Callistomordax kugleri* Schoch, 2008, which is interpreted as sister taxon to metoposaurids, had a manus with apparently four digits, as suggested by four almost similar-sized elongated metacarpals (Schoch, 2008).

It thus appears likely that the number of digits was not as phylogenetically constrained in Paleozoic and Mesozoic temnospondyls as in modern amphibians and varied at a low taxonomic level. In addition, we cannot be sure that reduction in the number of digits from five to four in these fossil taxa always involved digit V, and we cannot exclude the possibility that some of the four-fingered taxa evolved by the loss of digit I. This might represent the typical high peak of disparity described as a characteristic phenomenon of early clade history (Hughes *et al.*, 2013). We hope for and encourage the discovery and description of further material to clarify this question which has important implications for Batrachomorpha digital reduction in general.

## 5 | SUMMARY

The shoulder girdle and associated forelimb of a partial skeleton of *Metoposaurus krasiejowensis* (UOPB 00097) offer new data points on manus architecture and evolution in Temnospondyli. Specimen UOPB 00097 suggests that the manus was pentadactyl in *Metoposaurus krasiejowensis*, contrasting with the tetradactyl manus of the closely related *Dutuitosaurus*. A broader look at the entire group of Temnospondyli does not show a clear trend with respect to pentadactyly, either, and suggests that the number of digits was not phylogenetically constrained. Even if the ossification of five metacarpals described here were only a pathology, it still shows that

the presence of a five-digit manus among Temnospondyli is possible, as already had been suggested by the description of a pentadactyl manus in *Paracyclotossaurus* by Watson (1958) and pentadactyl trackways referred to a capitosaurid (Peabody, 1948; Welles and Cosgriff, 1965). Clearly, the manus of the holotype specimen of *Paracyclotossaurus* needs to be restudied. In addition, we cannot be sure that reduction in the number of digits from five to four in these fossil taxa always involved digit V, and the possibility that some of the four-fingered taxa evolved by the loss of digit I cannot be excluded. The new record of a five-digit manus is especially important for the interpretations of footprints, as it shows that trackmaker of a five-digit manus inprint could be a member of Temnospondyli.

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### AUTHOR CONTRIBUTIONS

DK-M designed the study, DK-M, EMT, and PMS performed the research, DK-M, EMT, and PMS wrote the manuscript, EMT performed the photogrammetry, DK-M, EMT, AB, and PMS conducted the critical revision and approved of the final version of the manuscript.

### 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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Additional supporting information may be found online in the Supporting Information section.

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