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First evidence of spinal arthropathy and congenital block of the cervical vertebrae in Temnospondyli

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Despite recent reports, the fossil record of pathologies in vertebrates is still patchy in terms of phylogeny, geological age and paleogeography. Here, we report several cases of pathological vertebrae in several specimens of the Late Triassic temnospondyl *Metoposaurus krasiejowensis* from Krasiejów. The presence of cervical block vertebrae (atlas-axis complex) is the oldest such case reported for any fossil tetrapod and the first such case reported in temnospondyls. Spinal arthropathy (or spinal arthritis) is the first such case for a non-amniote. Based on different levels of fusion among the centra in the three specimens, this pathology revealed different stages of disease development. Finally, hemivertebra (congenital scoliosis) have been noted previously; however, this is the first example of scoliosis caused by hemivertebra in the genus *Metoposaurus*. These findings from the Upper Triassic site in Krasiejów allow for a better characterization of vertebral diseases in the fossil record. This was possible because of the very rich material of vertebrae from the Krasiejów Konzentrat Lagerstätte.

Metoposaurids are well-known representatives of Late Triassic terrestrial faunas across Pangea. Their remains were described from Europe (Poland, Germany, Portugal), Africa, North America and India[1–3]). Like many other representatives of Temnospondyli, metoposaurids had flattened bodies, large skulls, pectoral girdles with distinct ornamentation, and weak limbs. From many other temnospondyls, they can be discerned by having orbits located in front of the skull and well-developed lateral line canals.

Krasiejów is an Upper Triassic (Carnian – according to, e.g[4]., or Norian – according to, e.g[5,6]) locality, where fine-grained deposits yielded abundant vertebrate fossils that have been excavated for more than twenty years. Among the vertebrates described from the site, there are two genera of temnospondyl amphibians – *Metoposaurus*[7] and *Cyclotosaurus*[8]; several species of archosaurs – *Stagonolepis olenkae*[9], *Parasuchus* sp[10]., *Polonosuchus silesiacus*[11] and *Silesaurus opolensis*[12]; and some fish remains[13], including a new species of dipnoan *Ptychoceratodus*[14]. Invertebrate and plant remains (e.g[15–17]) and microvertebrate remains[18] are also known from the site.

The remains of *Metoposaurus krasiejowensis* are the most numerous fossils at the site. Rich collection enabled detailed descriptions of the anatomy and biology of the species (e.g[19–22]). Among the isolated skeletal remains, heavy-built skulls, mandibles, elements of the pectoral girdle and appendicular skeleton are common, but the most numerous bones of *Metoposaurus* at the University of Opole collection are isolated vertebrae. They possess typical stereospondylus characteristics[7,23,24]). The intercentra are strongly ossified and disc shaped.

The term "temnospondyli" translates into "cut vertebrae", which refer to the fact that they can be divided into separate elements: intercentra, pleurocentra and neural arches. Vertebrae of many temnospondyl amphibians (e.g., *Cyclotosaurus*) are partially cartilaginous and, in general, are not strongly ossified, in contrast to jaws, skulls and pectoral girdles, in connection with their mostly aquatic mode of life (cf. heterochronic ontogeny[25]). This finding was confirmed by histological analysis, which revealed that stereospondyl vertebrae possess high amounts of calcified cartilage preserved in endochondral trabeculae[26].

Metoposaurus vertebrae are fully ossified, presenting a disc shape with ophistocelous to amphicoleus articular surfaces. The ventral and lateral surfaces of intercentra bear depressions and pits. Intercentra are preserved separately in a typical temnospondyl manner. Neural arches are ossified with the intercentrum only in atlases and axes[7]. Intercentra are usually found isolated from each vertebra, and several sets of articulated vertebrae of *Metoposaurus krasiejowensis* are known, showing large spaces (synovial joints) between each vertebra[7]; personal observation).

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Several temnospondyl vertebrae from Permian and Triassic deposits are known to present pathological conditions—congenital malformations[24,27]. Surmik et al.[28] described pathological vertebrae as an example of tissue affected by a tumor.

Here, we describe new pathological specimens of fused *Metoposaurus* vertebrae, including – for the first time in temnospondyls – congenitally fused atlas and axis and spinal arthropathy.

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Materials and methods

Six specimens of fused pairs of vertebrae described herein were collected during the excavations camp at the Late Triassic site in Krasiejów (SW Poland) and are housed at the Paleobiology Collection of the Institute of Biology of the University of Opole (UOPB). The specimens were collected from the so-called lower bone-bearing horizon, fine-grained (claystone and mudstone) sediment layer, which is the section of the Krasiejów profile with the most abundant fossil assemblage (Fig. 1). The supposed origin of the bone bed is deposition of the material provided from a larger area by seasonal sheet flows[29]. More details on the geology and stratigraphy of the site can be found in multiple detailed analyses, including[5,6 and 30].

The specimens were prepared manually. Photographs were taken using a Canon EOS 250D.

The location of a single vertebra within the vertebral column can be identified on the basis of the position and shape of the parapophyses, as shown in[7].

Results

UOPB 3652

The specimen consists of two fused cervical vertebrae, an atlas and an axis, with partially preserved neural arches that are also fused together. It represents the vertebrae of a probably subadult individual, as evidenced by the complete and strong ossification of the centra and its small size. At the same time, the collection from the Krasiejów site includes many atlas and axis specimens belonging to *Metoposaurus* of larger sizes.

The anteroposterior length of the two fused vertebrae (measured on the ventral surface at the midline) was 29.8 mm. The anterior element is 15.6 mm in length, and the posterior element is 13.2 mm in length. The posterior articular surface of the axis has a width to height ratio of approximately 5:3 (36.9 mm to 20.7 mm).

The anterior surface of the intercentrum of the first vertebra is bifurcated, and two, approximately round and deep, articular surfaces are visible, originally connecting with the occipital condyles of the skull. Prominent bony ridges are formed at the point of contact of these articular surfaces and along their entire outer circumference. The neural arch is completely fused at its base with the intercentrum. It is not completely preserved, and the upper part is missing. The preserved section of the neural arch just above its base is broken and shifted to the left, and its frontal surface is partially turned to the right. A prominent oval neural canal is located between the intercentrum and the neural process. In frontal view, the shape of the intercentrum is oval and wider than high. The right lateral edge of the vertebra bordering the second intercentrum has a visible bony ridge running vertically. The left surface of the atlas intercentrum lacks a visible ridge and is closely fused with the anterior surface of the axis. The axis intercentrum is closely fused to the posterior surface of the atlas. The border between both vertebrae on the left side is very poorly visible, but on the right surface of the specimen, it is much better marked. The posterior surface of the axis intercentrum is clearly concave and oval in shape (Fig. 2).

Diapophyses and parapophyses on both sides of the intercentrum are poorly preserved but visible, approximately circular and of similar size. The posterior edges of the parapophyses are fused with the edge of the intercentrum. The neural process is fused at the base with the intercentrum. Its deformation is visible, as a result of which it is clearly shifted to the left. The left part of the base of the neural process is located clearly higher than the right part of the base. As a result of deformation, the neural canal is distorted and directed to the left (with a tri-lobed shape) and not along the intercentrum axis. Just below the right base of the neural arch, a distinct depression with a cracked intercentrum surface is visible, being perhaps a remnant of in vivo mechanical trauma. There are no signs of adhesions or damage healing. Both vertebrae are strongly fused and compressed together. The border between them is visible on the right surface of the specimen, where there is spongy bone tissue between the two intercentra. On the ventral side of the specimen, there are two sections where the fusion between the vertebrae is so strong that there is no visible boundary. In the central part of the connection of both vertebrae on the ventral side, there is still a small, barely visible fragment of spongy bone tissue. The entire ventral surface of the intercentera is covered with numerous small pores, a normal condition.

UOPB 3631

The specimen consists of two fused vertebrae, which are presacral vertebrae, as evidenced by the presence of both anterior and posterior parapophyses on each centrum (fovea costalis superior and inferior) and the shape of the constriction between them (under the missing pediculus arcus, centrodiapophyseal fossa)[7] (Fig. 3).

The anteroposterior length of the two fused vertebrae (measured on the ventral surface at the midline) was 47.2 mm. The anterior element is 26.1 mm in length, and the posterior element is 21.1 mm in length. The exposed articular surfaces (anterior surface for the anterior vertebra and posterior surface for the posterior vertebra) are slightly concave (amphicoelous). Both vertebrae are slightly elliptical, with an articular surface width to height ratio of approximately 4:3 (39.9 mm to 30.1 mm in the anterior element). In the anterior element, the ventral part of the articular surface is tilted anteriorly. The articular surface slightly exceeds the outline of the vertebral intercentra. The neural arches are not preserved; probably, they are not involved in vertebral fusion. Vertebra centra are covered with extensive nets of pits and grooves, which can often also be observed in isolated vertebrae of *Metoposaurus*. The dorsal surface of the specimen is poorly preserved, making it impossible to determine its original structure more accurately. The ventral surface of the specimen is well preserved. The

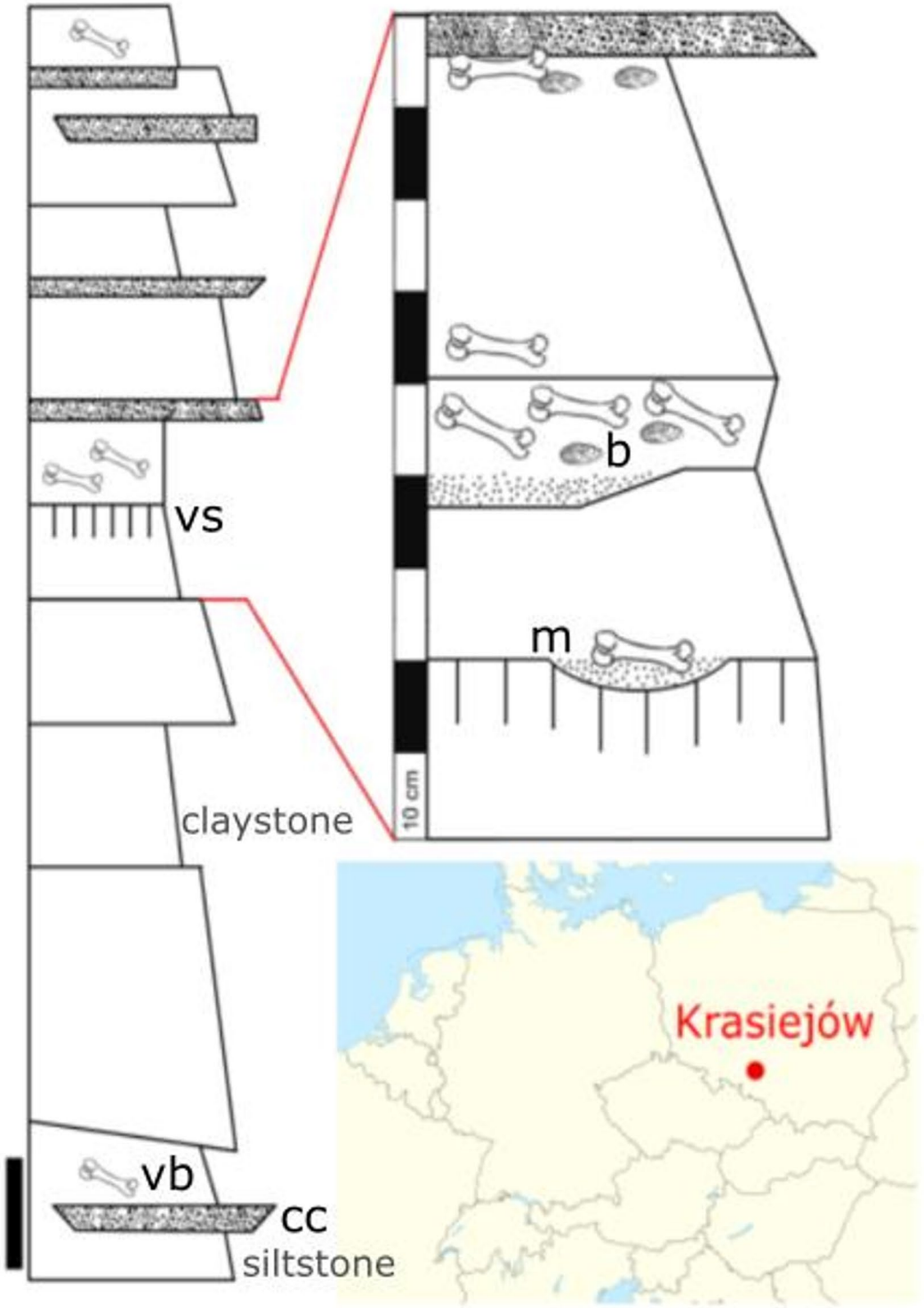

Fig. 1. Location and geological profile of the Krasiejów site. b – Bivalves, cc - Calcareous concretions, M – microfossils, Vb – Vertebrate bones, Vs - vertisol.

anterior parapophyses in the first vertebra are small and semicircular in shape. The right anterior parapophysis of the posterior vertebra is similar in size and shape to that of the anterior vertebra, whereas the left anterior parapophysis of the posterior vertebra is slightly deformed and elongated. The posterior parapophyses of both vertebrae on both sides are similarly structured and approximately semicircular with a slightly dorsally extended upper portion. The surfaces of the posterior parapophyses are noticeably larger than those of the anterior parapophyses. On both vertebral centra between the anterior and posterior parapophyses in the dorsal part

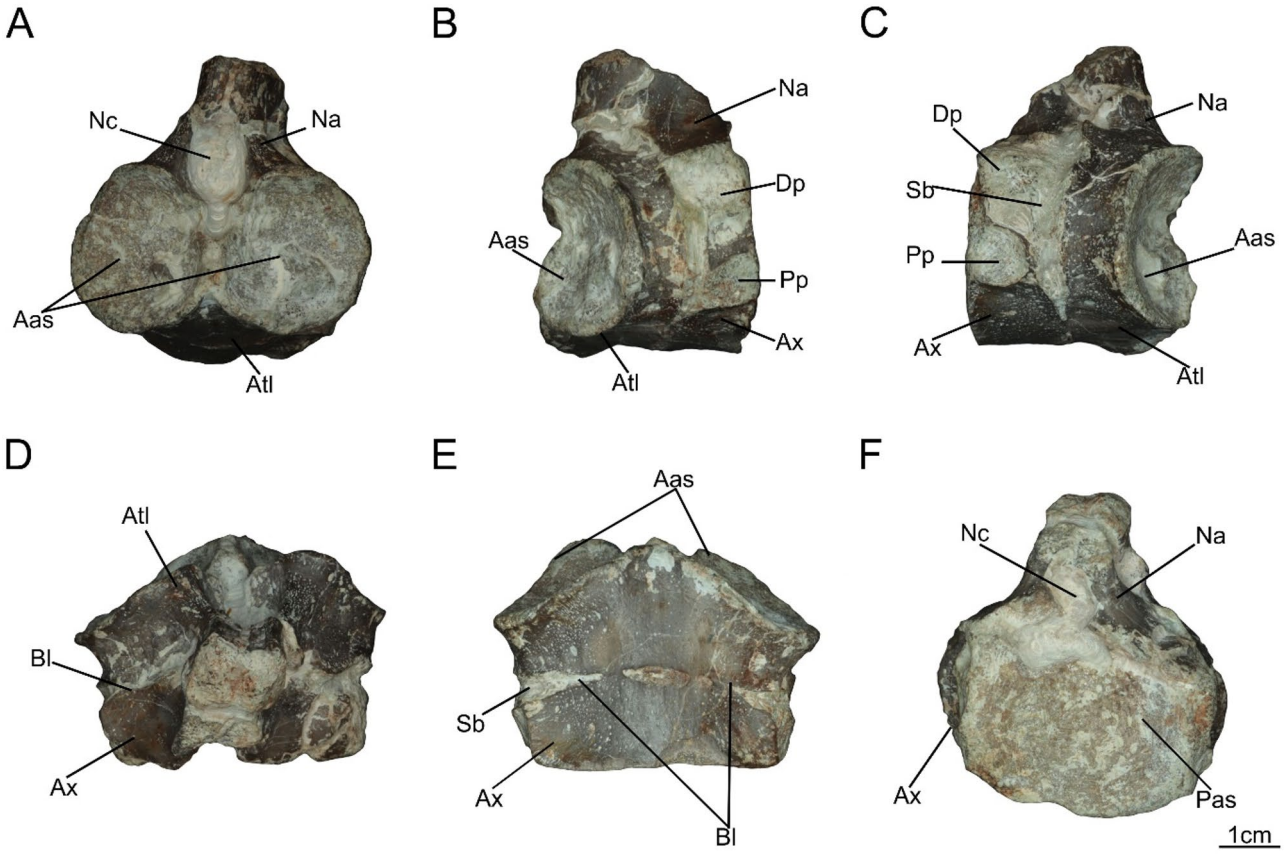

Fig. 2. UOPB 3652. Fused cervical vertebrae (atlas and axis) of *Metoposaurus krasiejowensis*. A – Anterior view, B – Left lateral view, C- Right lateral view, D – Dorsal view, E – Ventral view, F – Posterior view. Aas – Anterior articular surface, Atl – Atlas, Ax – Axis, Bl – Border line, Dp – Diapophysis, Na – Neural arch, Nc – Neural canal, Pas – Posterior articular surface, Pp – Parapophysis, Sb – Spongy bone tissue.

of the vertebral bodies, a very prominent and deep rhomboidal fossa is visible, the top of which is directed obliquely backward.

The two elements of the vertebral column are fused by several millimeter-thick spongy sutures. The connection is strongest on the ventral surface in the midline, where two thick bars of solid bone connect the two elements (Fig. 3). The suture extended to the area between the parapophyses. On the lateral surfaces, the suture forms an elevated bulge. The bone is porous, but the texture is much finer than the porous texture of the intercentrum surface.

UOPB 3632

The specimen consists of two fused vertebrae, which are presacral vertebrae, as evidenced by the presence of both anterior and posterior parapophyses on each centrum (fovea costalis superior and inferior) and the shape of the constriction between them (under the missing pediculus arcus, centrodiapophyseal fossa)[7] (Fig. 4).

The anteroposterior length of the two fused vertebrae (measured on the ventral surface at the midline) was 42.7 mm. The anterior element is 22.6 mm in length, and the posterior element is 20.1 mm in length. The exposed articular surfaces (anterior surface for the anterior vertebra and posterior surface for the posterior vertebra) are slightly concave (amphicoelous). Both vertebrae are slightly elliptical, with an articular surface width to height ratio of approximately 4:3 (32.9 mm to 26.9 mm in the posterior element). The articular surface slightly exceeds the outline of the vertebral intercentrum, with a distinct indentation in the midline of the ventral surface. The neural arches are not preserved; probably, they are not involved in vertebral fusion. Vertebra centra are covered with extensive networks of pits and grooves (much more prominent and deeper, which is particularly evident in the posterior part of the second vertebra near the edge of the vertebral body), which can often also be observed in isolated vertebrae of *Metoposaurus*.

The dorsal surface of the specimen is covered with strongly cemented sediment to which a very poorly preserved fragment of long bone (most likely a rib) is attached. The fragment was additionally coated with cyanoacrylate glue to secure the specimen, making preparation difficult. The entire right dorsal portion of the specimen above the parapophyses was damaged during excavation, and a prominent defect was visible, exposing the cancellous tissue of the bone. The anterior and posterior parapophyses on the left side of the vertebral bodies are well preserved. The anterior parapophyses are semicircular in shape, whereas the posterior parapophyses are slightly larger, and their surface is more angular and more strongly drawn toward the dorsal part of the vertebral

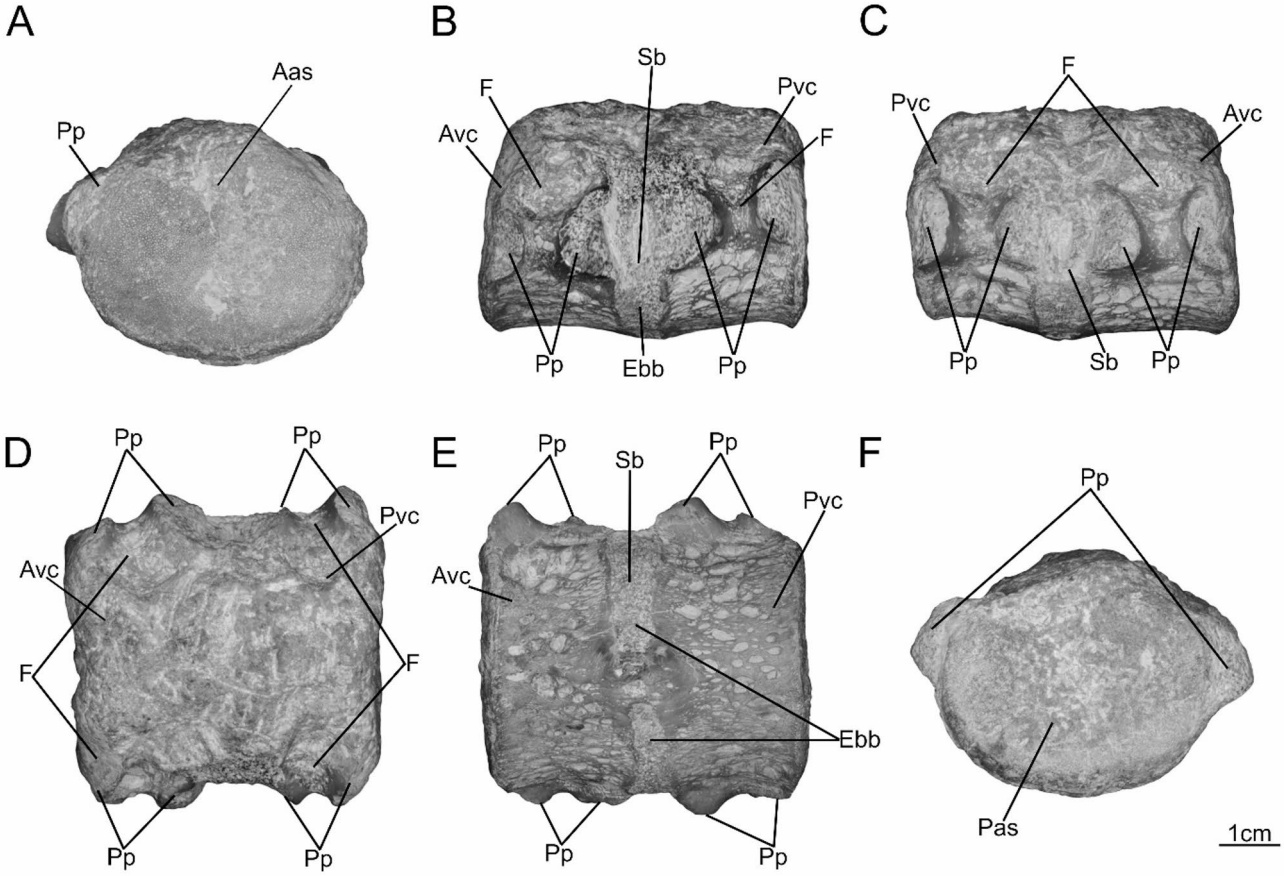

Fig. 3. UOPB 3631. Fused presacral vertebrae of *Metoposaurus krasiejowensis*. A – Anterior view, B – Left lateral view, C- Right lateral view, D – Dorsal view, E – Ventral view, F – Posterior view. Aas – Anterior articular surface, Avc – Anterior vertebral centrum, Ebb – Elevated bony bulge, F – Fossae, Pas – Posterior articular surface, Pp – Parapophyses, Pvc – Posterior vertebra centrum, Sb – Spongy bone tissue.

centers. The parapophyses on the right side of the vertebral bodies, except for the anterior parapophysis of the second vertebra in the row, are very poorly preserved and partially broken. Fossae in the vertebral bodies above the parapophyses on the left side of the specimen are visible but are clearly obliterated and partially covered by sediment. On the right side of the specimen, these fossae are not preserved.

The two elements of the vertebral column are fused more firmly than those in specimen UOPB3631. No spongy suture is visible; instead, there is a thick (5–6 mm) firm connection between the elements (Fig. 4). The suture extends from the ventral surface up to the area between parapophyses. On the lateral surfaces, the suture forms an elevated bulge. While the surface of the intercentra is distinctly porous, the surface between the vertebrae is smooth and shiny.

UOPB 3633

The specimen consists of two fused vertebrae, which are the anterior caudals. Although the dorsal surface of the specimen is heavily damaged (probably post mortem), a notch for chordal canal indentation running through the entire length of both centra is clearly visible. The anteroposterior length of the two fused vertebrae (measured on the ventral surface at the midline) was 34.2 mm. The anterior element is 17.4 mm in length, and the posterior element is 16.7 mm in length. Both vertebrae are slightly trapezoidal, with an articular surface width to height ratio of approximately 7:6 (27.7 mm to 24 mm in the anterior element and 27.1 mm to 23.6 mm in the posterior element). The anterior articular surface of the anterior vertebra is convex, and the posterior surface of the posterior vertebra is strongly concave (opisthocoelous). The neural arches are not preserved; probably, they are not involved in vertebral fusion. Vertebra centra are covered by few pits and grooves (far less numerous than in the previously described specimens). Both vertebrae have single, prominent and horizontally elongated parapophyses on each side (Fig. 5).

The two elements of the vertebral column are fused by several millimeter-thick spongy sutures. In the lower part of the specimen, a faint border between the centra is visible on the suture. The connection is strongest on the lateral sides of the vertebrae just below the line of the parapophyses. On the lateral surfaces, the suture forms an elevated bulge. The bone is porous, but the texture is much finer than the porous texture of the intercentrum surface.

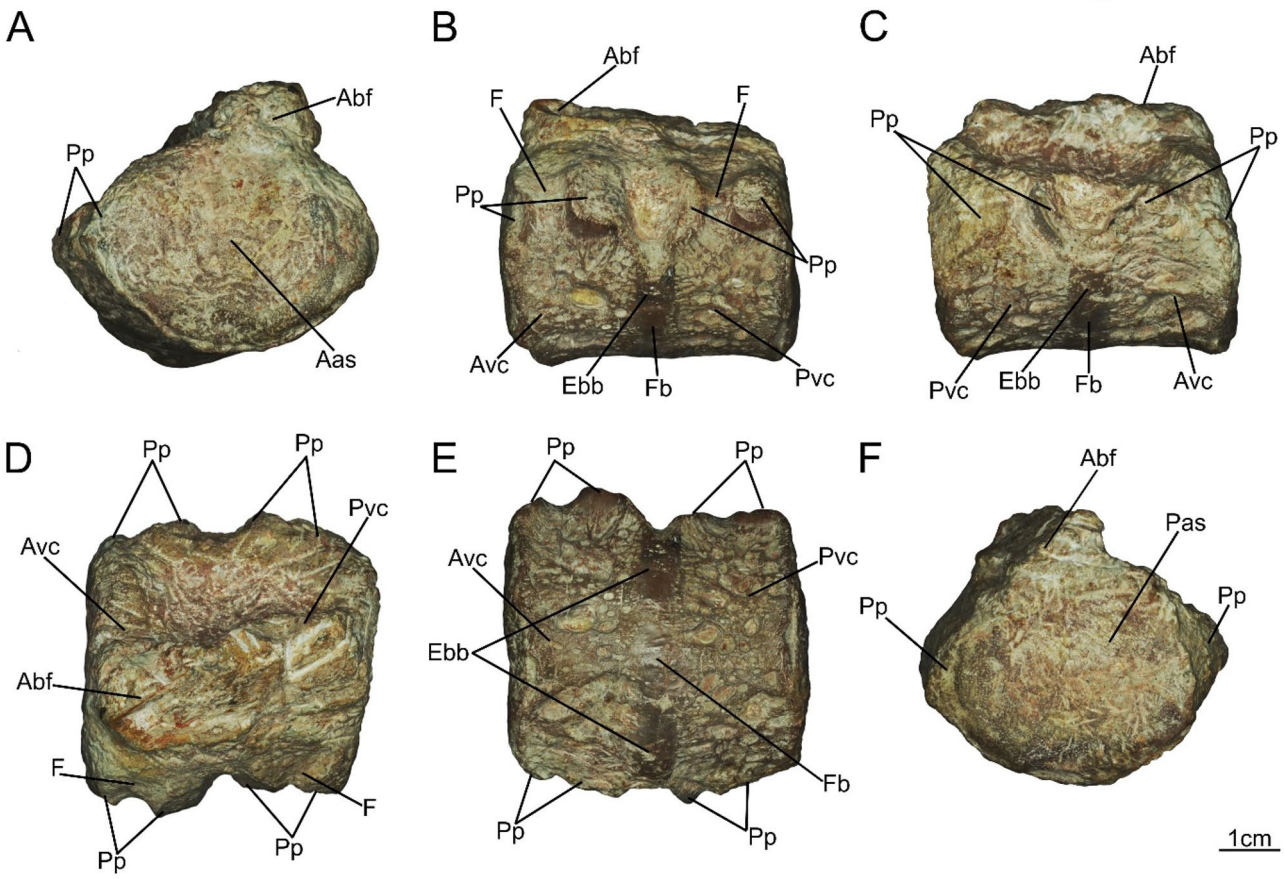

Fig. 4. UOPB 3632. Fused presacral vertebrae of *Metoposaurus krasiejowensis*. A – Anterior view, B – Left lateral view, C- Right lateral view, D – Dorsal view, E – Ventral view, F – Posterior view. Aas – Anterior articular surface, Abf – Attached bone fragment, Avc – Anterior vertebral centrum, Ebb – Elevated bony bulges, F – Fossae, Fb – Fused bone, Pp – Parapohyses, Pvc – Posterior vertebral centrum.

UOPB 3634

The specimen consists of well-preserved co-ossified one and a half intercentra, which are anterior dorsals on the basis of the shape of the parapophyses and the shape of the constriction behind it (centrodiapophyseal fossa)[7] (Fig. 6).

The length of the posterior element (full vertebra) was 21.1 mm. The articular surface (posterior) is amphicoelous and slightly transversely elongated (elliptical – 36.5 mm × 27.3 mm). On the lateral surfaces of the posterior vertebra, prominent deltoid parapophyses are visible, connecting to the posterior margin of the vertebra. A single parapophysis located on the middle of the shaft of the first vertebra (on the right surface of the specimen) is deformed and displaced toward the dorsal side. The ventral surface of the intercentrum is less porous than in specimens UOPB 3661 and 3662 but contains far more cavities than UOPB 3663. The pores are irregularly distributed, oval shaped and are both oriented parallel to the axis of the vertebral body and perpendicular to it. On the right side, the fully developed vertebra is connected with another, which is only partially developed. Half of the anterior vertebra is smoothly connected with the posterior vertebra. A slight suture between the elements is visible, resembling sutures in the skull rather than the pathological overgrowths observed earlier.

The angle between the transverse axes of the intercentra was measured as proposed by[27]. The angle is 30°.

UOPB 3653

The specimen consists of poorly preserved and abraded co-ossified one and a half intercentra, which are probably anterior dorsal, on the basis of the presence of a single parapophysis on the lateral surfaces of the vertebrae and the shape of the constriction behind it (centrodiapophyseal fossa)[7] (Fig. 7).

The second (posterior) vertebral body in the specimen is severely deformed post mortem. The length of the ventral surface of the vertebra is 28.4 mm. In the dorsal direction, the vertebral body flattens strongly, and in the uppermost part, its length is 21.1 mm. The articular surface (posterior) is amphicoelous and slightly transversely elongated (elliptical – 48.5 mm × 39 mm). A single, prominent and elongated parapophysis is preserved on the lateral (left) surface of the posterior vertebra. The parapophysis on the right side of this vertebra is highly abraded and almost invisible. A single parapophysis located on the middle of the shaft of the first vertebra on the

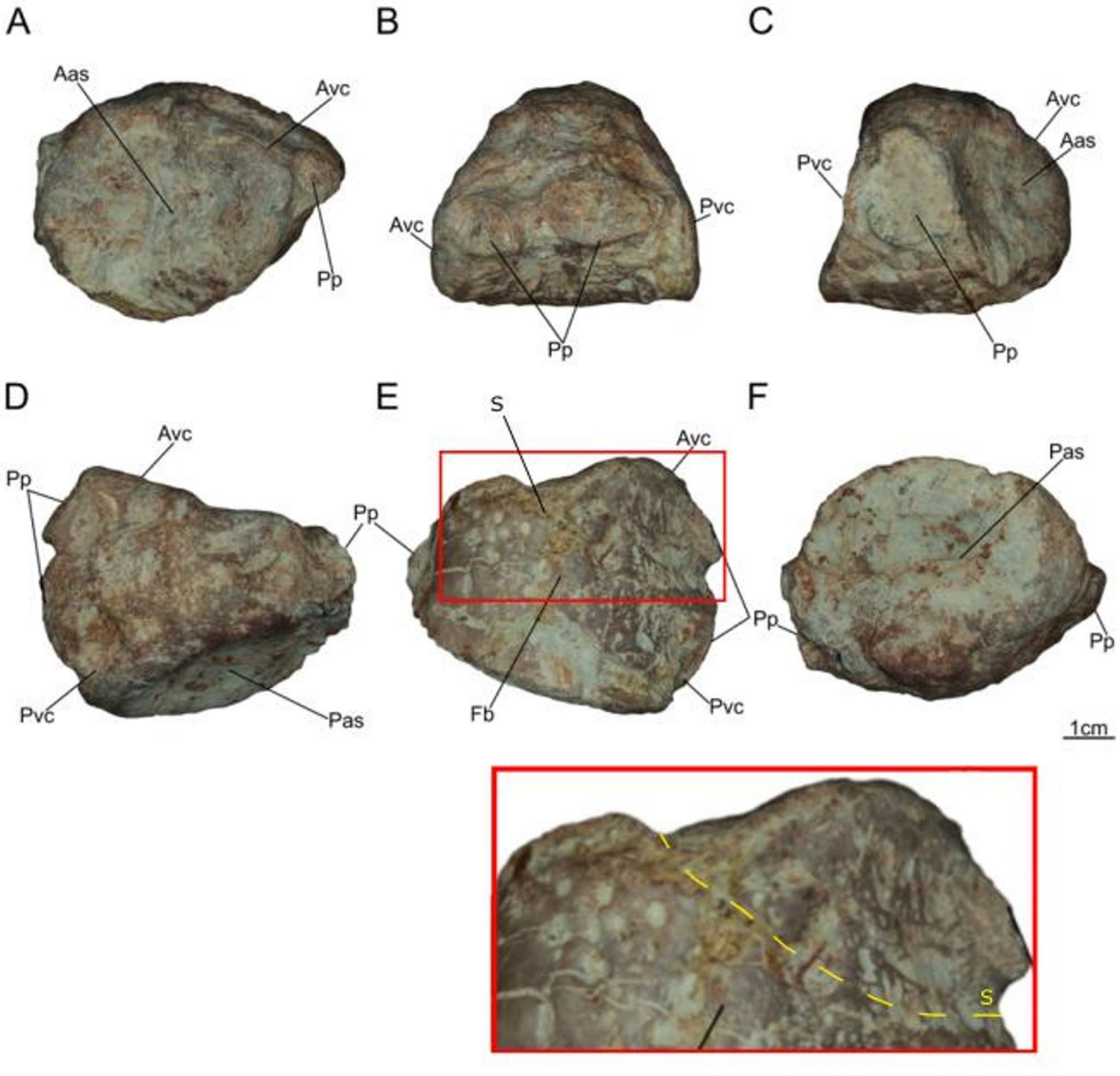

Fig. 5. UOPB 3633. Fused caudal vertebrae of *Metoposaurus krasiejowensis*. A – Anterior view, B – Left lateral view, C- Right lateral view, D – Dorsal view, E – Ventral view with magnification of suture framed, F – Posterior view. Aas – Anterior articular surface, Avc – Anterior vertebral centrum, Bl -Border line, Fb -Fused bone, Pp -Parapohyses, Pvc – Posterior vertebral centrum, S – suture, Sb – Spongy bone tissue.

left side is smaller and is directed slightly forward. The lower surface of the vertebrae is covered with numerous prominent pores, especially on the left side of the specimen. These pores diverge in a stellate manner from the suture between the vertebrae below the parapophyses. On the right side of the lower surface, the pores are less numerous and irregularly arranged. On the left side, the fully developed vertebra is connected with another, which is only partially developed. Half of the anterior vertebra is smoothly connected with the posterior one. A slight suture between the elements is visible. The anterior articular surface of the specimen is directed strongly to the right and slightly upward.

Discussion

The fused vertebrae in specimens UOPB 3631, 3632 and 3633 of *M. krasiejowensis* are most likely examples of spinal arthropathy. This term includes a group of different rheumatic diseases resulting in ossification of the vertebral column or other skeletal element synovial joints, tendons or ligaments[31]. This may be a result of injuries or bacterial infection[32]; *Brucella* spp. may cause arthritis in modern toads[33]).

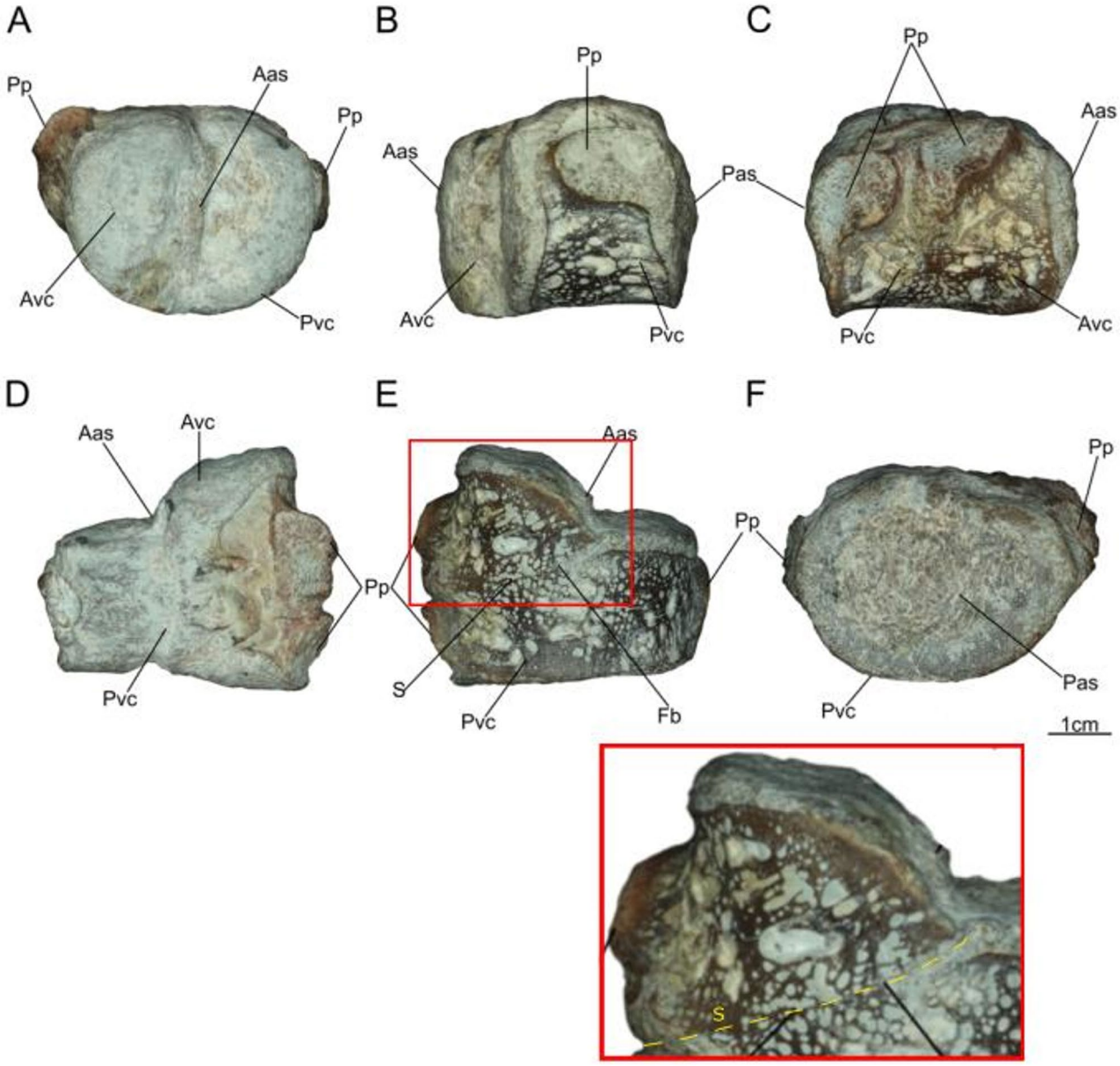

Fig. 6. UOPB 3634. Vertebra fused with hemivertebra of *Metoposaurus krasiejowensis*. A – Anterior view, B – Left lateral view, C- Right lateral view, D – Dorsal view, E – Ventral view with magnification of suture framed, F – Posterior view. Aas – Anterior articular surface, Avc – Anterior vertebral centrum, Fb – Fused bone, Pp – parapohyses, Pvc – Posterior vertebral centrum, S – Suture.

Spinal arthropathy results in the formation of new bone and erosion of old tissue. New bone forms within the synovial membrane[34] of the intervertebral joint. Thus, fracture and formation of a callus can be excluded.

Similar conditions were previously described in the fossil record, e.g., in proboscideans[35] and multiple representatives of ungulates[36]. However, in pre-Cenozoic vertebrates, it was noted only several times, e.g., in Triassic phytosaurs[34] and Cretaceous snakes[37]. The oldest evidence for pathological fusion of vertebrae is the case of Lower Triassic archosaurian reptile from the Karoo Basin (South Africa)[38]. Spinal arthropathy has also been found in modern amphibians, such as cane toads (*Chaunus marinus*)[39], but thus far, it has not been detected in Temnospondyli.

Specimen UOPB 3632, with a firm connection by a distinct bulge, resembles the condition of phytosaur vertebrae MB.R. 1972[34] interpreted it as arthropathic. A much smaller, thus not interpreted as arthropathic, bulge is also present between two fused *Metoposaurus algarvensis* centra in[24].

Specimens UOPB 3631 and 3633, with spongy connections, might represent earlier ontogenetic stages of vertebral fusion. The numerous pits and grooves on the ventral and ventrolateral surfaces of the vertebrae that form a spongy texture may be remnants of a partially cartilaginous character[25] or signs of erosion, which is often observed along with the ossification of the vertebral column joints[31].

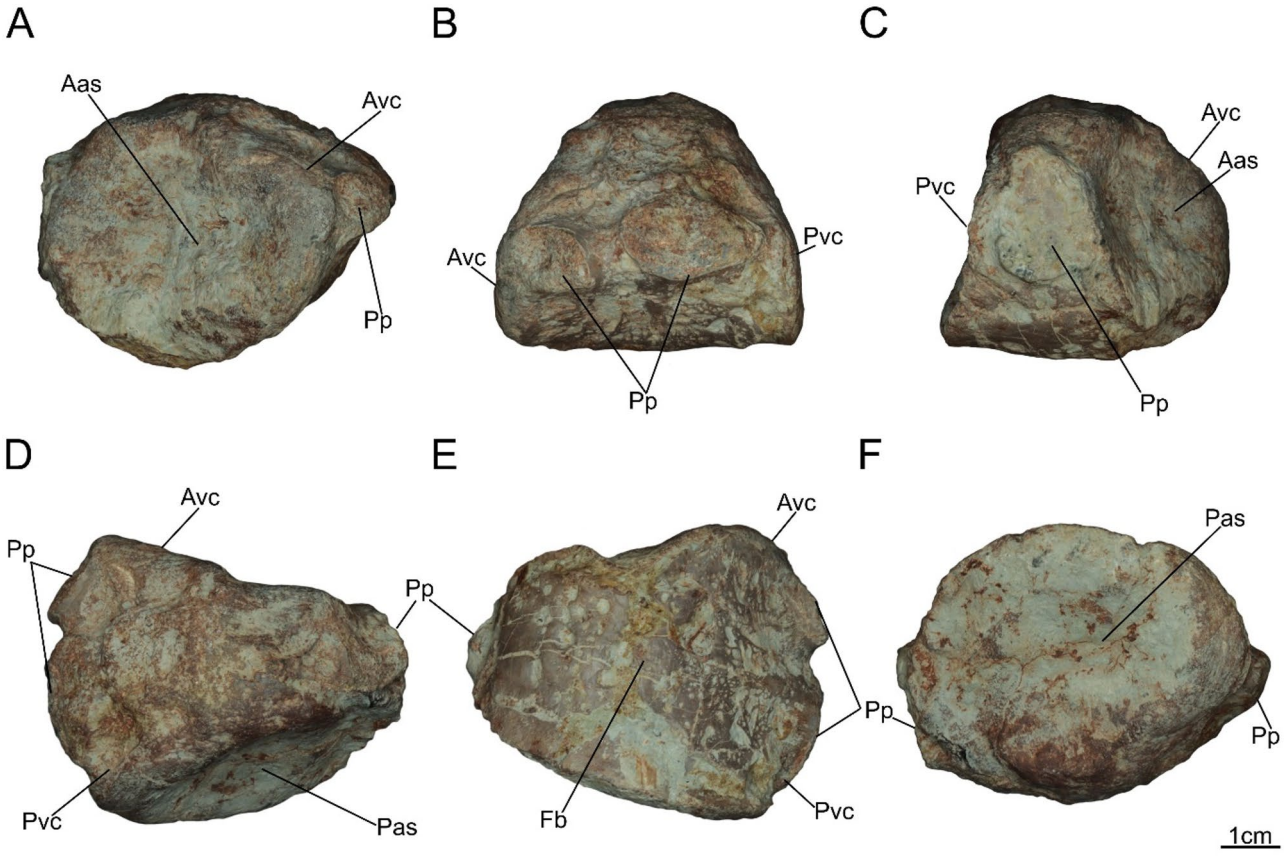

Fig. 7. UOPB 3653. Vertebra fused with hemivertebra of *Metoposaurus krasiejowensis*. A – Anterior view, B – Left lateral view, C – Right lateral view, D – Dorsal view, E – Ventral view, F – Posterior view. Aas – Anterior articular surface, Avc – Anterior vertebral centrum, Fb – Fused bone, Pp –Parapohyses, Pvc – Posterior vertebral centrum.

This state might be explained by several conditions: (1) spondyloarthropathy, (2) congenital fusion or (3) fusion of vertebrae caused by degenerative disease. In spondyloarthropathy, there should be signs of erosion on subchondral bone of joint surfaces. In the presented specimens such kind of erosion cannot be definitely recognised, because of poor state of preservation and signs of mechanical preparation. Moreover, the zygapophyses are not connected with intercentra, so it is impossible to determine if they were involved in vertebral fusion. This lack of evidence (no joint erosion; zygapophyses not preserved) precludes spondyloarthropathy as a definite diagnosis. Other possible explanation is congenital fusion, however less possible as in the case of failure of segmentation early in ontogenesis, the fused intercentra surface would be less prominent (without bulge) and more unified[26]. Presented specimens possess distinct fusion in form of elevated bulge - similar to outer ridges of articular surfaces of vertebra. This suggests the fusion of two separate elements rather than failure of segmentation. The last possible explanation is fusion of vertebrae cause by degenerative disease, however it is the least probable one, because of lack of outgrowths of degenerative tissue, as seen in e.g. *Plioplatecarpus*[32]. There are also no signs of injury.

The present pathological condition of the metoposaurid vertebrae is one of the oldest known examples in the fossil record, as well as the first evidence for this disease in fossil amphibians (i.e., temnospondyls) and the first example where different stages of the disease can be observed from one site.

Another pathological condition of the vertebral column observed in modern animals and their fossil relatives is scoliosis. Bending of the vertebral column may be the effect of soft tissue abnormalities (e.g., parasitic infection in tiger salamanders[40]), although it is usually associated with pathological growth of the vertebrae. In modern reptiles (snakes and sand lizards), the occurrence of vertebral scoliosis may be a result of extremely high incubation temperatures[41].

The nature of specimen UOPB 3634 is more likely the result of segmentation failure early in ontogeny, i.e., disruption of genes regulating embryonic somite formation[24]. A delicate suture between the elements and the partially formed posterior vertebra implies that they were formed in this way. These conditions are known from modern amphibian observations. The so-called lateral hemivertebra, characterized by the lack of formation of one half of the vertebra, might be fully segmented or fused with the anterior, posterior or both adjacent vertebrae[42]. Specimen UOPB 3634 is in a nonsegmented condition[43].

Hemivertebrae were previously noted in the fossil record for Permian *Sclerocephalus*, *Stereosternum* and Upper Jurassic *Dysalotosaurus*[24,44,45], the former being the oldest known example of congenital hemivertebra. Hemivertebra-induced scoliosis was also found in Middle Triassic temnospondyl[27].

Hemivertebra causes scoliosis due to bending of the vertebral column, which, in this case, is even greater than that described by[27]: 30° vs. 20°. This may affect the locomotion of the animal, reducing flexibility and impeding swimming. According to new interpretations, metoposaurids were rather active hunters/ambush predators that used direct biting instead of suction feeding[21,46,47]). The average size of the vertebrae may suggest that the individuals survived long enough thus the pathology did not prevent animals from foraging effectively.

Failure in the embryonic formation of vertebrae may also cause the formation of wedge block vertebrae where disc spaces between adjacent vertebrae are very narrow or fused[48]. In such cases, the vertebrae are firmly fused with no outgrowths or signs of the former synovial joint. This condition can be observed in the UOPB 3652 specimen, where the contact between vertebrae is smooth and a very narrow space between the intercentra can be observed. Although congenital vertebral pathologies are known from fossil reptiles and amphibians, including temnospondyls[24] dating back to the Permian[44], they are very rare in the cervical vertebrae. The joining of the atlas and axis (two first cervical vertebrae) has been described, e.g., in eastern wapiti[49], but not in Mesozoic tetrapods. The presented specimen is the oldest case of block vertebrae of the atlas and axis in the fossil record and is the first example among fossil amphibians.

For an alternative timing of the onset of this pathology, we note that in recent amphibians, thyroid hormone activity during metamorphosis has a major impact on skeletogenesis[50], but considering that a distinct tadpole stage was not present in stereospondyls[51], we favor the embryonic stage as the time of origin of the pathology present in UOPB 3652. Permanent neck sprain in juvenile specimens may be the cause of death before adult size is acquired.

Conclusion

Pairs of fused vertebrae of *Metoposaurus krasiejowensis* show three different pathological conditions. One (UOPB 3634 and 3653) is previously known from temnospondyl records as an example of lateral hemivertebra resulting in scoliosis. The second category includes wedge block vertebrae of the atlas and axis. Both of these effects involve the disruption of genes during embryonic development and failure of spine segmentation[24]. The third example (UOPB 3631, 3632, 3633) is most likely an example of spinal arthropathy scarcely represented in the fossil record; it is one of the oldest known examples of this condition and was first described in nonamniotic tetrapod representatives[31]. Two kinds of preservation of fusion between adjacent vertebrae possibly represent two stages of pathological conditions. Specimens UOPB 3631 and 3633, with porous, spongy structures in place of cartilaginous joints between vertebrae, represent the first stage of ossification. Specimen UOPB 3632 has a firm bony connection between adjacent elements, forming a distinct bulge that represents the final stage of arthritis after continuous ossification of the vertebral joint. Specimen UOPB 3652 represents the oldest known example of a block joint between the atlas and the axis. UOPB 3631-33 are the first described examples of spinal arthritis in fossil amphibians (Temnospondyli).

Data availability

All data pertaining to this research are included in the paper. The specimens are housed in the collection of the University of Opole and have been described and photographed with the consent of the Head of the Department of Paleobiology and University of Opole Rector's authorized representative for the paleontological site in Krasiejów. The paleontological excursions at the 'Trias' documentation site were conducted under the supervision of the Department of Paleobiology with the permission of local municipality (Gmina Ozimek).

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Author contributions

M.A., J.K., D.M. and K.K. wrote the main manuscript text and P.J. and M.A. prepared the figures. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

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