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An early Late Triassic long-necked reptile with a bony pectoral shield and gracile appendages

JERZY DZIK and TOMASZ SULEJ



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Several partially articulated specimens and numerous isolated bones of *Ozimek volans* gen. et sp. nov., from the late Carnian lacustrine deposits exposed at Krasiejów in southern Poland, enable a reconstruction of most of the skeleton. The unique character of the animal is its enlarged plate-like coracoids presumably fused with sterna. Other aspects of the skeleton seem to be comparable to those of the only known specimen of *Sharovipteryx mirabilis* from the latest Middle Triassic of Kyrgyzstan, which supports interpretation of both forms as protorosaurians. One may expect that the pectoral girdle of *S. mirabilis*, probably covered by the rock matrix in its only specimen, was similar to that of *O. volans* gen. et sp. nov. The Krasiejów material shows sharp teeth, low crescent scapula, three sacrals in a generalized pelvis (two of the sacrals being in contact with the ilium) and curved robust metatarsal of the fifth digit in the pes, which are unknown in *Sharovipteryx*. Other traits are plesiomorphic and, except for the pelvic girdle and extreme elongation of appendages, do not allow to identify any close connection of the sharovipterygids within the Triassic protorosaurians.

Key words: Archosauromorpha, *Sharovipteryx*, protorosaurs, gliding, evolution, Carnian, Poland.

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Introduction

Relatively well-articulated, large tetrapod skeletons abundantly occur in dense concentrations of hundreds of specimens in the lacustrine sediment bed in the former clay-pit at Krasiejów in Upper Silesia, south-western Poland (Dzik and Sulej 2007). These large skeletons overshadow the more uniformly distributed smaller reptile fossils from the same beds. The most common of these smaller reptiles belong to a species that remarkably shows extremely elongated appendages and neck, thin-walled long bones with an empty interior and a shield-like pectoral girdle. This anatomy resembles that of *Sharovipteryx mirabilis* from the latest Middle Triassic of Kyrgyzstan, preserved with patagium, which suggests a gliding adaptation. Most examples of this small reptile are partial skeletons probably dismembered by decay, which may explain the chaotic distribution of bones, or by scavengers. Some specimens are curled with most bones displaced and closely packed, which suggests that these are possibly coprolites or regurgulites. In this paper we restore the skeleton of this enigmatic animal and compare it with Triassic reptiles of more or less similar anatomy in the hope of determining its evolutionary relationships and possible mode of life.

Institutional abbreviations.—UOPB, Chair of Biosystematics, University of Opole, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting

The former clay-pit at Krasiejów in southern Poland (now protected by law as a geological sanctuary) exposes a sequence of variegated, mostly fine-grained mudstone and claystone beds with thin lenses of calcareous grainstone (Dzik et al. 2000). Such rock units are known from various levels of the Keuper in the Germanic Basin and because of generally uniform lithology, the age and sedimentological interpretation of the strata continue to be subject to controversy (reviewed by Dzik and Sulej 2007; Szulc et al. 2015). Most of the sequence is unquestionably of fluviatile origin but the fossils under study occur in the one-meter thick la-

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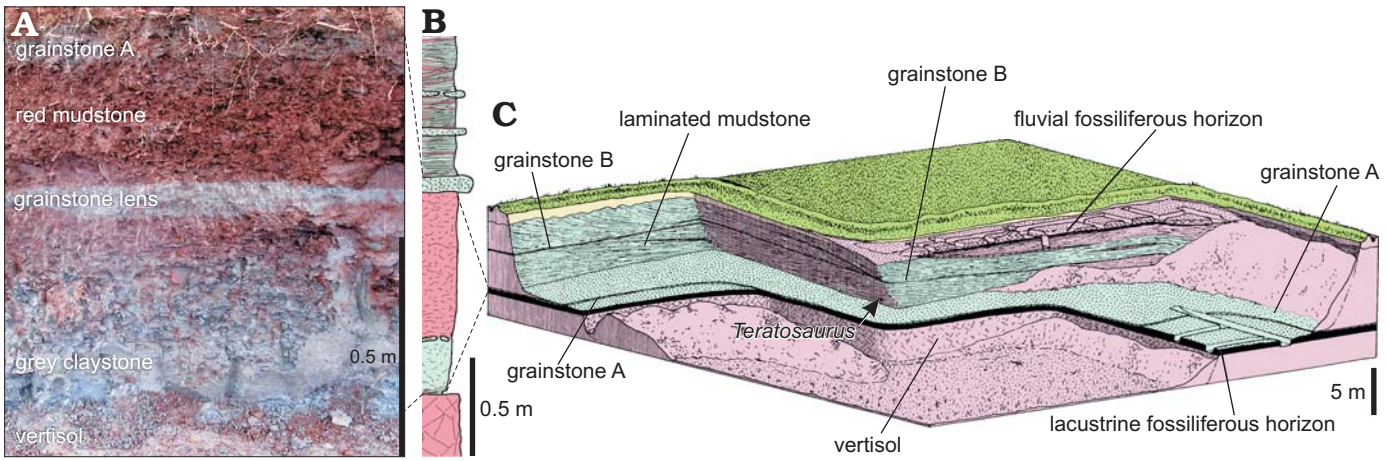


Fig. 1. Krasiejów claypit yielding *Ozimek volans* gen. et sp. nov. **A**. Photograph of the quarry wall with exposed fossiliferous lacustrine horizon. **B**. Rock column of strata of lower Upper Triassic exposed at Krasiejów and position of the lacustrine bed (modified after Dzik et al. 2000). **C**. Diagrammatic representation of the NW corner of the quarry with location of the lacustrine bed indicated (modified after Dzik 2003).

custrine horizon in the upper part (Fig. 1) where the dominant species are aquatic or semi-aquatic animals. These include the temnospondyl *Metoposaurus* and the phytosaur *Parasuchus* (Kammerer et al. 2016). They are followed in abundance by their probable prey consisting of ganoid and dipnoan fishes, as well as aquatic invertebrates and charophyte algae (Dzik and Sulej 2007). There was also a steady contribution from the surrounding terrestrial environments to the lake environment. These include the armored aetosaur *Stagonolepis*, possible dinosauriform *Silesaurus*, crocodile-like labyrinthodont *Cyclotosaurus*, and the predatory rauisuchian *Polonosuchus*. Charophyte gyrogonites are abundant throughout the entire lacustrine horizon (Zatoń et al. 2005), which indicates that shallow freshwater conditions existed at deposition. This taken together with conchostracans occurring within the fauna (Olempska 2004) suggest an abundance of periodic ponding at a lake shore. Forest flora and insect remains indicate that these ponds were part of a complex terrestrial ecosystem. Small reptiles are generally rare within the fauna and are represented by the new species documented in this work, sphenodonts and a few unidentified species (Dzik and Sulej 2007). Presumably, gliding individuals of *Ozimek volans* gen. et sp. nov. sunk into a lake environment and their cadavers decayed there or else were scavenged by aquatic amphibians and reptiles.

According to Bodzioch and Kowal-Linka (2012) the barite infill of the osteonal and trabecular spaces of bones of the armored terrestrial aetosaur from Krasiejów indicates that their early diagenetic history was outside the aquatic environment and that they were subsequently transported to the lacustrine environment. In this respect the bones of terrestrial reptiles differ from the co-occurring bones of metoposaurid temnospondyls that were adapted to aquatic life. This suggests periodic flooding events as the cause of redeposition. The adaptation to an aquatic lifestyle of the majority of the fossilized inhabitants of the Krasiejów lake argues against the scenario raised by Bodzioch and Kowal-Linka (2012) who proposed that this was a periodic pond that quickly dried and filled with sediment. Such a scenario may be applicable to the bone-bearing mudstone bodies below and above the main lake horizon in Krasiejów where fossils of aquatic organisms are entirely absent. It does not also seem consistent with the inferred biology of *Metoposaurus*, an animal that was apparently unable to walk on the land (Sulej 2007). Its shortened tail suggests that it used an underwater locomotion style of the synchronous movement of its appendages (Sulej 2007). Equally strong was the adaptation to semi-aquatic life by the phytosaur *Paleorhinus* (*Parasuchus*), which had nostrils near the top of the head (Sereno 1991). The dipnoan fish *Ptychoceratodus* that is commonly found in the lacustrine horizon (Skrzycki 2015) was of size and morphology similar to the present day Australian *Neoceratodus*. This fish is incapable of surviving complete desiccation of its habitat (Kemp 1985), and apparently reached its large size after many years of life in the lake. However, a possibility remains that the great accumulations of disarticulated *Metoposaurus* and phytosaur skeletons in the middle of the lacustrine bed may have resulted from catastrophic causes. This includes a prolonged drought and subsequent desiccation of the lake, which may be seen by metoposaurs gathering and dying in the disappearing ponds. At this level of the lacustrine bed lenses of a grainstone composed of small limestone concretions occur that were apparently concentrated by winnowing (Fig. 1A). They may mark the first stage of restoration of the lacustrine regime after its retreat. The bed above is a red mudstone full of disarticulated bivalves of the genus *Silesunio*, chaotically distributed probably as a result of bioturbation and storms. Locally, winnowed calcareous grains and bones form lenses. There are also horizons with bivalves in life position that were probably killed by a sudden deposition of the mud (Skawina 2013). Most of the articulated *Ozimek* gen. nov. specimens were found at the boundary between the red upper and grey lower units of the lacustrine horizon, but not in the grainstone lenses. ZPAL AbIII/2012 (Figs. 2, 3) has its neck exposed at the discontinuity surface locally separating these units.

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The bed below the largest bone accumulation (Fig. 1A) does not differ from that above it except for its variegated red and grey coloration. Basally it gradually changes into a compact grey claystone with rare bivalves preserved with open articulated valves (Skawina and Dzik 2011) and conchostracans. Locally the bed is cut by chaotically distributed fissures filled with the sediment from above, which probably resulted from dehydration of the clay. Whether the fissures developed in connection with desiccation or it was an underwater process remains to be shown. Locally, a fine lamination of the claystone is visible. The base of the gray unit is marked by a thin layer of a soft laminated clay deposited on the vertisol erosional surface. In some depressions it is enriched with calcareous grains, plant detritus and small bones. Accumulations of partially articulated aetosaur and phytosaur skeletons have been found at this level. Fossils are absent in the red vertisol bed below (Gruszka and Zieliński 2008; erroneously attributed to the lacustrine unit by these authors).

Biostratigraphic evidence in support of a late Carnian age of the Krasiejów strata is offered by the conchostracan *Laxitextella laxitexta* (Jones, 1890) and the phytosaur *Parasuchus* (*Paleorhinus*) of ranges restricted to formations in the German part of the basin correlated with the marine late Carnian (Dzik et al. 2000; Dzik 2001; Olempska 2004; Dzik and Sulej 2007; Butler et al. 2014), as well as the Krasiejów flora that shows close similarity to that of the Coburg sandstone, of generally accepted Carnian age (Pacyna 2014). Szulc et al. (2015) and Szulc and Racki (2015) proposed Norian age for the Krasiejów strata based on lithostratigraphic correlation with formations of such an age in Germany, as interpreted by these authors. We are not able to support such dating on paleontological grounds.

Systematic palaeontology

Archosauromorpha von Huene, 1946

Family Sharovipterygidae Tatarinov, 1989

Genus *Ozimek* nov.

Type species: *Ozimek volans* gen. et sp. nov.; see below

Etymology: After the borough town Ozimek nearby the type locality.

Diagnosis.—As for type and only species.

Ozimek volans gen. et sp. nov.

Fig. 7.

Etymology: From Latin *volans*, flying.

Holotype: Incomplete skeleton ZPAL AbIII/2512 (Fig. 7).

Type locality: Krasiejów near Ozimek, Upper Silesia, Poland.

Type horizon: Lacustrine bed, probably late Carnian, early Late Triassic.

Material.—Articulated skeletons: ZPAL AbIII/2012 (Figs. 2, 3), partial skeleton including a crushed skull, that is somewhat displaced with respect to the almost complete neck, that is extended over the bedding plane surface, and which is continuous with the vertically oriented anterior part of the trunk. Incomplete humeri and partial radii and ulnae; are preserved in articulation. ZPAL AbIII/2511 (Figs. 4–6), the most complete, partially disarticulated skeleton, although without a skull. Its parts are distributed within the rock at different levels. The proximal part of the neck is crushed and continues into the similarly crushed anterior part of the thoraxin another piece of the rock, which shows also front appendages bones at a different level. The counterpart shows more details of the long bones and posterior part of the thorax in partial disarticulation, caudal vertebrae, and many other bones, which are chaotically distributed on the slab. After being superimposed on top of each other, bones from separate slabs show an almost complete skeleton (Fig. 4). ZPAL AbIII/2512 (Fig. 7; SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Dzik_Sulej_SOM.pdf), an almost complete curled skeleton lacking its head. Bones are preserved three-dimensionally in a limestone concretion and enable an accurate restoration of the pectoral girdle and a part of the vertebral column. ZPAL AbIII/3191 (Fig. 8, SOM 2), an almost complete partially articulated skeleton with disarticulated skull bones in the centre. The bones are preserved in a rather chaotic manner but several skull bones can be identified with some confidence. The specimen UOPB 1148: cervicals 5–8 in articulation, fragmentary coracoids(?), femur, humerus, and a partial pes. Cervicals: ZPAL AbIII/2051, c3; ZPAL AbIII/2456, c6; ZPAL AbIII/2499, c7–c9; ZPAL AbIII/2454, fragmentary c6 and c7, and crushed cervical found in proximity; ZPAL AbIII/2528, c7 and c8 in articulation; ZPAL AbIII/3196, c4. Dorsals: ZPAL AbIII/3192, d1–d4 in articulation; ZPAL AbIII/3202, d?. Humeri: ZPAL AbIII/2026; ZPAL AbIII/2028; ZPAL AbIII/2033, distal parts of humerus and femur; ZPAL AbIII/2459, humerus with crushed proximal part; ZPAL AbIII/2529, almost complete humerus with broken proximal head; ZPAL AbIII/3193, crushed. Femuri: ZPAL AbIII/2027, incomplete in articulation with incomplete tibia, fibula, and fragmentary gastralia; ZPAL AbIII/2451, distal part; ZPAL AbIII/2452; ZPAL AbIII/2458, distal part; ZPAL AbIII/2530, proximal part; ZPAL AbIII/3195, almost complete femur; ZPAL AbIII/3194, middle and distal portion; ZPAL AbIII/3197, incomplete with tibia and fibula in articulation; ZPAL AbIII/3199, distal part; ZPAL AbIII/3200, proximal part; ZPAL AbIII/3203, almost complete; ZPAL AbIII/3201, distal part with well preserved head. ZPAL AbIII/2525, tibia, fibula, and complete cervical rib; ZPAL AbIII/2526, tibia, fibula, and proximal part of tarsus; ZPAL AbIII/2527, complete broken tibia.

Diagnosis.—Enlarged coracoids that meet along the midline forming a slightly convex ventral shield; low, crescent shaped scapula.

Description.—*Skull*: Although fragmented, the two skulls provide information that enables a provisional restoration of

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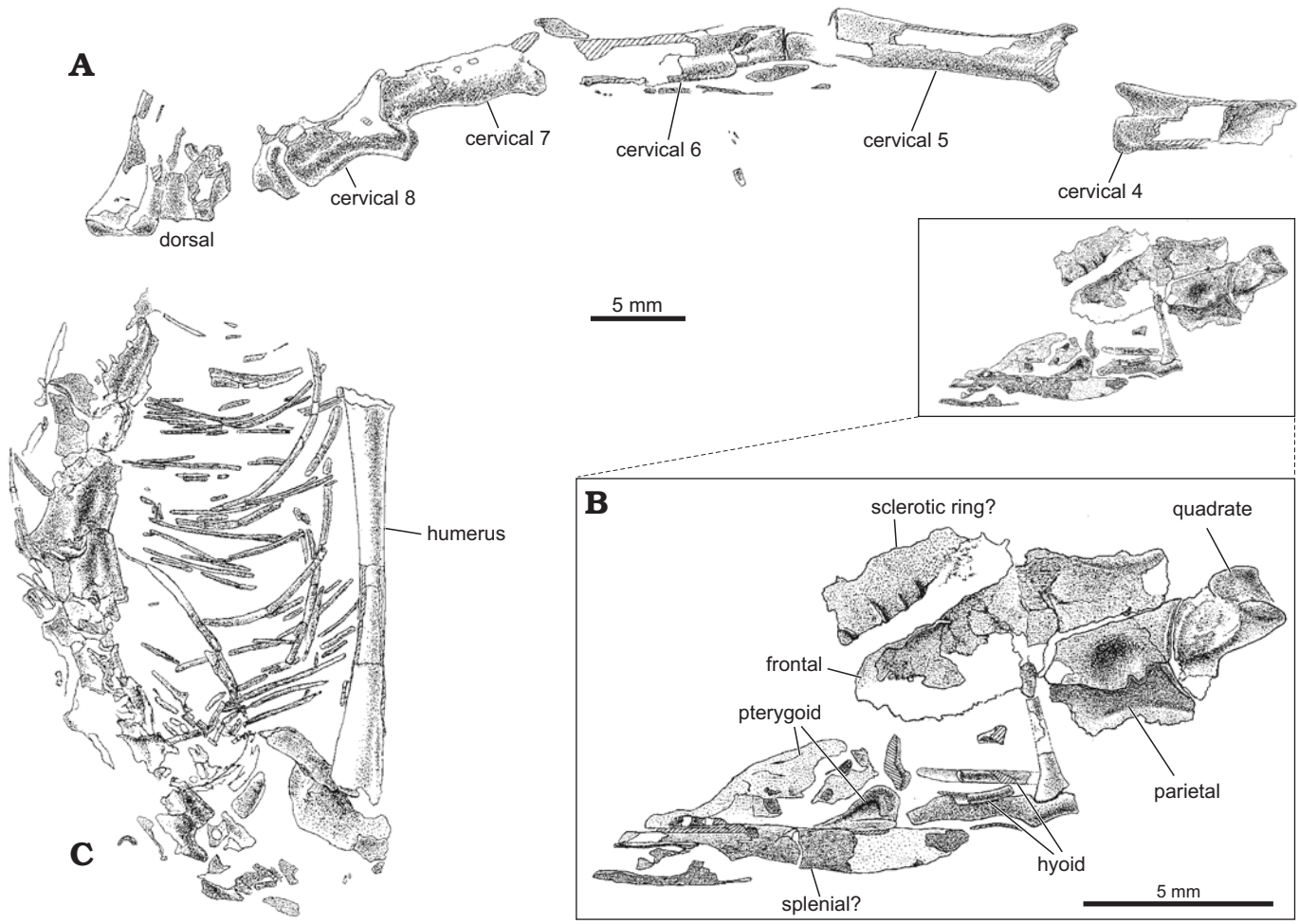


Fig. 2. Camera lucida drawings of ZPAL AbIII/2012, incomplete articulated skeleton of long-necked reptile *Ozimek volans* gen. et sp. nov. (see photographs Fig. 3). Neck with skull (**A**), skull (**B**), and torax (**C**).

the original disposition of the main bones (Fig. 8, SOM 2). The most striking aspect of the skull is its wide roof. This is apparent in ZPAL AbIII/2012 (Figs. 2, 3), in which crushed parietals and frontals are associated with palate and jaws, both poorly preserved and incomplete but showing proportions. An isolated parietal in ZPAL AbIII/3191 and a frontal with irregularly broken margins (Fig. 8, SOM 2) show a closely similar pattern.

The set of identified bones is incomplete. Thus, no remains of nasals or premaxillae have been identified. Significant parts of both left and right maxillae are preserved in ZPAL AbIII/3191 (Fig. 8, SOM 2) in occlusion with dentaries. Maxillary teeth are minute and sharp. Their size decreases posteriorly and it seems that about half of the jaw length was with dentition. A shallow shelf, thickening anteriorly, delimits the lower margin of the maxilla. This tooth-bearing part of the bone is robust and relatively wide, with its thickness equal to height. The wall of the maxilla joins the tooth-bearing part close to its dorsal external margin and is gently curved adaxially. The posterodorsal oblique suture of the maxilla with the jugal and other (not preserved) bones runs straight. Teeth are present almost to its tip, which suggests that this part of the bone was located well below the orbit. This leaves virtually no space for an antorbital fenestra, which was apparently missing.

The L-shaped robust bone found in the same specimen is interpreted here as the prefrontal, although there is rather poor support for its location in the skull. The bone shows an elevation along its central region, interpreted as an external "brow". The inferred dorsal margin is thin and oriented almost vertically. If it truly contacted the frontal, the skull roof was rather convex.

In ZPAL AbIII/2012 (Figs. 2, 3) there is an enigmatic bone that borders the frontal. It was apparently very thin and its imprint on the rock surface shows transverse ridges near the margin, probably reflecting furrows on the original bone surface. We interpret it as an ocular sclerotic ring with fused individual ossifications, although evidence for this is scarce.

The frontals are thin with straight external margins in its anterior and posterior parts, and which narrows anteriorly, as suggested by both ZPAL AbIII/2012 (Fig. 2, 3) and ZPAL AbIII/3191 (Fig. 8, SOM 2). It is difficult to infer anything about their geometry from the poorly preserved available specimens, in which other skull bones in close contact are hard to delimit. Much more informative are parietals. The right parietal in ZPAL AbIII/2012

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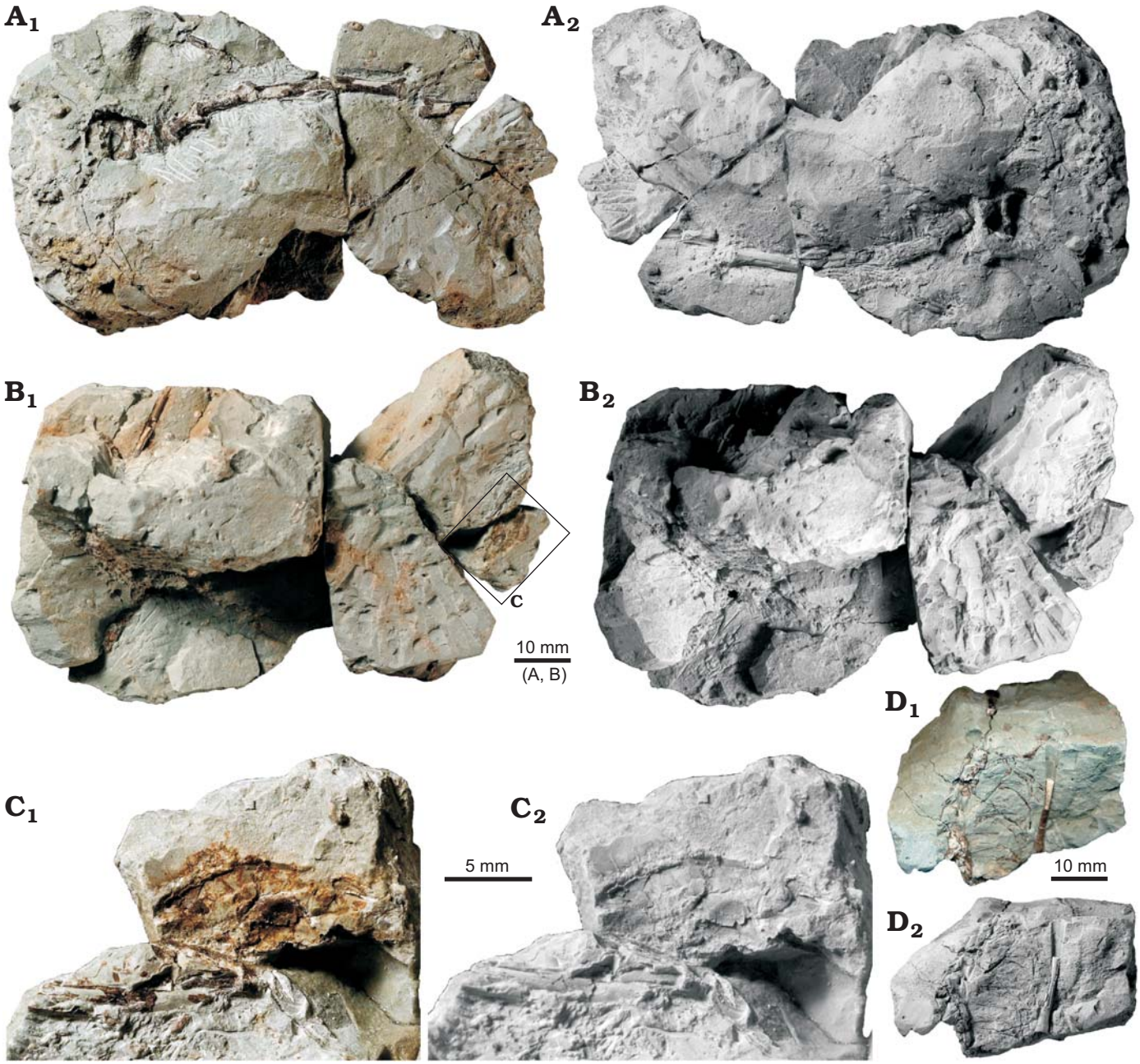


Fig. 3. Incomplete articulated skeleton ZPAL AbIII/2012 of long-necked reptile *Ozimek volans* gen. et sp. nov. from Krasiejów, lower Upper Triassic, preserved at a local sedimentary discontinuity surface between grey claystone and red fine-grained mudstone. View of the block from below (**A**) and above (**B**), showing location of the crushed skull; enlarged skull (**C**); part of the thorax (**D**), preserved in vertical orientation. Photographs of specimen whitened with ammonia chloride (A_2–D_2). See also explanatory drawing (Fig. 2).

(Figs. 2, 3) is the most complete. Its posterior margin is strongly thickened and concave. The central region of the bone is distinctly concave on its ventral surface. The posterolateral corner extends into a prominent process, which is completely preserved in ZPAL AbIII/3191. It apparently articulated with the squamosal, bordering the upper temporal fenestra. The dorso-medial margin of the fenestra was slightly angular in the middle.

The squamosal is relatively well preserved in ZPAL AbIII/3191 (Fig. 8, SOM 2). It is gently arched in dorsal view. Its anterior branch shows a deep indentation extending into a furrow, apparently the articulation site for the postorbital. The bone is of a rather large size, similar to that of *Langobardisaurus* (Saller et al. 2013). The very low ventral process of the squamosal is similar to that in *Tanystropheus longobardicus* (Wild 1973: fig. 9).

An incomplete quadrate left an imprint behind the parietal in ZPAL AbIII/2012 (Figs. 2, 3) and both right and left quadrates are three-dimensionally preserved in ZPAL AbIII/3191 (Fig. 8, SOM 2). They both show a robust dorsal head, articulating with the squamosal and two-headed ventral condyle joint with the lower jaw. These dorsal and

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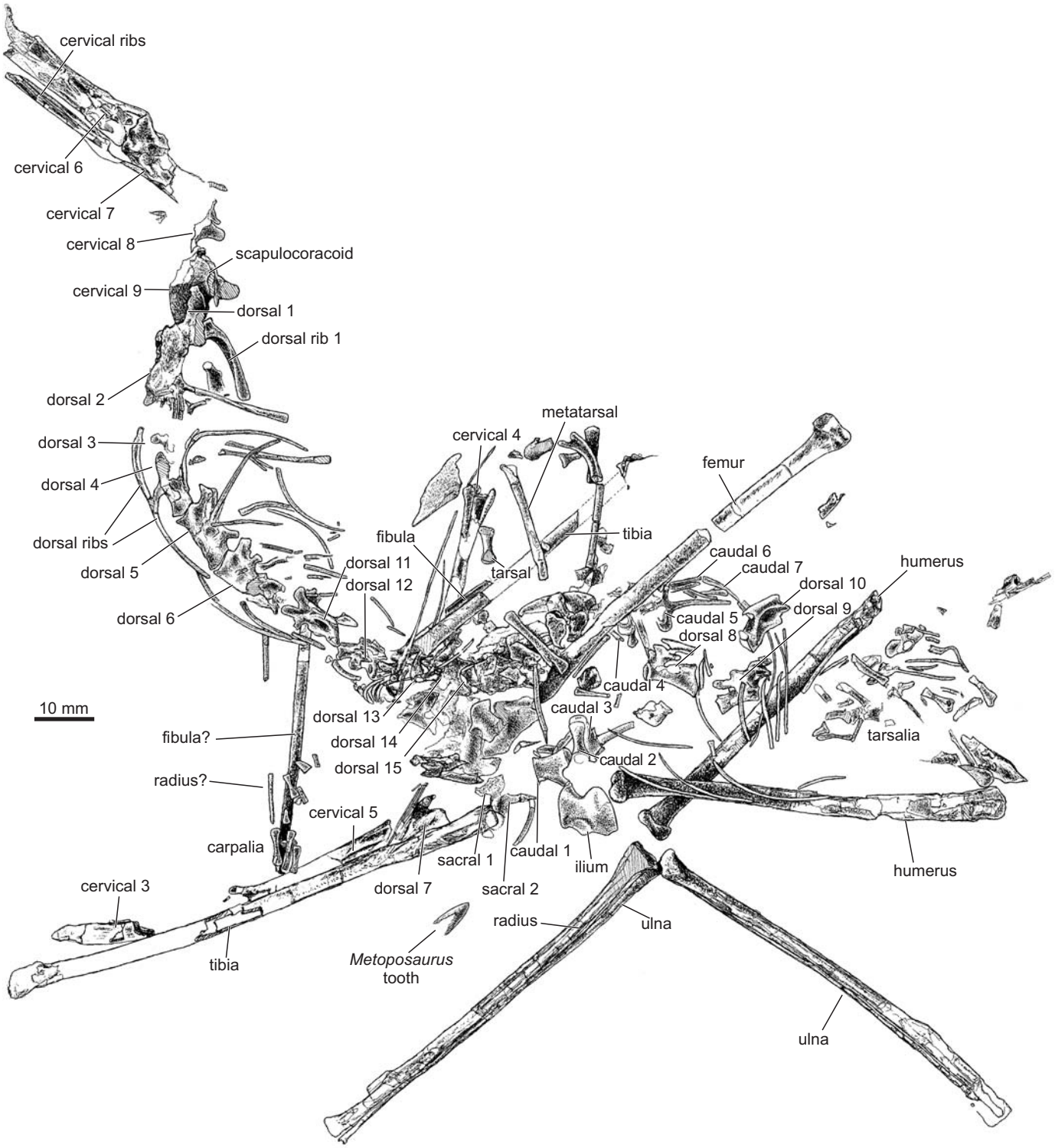


Fig. 4. Composite drawing of skeleton ZPAL AbIII/2511 of long-necked reptile *Ozimek volans* gen. et sp. nov. with bones from all layers superimposed (see photographs Figs. 5, 6).

ventral massive structures are connected by a robust but strongly compressed, relatively sharp, posterior ridge. Its posterior emargination (excavation) is gentle and relatively deep, with a depth of about one third of the bone height. The blade connecting the quadrate body with the pterygoid emerges at almost a right angle from the posterior ridge and is very thin. The external blade is gently concave and bears a dorsally oriented furrow in its ventral part, presumably the articulation with the quadratojugal. In the upper part of the bone an indistinct lateral crest is visible in Fig. 8D, E.

We tentatively interpret the second kind of L-shaped bone found in ZPAL AbIII/3191 as the quadratojugal (Fig. 8,

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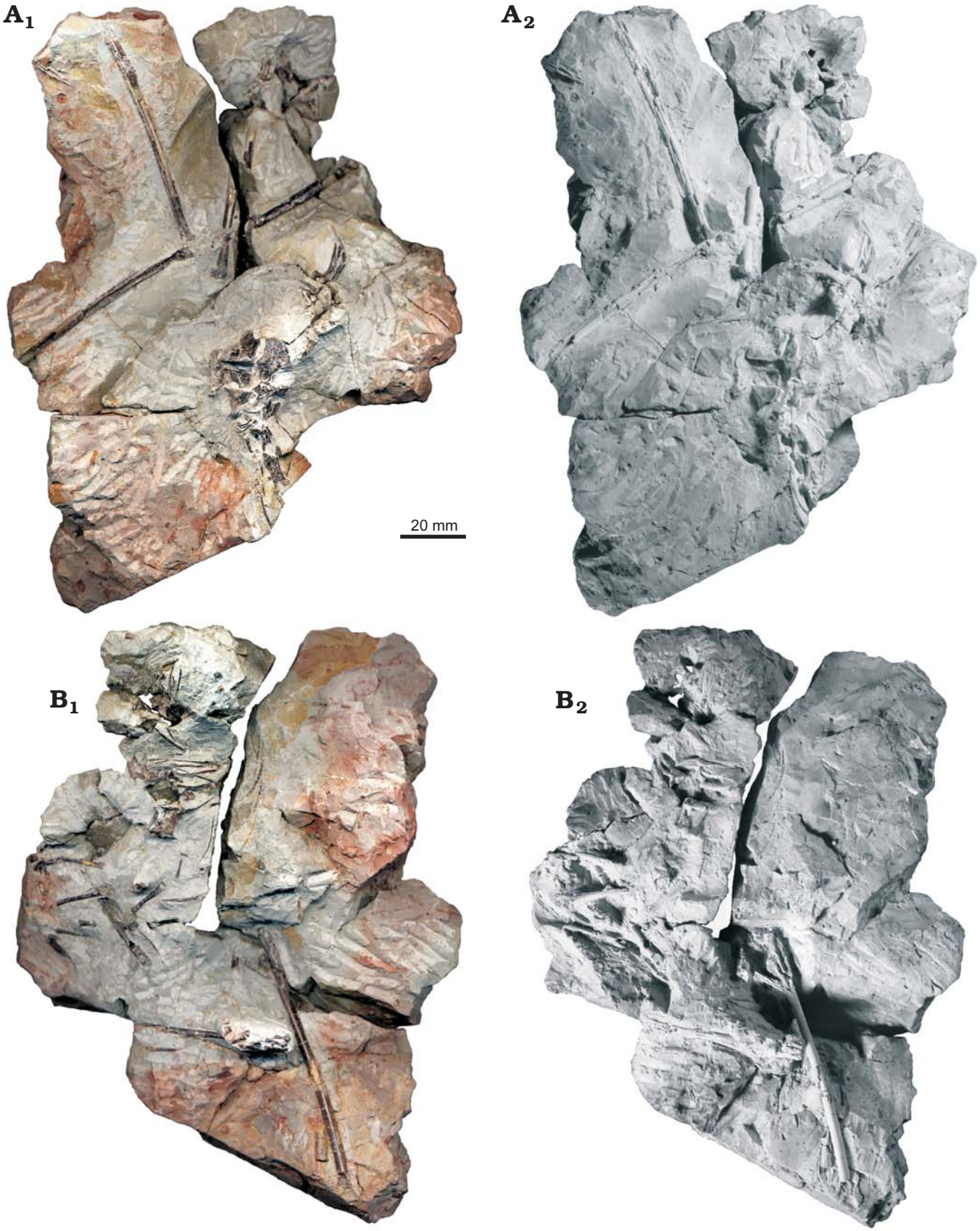


Fig. 5. Partially articulated skeleton ZPAL AbIII/2511 of long-necked reptile *Ozimek volans* gen. et sp. nov. from Krasiejów, lower Upper Triassic, preserved in claystone; two slices of the rock (**A**, **B**). Photographs (A_1, B_1) and specimens coated with ammonium chloride (A_2, B_2). See also explanatory drawing (Fig. 4) and additional photographs (Fig. 6).

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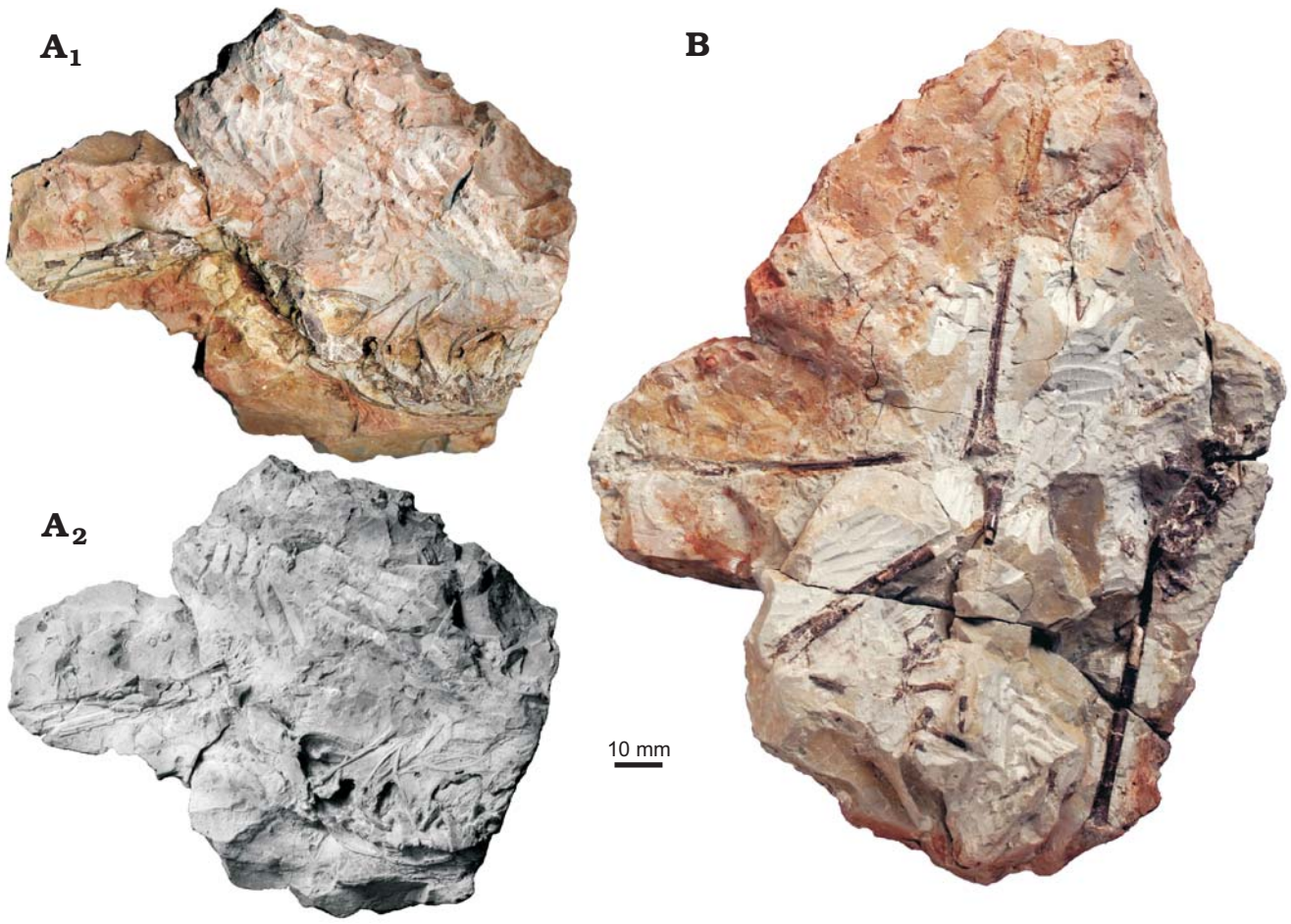


Fig. 6. Partially articulated skeleton ZPAL AbIII/2511 of long-necked reptile *Ozimek volans* gen. et sp. nov. from Krasiejów, lower Upper Triassic, preserved in claystone (see Fig. 4 for camera lucida interpretive drawings). **A**. Proximal part of the neck and anterior part of the thorax. **B**. Disarticulated long bones and part of thorax (probably from above). Photograph of specimen coated with ammonium chloride (A_2).

SOM 2), although the presence of a quadratojugal with a prominent anterior process would be quite surprising for a protorosaur-grade reptile; most of them have a narrow, splint-like quadratojugal that lacks an anterior process. Unlike the bone interpreted as lacrimal, it is flat and with well defined tips. Its anterior sharp end fits well into a furrow in the bone interpreted as the jugal. The proposed jugal has a dorsal lobe and an oblique anterior margin.

The dentaries of both sides are preserved in ZPAL AbIII/3191 (Fig. 8, SOM 2), although both their posterior and anterior parts are missing. They show numerous sharp teeth of the same kind as those in the articulated maxillae. Isolated bones of the same specimen seem to represent the surangular and articular. They are gently convex and of rather indifferent morphology, being similar to crushed bones preserved in the skull of ZPAL AbIII/2012 (Figs. 2, 3), which supports their identification.

Fragmentary rod-like bones associated with the skull of ZPAL AbIII/2012 (Figs. 2, 3) are probably parts of the hyobranchial skeleton.

Although most of the skull bones are missing in the available material, a tentative restoration may be attempted. It is apparently a diapsid with a complete jugal arch and of a rather compact appearance unlike other small-bodied archosauromorphs (Fig. 8).

Vertebral column: All vertebrae of *Ozimek* gen. nov. are procoelous. They also occur in the tanystropheids *Tanytrachelos* (Olsen 1979) and *Langobardisaurus* (Pritchard et al. 2015). The posterior surface of the centrum is more or less hemisphaerical and the anterior end develops a concavity of corresponding shape. In this aspect the vertebrae are different from those of other early diapsids, including the elongated cervical vertebrae of *Czatkowiella* (Borsuk-Białynicka and Evans 2009) and *Tanystropheus* (Wild 1973, 1980a). Specimens in articulation show that there was not much space for cartilage on the contact between centra. Only cervicals deviate from the rather generalized plan of the vertebrae, in that they are strongly elongated and the spinal processes are very low (Fig. 6). The very low neural spines in *Ozimek* gen. nov. closely resemble the condition in *Tanystropheus* and *Tanytrachelos*. The proximal cervicals, dorsals, sacrals, and caudals differ mostly from each other in location, length, and orientation of their diapophyses. The inferred number of vertebrae is nine (or more) cervicals, sixteen dorsals, two or three sacrals (the anterior one with ribs not in contact with ilium), and probably a large number of

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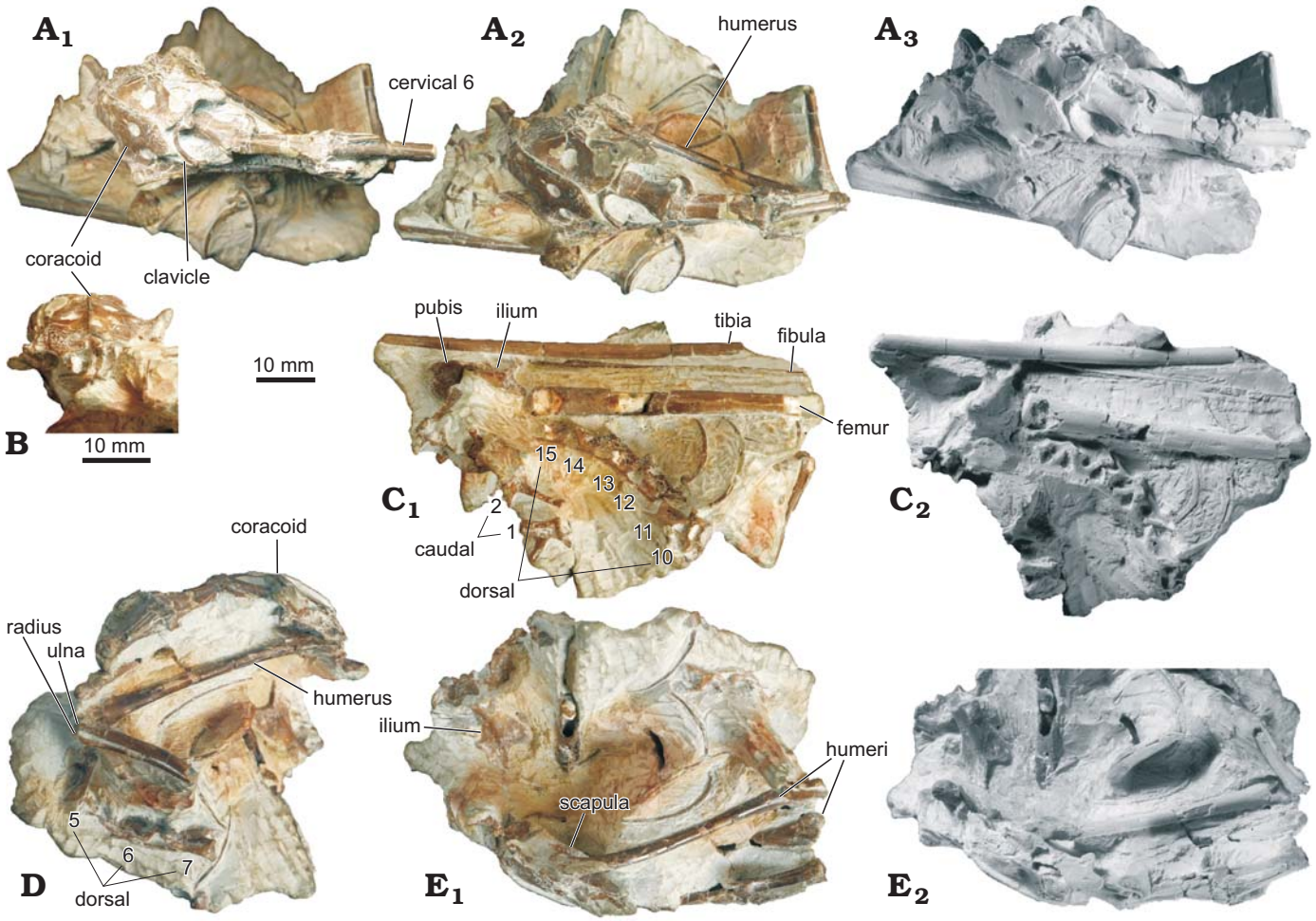


Fig. 7. Curled skeleton ZPAL AbIII/2512, holotype of long-necked reptile *Ozimek volans* gen. et sp. nov. from Krasiejów, lower Upper Triassic, preserved in a limestone concretion. **A**. Neck and pectoral girdle in ventral (A_1) and oblique right lateral (A_2, A_3) views. **B**. Pectoral girdle in anterior view. **C**. Thoracic vertebrae, ilium, and long bones of the hind leg. **D**. Dorsal vertebrae, coracoid, and long bones of the front leg. **E**. Humeri, scapula, ilium. Photographs of specimens coated with ammonium chloride (A_3, C_2, E_2).

caudals, the proximal seven of them bearing disproportionally elongated transverse processes (Fig. 9).

Cervicals: No specimen with all cervical vertebrae in articulation with the skull is represented in the collection. The most complete is the neck in ZPAL AbIII/2012 (Figs. 2, 3), but it has only four elongated cervical vertebrae, although in other specimens there are more of them. The minimum number of cervicals can thus be inferred only indirectly.

A part of the neck is preserved in articulation also in specimen ZPAL AbIII/2511 (Figs. 4–6). Below the anteriormost of the three preserved elongated cervicals, laterally crushed, 27.6 mm long, there are four cervical ribs preserved. This means that each individual rib extends for two vertebrae and thus one more articulated vertebra was originally present in the specimen. Such an assumption is consistent with the length of complete cervical ribs found displaced in the same, 49.0 mm in length. The elongate ribs, much longer than their respective centra, are like those in many "protorosaurs" (e.g., Rieppel et al. 2003). Apparently the isolated vertebra, 34.7 mm long, was displaced to near the pelvis together with a pair of cervical ribs (including the one referred to) in the specimen, and must have originated from an even more anterior part of the neck. The ribs associated with it indicate that yet another missing vertebra posterior of it was displaced from its original articulation. Possibly, this is the one hidden under the probable femur. Thus, at least five elongated cervicals were present in this specimen, the three anterior ones being strongly elongated.

The position of the cervical missing in ZPAL AbIII/2511 is represented by the anterior one of two articulated long vertebrae of equal length from UOPB 1148. The posterior one corresponds to the anteriormost preserved vertebra in ZPAL AbIII/2512 (Fig. 7). Three cervical ribs occur on its left side. This means that some ribs were extended for three of the cervicals. Such variation in rib length was observed also in the associated *Silesaurus*.

The probable atlas and axis are preserved close to the crushed skull in ZPAL AbIII/3191 (SOM 2). The atlas is represented only by a triramous neural arch with the ventro-lateral ramus bearing a terminal thickening and the posterior ramus enabling articulation with the zygapophysis of axis. The probable axis is strongly elongated and differs from

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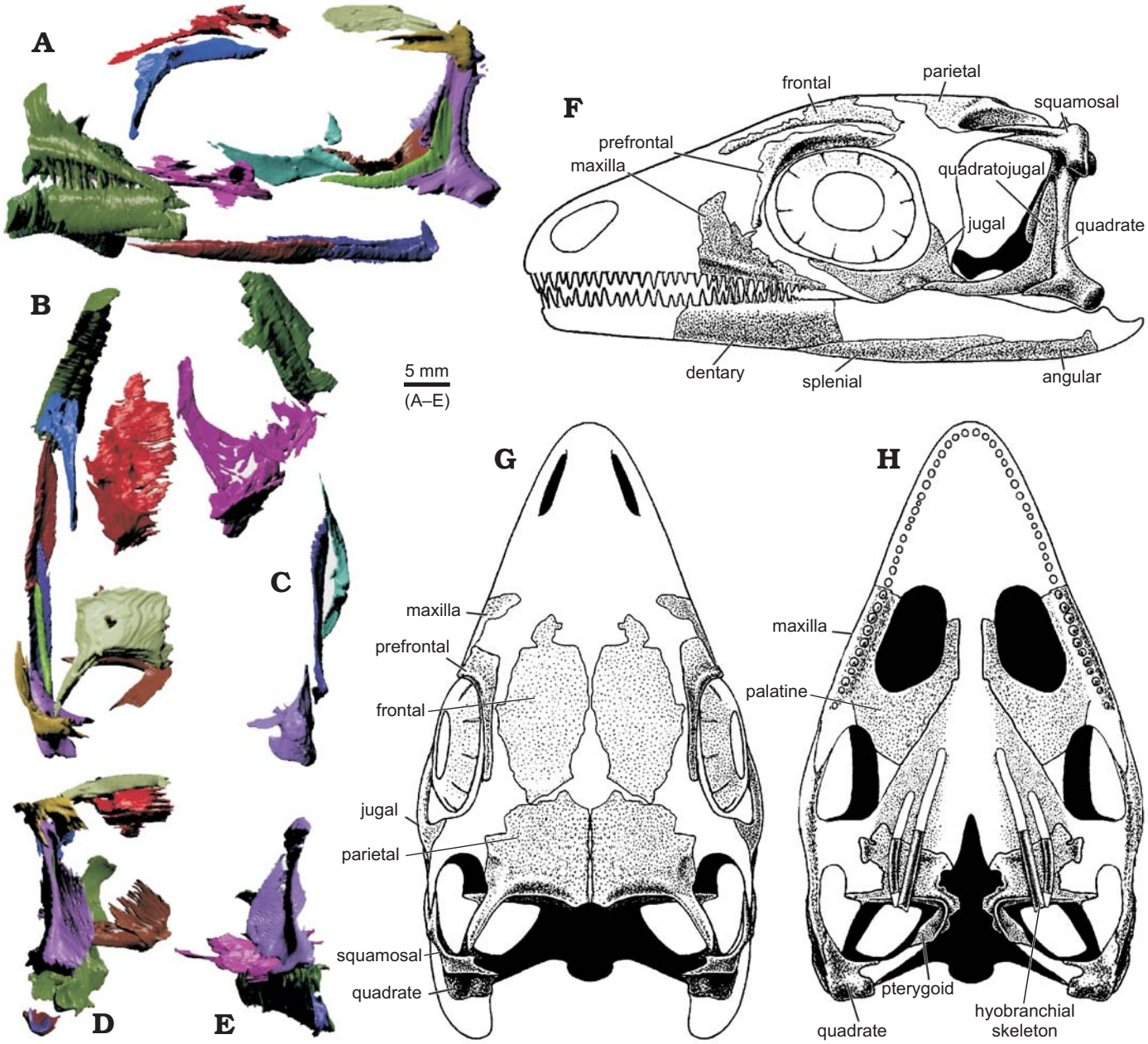


Fig. 8. Tomographic three-dimensional representations of the skull bones of ZPAL AbIII/3191 long-necked reptile *Ozimek volans* gen. et sp. nov. in their proposed original arrangement (A–E) and restorations of the skull (F–H); in lateral (**A**, **F**), dorsal (**B**, **G**), palatal (**C**, **H**), posterior (**D**), and anterior (**E**) views. F–H not to scale.

other cervicals in having a more prominent longitudinal ridge along ventral surface of its centrum. The axial neural spine is anterodorsally inclined in its anterior part. This is a characteristic of Tanystropheidae (character 244 in Nesbitt et al. 2015). The anterior end of the centrum is crushed and it remains unknown whether the atlantal centrum was unified with it.

Isolated cervical ZPAL AbIII/2051 has proportions that differ from all cervicals represented among the articulated specimens. It cannot be fit into any of the series of articulated vertebrae represented in the material, therefore we propose that it represents the anterior location closest to the axis. If a conservative count is assumed that only the atlas and axis were in front of this location, than it was cervical 3. Consecutive numbering of identified vertebrae would then be as follows here. Isolated, relatively well preserved slender cervical ZPAL AbIII/3196 may be cervical 4. Cervical 5 has been found in UOPB 1148 associated with cervical 6, which corresponds to the anteriormost unit in the articulated series ZPAL AbIII/2511 (Figs. 4–6) and ZPAL AbIII/2512 (Fig. 7). ZPAL AbIII/2056 is an isolated specimen representing either the location 5 or 6 in the neck. A fragmentary cervical near the distal end of a probable humerus in ZPAL AbIII/2511 (Figs. 5, 6) may represent the same location, whereas the two other displaced cervicals from the same specimen are from locations 4 and 5 in the neck.

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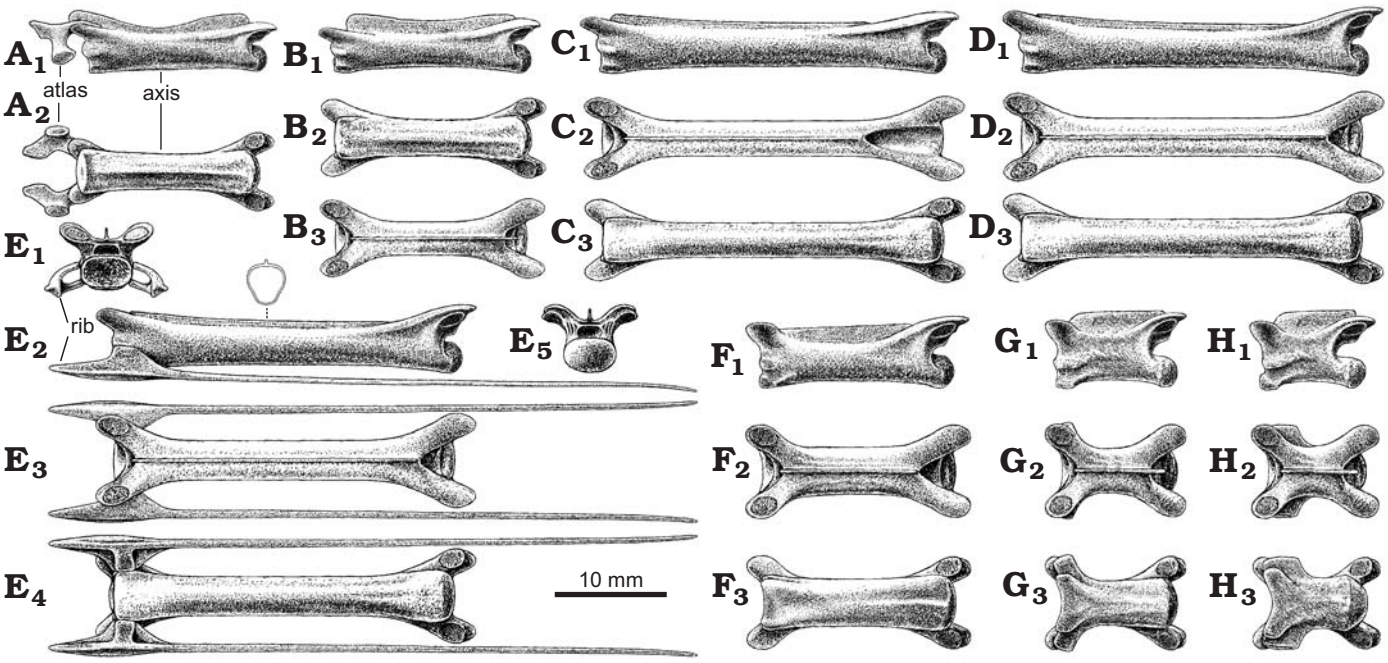


Fig. 9. Restoration of cervicals of long-necked reptile *Ozimek volans* gen. et sp. nov. **A**. Neural arches of atlas and complete axis, ZPAL AbIII/3191. **B**. Cervical 3, ZPAL AbIII/2051. **C**. Cervical 4, ZPAL AbIII/2511. **D**. Cervical 5, UOPB 1148. **E**. Cervical 6 with ribs, based on UOPB 1148, ZPAL AbIII/2456, /2511, /2512. **F**. Cervical 7, based on UOPB 1148, ZPAL AbIII/2528, /2494, /2454, /2511. **G**. Cervical 8, based on UOPB 1148, ZPAL AbIII/2528, /2499, /2511, /2512. **H**. Cervical 9, based on UOPB 1148 and ZPAL AbIII/2499. In left lateral (A_1–D_1, E_2, F_1–H_1), ventral (A_2–D_2, E_3, F_2–H_2), and dorsal (A_3–D_3, E_4, F_3–H_3), anterior (E_1), and posterior (E_5) views.

Articulated, but crushed cervicals 6 and 7 occur in ZPAL AbIII/2054. The latter is significantly shorter. Cervical 7 in ZPAL AbIII/2511 (Figs. 4–6) is 18.7 mm long, and in strict articulation with the preceding vertebra. However, its posterior end is missing with only a shallow impression left in the matrix indicating that it was crushed by sediment compaction. The base of the anterior zygapophyses is rather well preserved, as well as the articulation surface for the rib heads below.

Only the tips of deformed posterior zygapophyses of cervical 8 have survived exfoliation of bone remnants in ZPAL AbIII/2511 (Figs. 4–6); their orientation suggests displacement of the vertebra to an almost transverse orientation in respect to the rest of the vertebral column. In ZPAL AbIII/2512 (Fig. 7) relatively well preserved vertebra 8 bears tips of two cervical ribs of preceding vertebrae. Also in UOPB 1148 cervicals 7 and 8 are in articulation (but isolated from the vertebrae in front of them). Only the anterior margin of vertebra 9 survived in this specimen and is preserved underneath the poorly preserved scapulocoracoid. Three-dimensionally preserved cervicals 7 and 8 ZPAL AbIII/2528 were found articulated in part owing to a pyritic crust. Cervical 7 is more elongated than in other specimens, and especially in respect to ZPAL AbIII/2499, in which slightly displaced, but still in close proximity are cervicals 7, 8, and 9. The latter shows massive diapophyses for the ribs. There was apparently a significant change in the rib morphology between cervical 8 and 9 but the diapophyses are in ventral location, like in other cervicals, but unlike dorsal 1.

Dorsals: Only a small piece of the posterior end of the 1st dorsal is preserved in specimen ZPAL AbIII/2511 (Figs. 4–6, 10), which is preserved in its original location inserted between folded coracoids. It was in articulation with dorsal 2, of which only a piece of the anterior zygaphophysis, visible under the broken coracoid, and somewhat more complete posterior zygaphophysis remained. Similarly, only posterior zygaphophysis proves the presence of dorsal 3, which is in articulation with the first of a series of mostly complete dorsals from 4 to 6. Dorsal 4 is 11.3 mm, dorsal 5 is 10.6 mm, and dorsal 6 is 11.1 mm long (differences may be due to deformation). Posteriorly, there is some disorder in the orientation of vertebrae and it is proposed that the vertebral column was disassociated with a series of vertebrae removed and displaced behind the trunk.

Two very robust ribs occur in the anterior part of the trunk of ZPAL AbIII/2511 (Figs. 4–6), and presumably they belong to dorsal 1. They are deformed, and this may be the cause of difference in their length and proportions. The rib interpreted as the left one seems to bear a small anterior process, which is possibly serially homologous to the anterior processes of the cervical ribs.

Altogether four dorsals of ZPAL AbIII/2511 (Figs. 4–6) are displaced from their original location. It is unlikely that they belong to another specimen as there is no "surplus" in other bones that could substantiate such an interpretation. At Krasiejów, protorosaurian skeletons are very rare and occur in complete isolation. The only place in the vertebral column where vertebral zygapophyses are not in contact and the orientation of vertebrae is suddenly different, is behind

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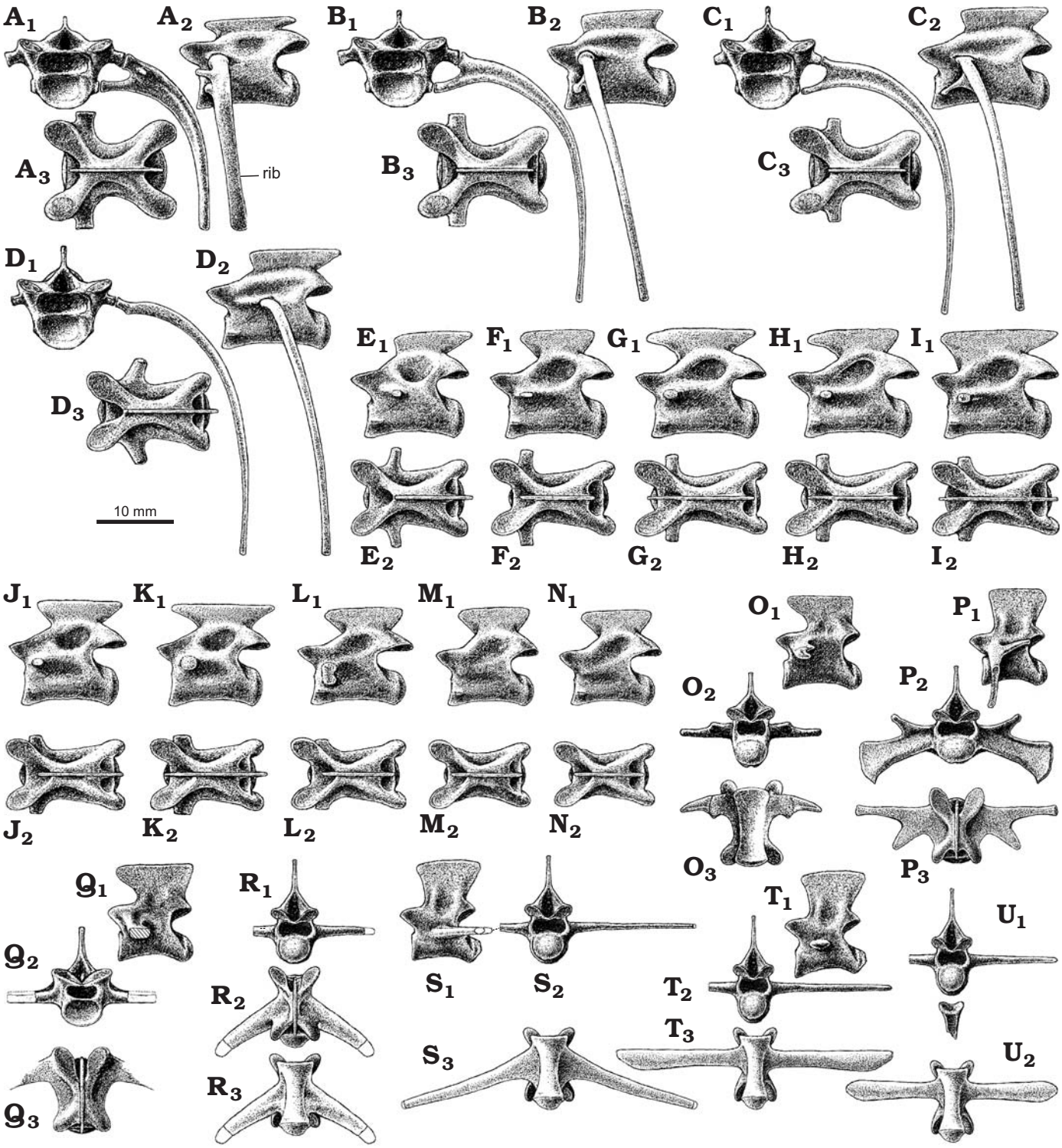


Fig. 10. Restoration of postcervical vertebrae of long-necked reptile *Ozimek volans* gen. et sp. nov. Dorsal 1 with ribs (**A**), dorsals 2–16 (**B**–**N**), based on ZPAL AbIII/2511, /2512, /3191. Sacrals 1–3 (**O**–**Q**), based on ZPAL AbIII/2511. Caudals 1, 2, 4 (**R**–**T**), caudal 6 with chevron (**U**), based on ZPAL AbIII/2512. In anterior (A_1–D_1, P_2, Q_2), left lateral (A_2–D_2, E_1–T_1), and dorsal (A_3–D_3, E_2–N_2, P_3–R_3), posterior (O_2, P_2, R_2, S_2, T_2, U_1), and ventral (O_3, R_4, S_3, T_3, U_2) views.

vertebra 6. It is thus proposed that these dorsals represent locations 7–10 in the trunk. An isolated vertebra identified as dorsal 7 is closest to its original location. It is deformed, incomplete and occurs below the pelvis. Vertebrae 9 and 10 are imbedded even deeper in the rock, in association with a series of ribs in an almost original disposition. Probably a segment of the decaying body was transferred there, perhaps together with the front limbs, as these are preserved 10 mm above. The vertebrae are displaced but still close to each other.

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As can be seen in the articulated vertebral column of ZPAL AbIII/2511 (Figs. 5, 6), a 12.3 mm long vertebra proposed to be dorsal 11, is rotated around its axis in respect to the vertebrae anterior to it, but more or less in the same orientation as the vertebrae behind with some disarticulation between them.

The three dorsals following behind (12–14) are in articulation but are strongly crushed and deformed. Dorsal 13 shows a prominent round articulation surface of the upper diapophysis. Dorsal 14 is at the split between rock blocks in which the skeleton is imbedded. It bears the right rib in articulation, with heads of similar size and, in proximity to each other and in strictly vertical arrangement. The centrum is strongly flattened. Dorsals behind are strongly crushed and hardly provide any specific information on their morphology.

In ZPAL AbIII/2512, the dorsal interpreted to represent location 1 is displaced behind the scapulocoracoid. A rib with two relatively strong heads is preserved in proximity, another rib is displaced further away. They are not as robust as the first dorsal rib in ZPAL AbIII/2511, but the specimens significantly differ in size and, presumably, ontogenetic age.

Dorsal 2 of ZPAL AbIII/2512 is also isolated, but its ribs are nearly in articulation. They are more gracile than in the preceding dorsal, and both heads are well developed. Vertebrae from more posterior locations are not preserved in this specimen and the series is known from articulated cervicals 5–7 and 10–16. The anterior part of the series is characterized by delicate dorsal diapophyses with inclination changing from slightly posterior to slightly anterior. In the posterior part of the series only a piece of the centrum is preserved of the dorsal 10th, but other dorsals are three-dimensionally preserved, and ribs are almost in articulation in the two anterior locations. They seem to have only one head. In dorsal 16, diapophyses cannot be traced. The ribs were possibly not present there. The neural arches and spines are very wide, with a straight dorsal margin that is slightly thickened, like in *Macrocnemus* (Peyer 1937: pl. 57).

Sacrals: In ZPAL AbIII/2511 (Figs. 5, 6) three vertebrae presumably representing sacrals are preserved in a separate piece of the rock that cannot be precisely fitted in the space between two slabs, from where it certainly comes. Although all are in proximity to each other and to other pelvic bones, they are displaced preventing decisive identification of their order in the pelvis. It is conjectured that the vertebra, which bears short, tapering ribs, was the anterior sacral. The alternative, that it was located behind the two other sacrals, would require a sudden change in morphology and orientation of transverse processes (diapophyses) between the sacrum and the first caudal. If true, then the ribs of this sacral were not in contact with the ilium. The sacral interpreted as 2nd is preserved with only the base of diapophysis, which is suggestive of the rib being vertically widened. Sacral 3 bears partially preserved ribs that are horizontally widened. This seems to fit roughly the morphology of the attachment area on the ilium.

An almost complete sacral 2 is preserved in isolation in specimen ZPAL AbIII/2512. Its rib has two branches like in *Mesosuchus browni* (Dilkes 1998: fig. 13a), *Prolacerta broomi* (Gow 1975: fig. 22), and *Macrocnemus bassanii* (Peyer 1937: pl. 63), the stronger anterior one is strongly widened at its tip, whereas the shorter posterior ones is directed obliquely towards the ilium. It probably contributed to a non-ossified part of the pelvis.

Caudals: Seven proximal caudals are preserved in ZPAL AbIII/2511 (Figs. 4–6). The proximal three are almost in articulation and others in close proximity to each other but rotated transversely to the body axis. The lateral processes of the first caudal are strongly bent posteriorly, in the 2nd they are less oblique, whereas in caudals 4–7 they are almost transverse and very long like in *Tanytrachelos ahynis* (Olsen 1979). Their length is considerable but diminishes posteriorly, and the base of the tail had thus a rhomboidal shape. Five distal caudals have been found displaced from their original location; they show that the tail was very narrow. Only three proximal caudals have been identified in ZPAL AbIII/2512 and they confirm our interpretation based on the most complete specimen.

Gastralia: Numerous broken and incomplete gastralia are represented in both articulated specimens (at least thirty in ZPAL AbIII/2511; Figs. 4–6) but some of them are difficult to distinguish from fragmentary thoracic ribs. Among the most complete elements, there are two classes, probably corresponding to the ventral main series and lateral ones. Only a few ventral gastralia are preserved completely enough to enable a provisional restoration. They are extremely variable and apparently their disposition on the venter was rather irregular. In each of the articulated specimens, a V-shaped gastralium was found near the scapulocoracoid. They may represent the anteriormost element of the whole series. Another gastralium from ZPAL AbIII/2512, preserved in proximity to the previous one, shows a T-shaped arrangement of arms, with the shortest arm transversely truncated in a way suggesting its connection with an anteriorly located gastralium by a suture. The length of this arm shows the distance separating subsequent gastralia. Some gastralia are gently curved in their probable mid-length. Much less variable are the lateral gastralia. They are rather robust, with both ends sharp and angular, and bending in the middle. This bending roughly fits the cross-section of the coracoid. The animal's venter was probably gently convex.

Pectoral girdle: The largest bone in the whole skeleton of the Krasiejów reptile is the scapulocoracoid (Fig. 11A). Its coracoid part is disproportionately enlarged with respect to the scapula. The scapula is very low (like in *Tangasaurus*; Currie 1982; Reisz et al. 2011) and posteriorly expanded, with a crescent shape, like in *Tanystropheus* (Wild 1973) and *Tanytrachelos* (Olsen 1979: fig. 4). It is firmly unified with the coracoid, but the glenoid seems to be composed completely of the coracoid part, although no signs of its fusion are recognizable. It is horizontal, with a thickened ventral region. The coracoids are extremely widened an-

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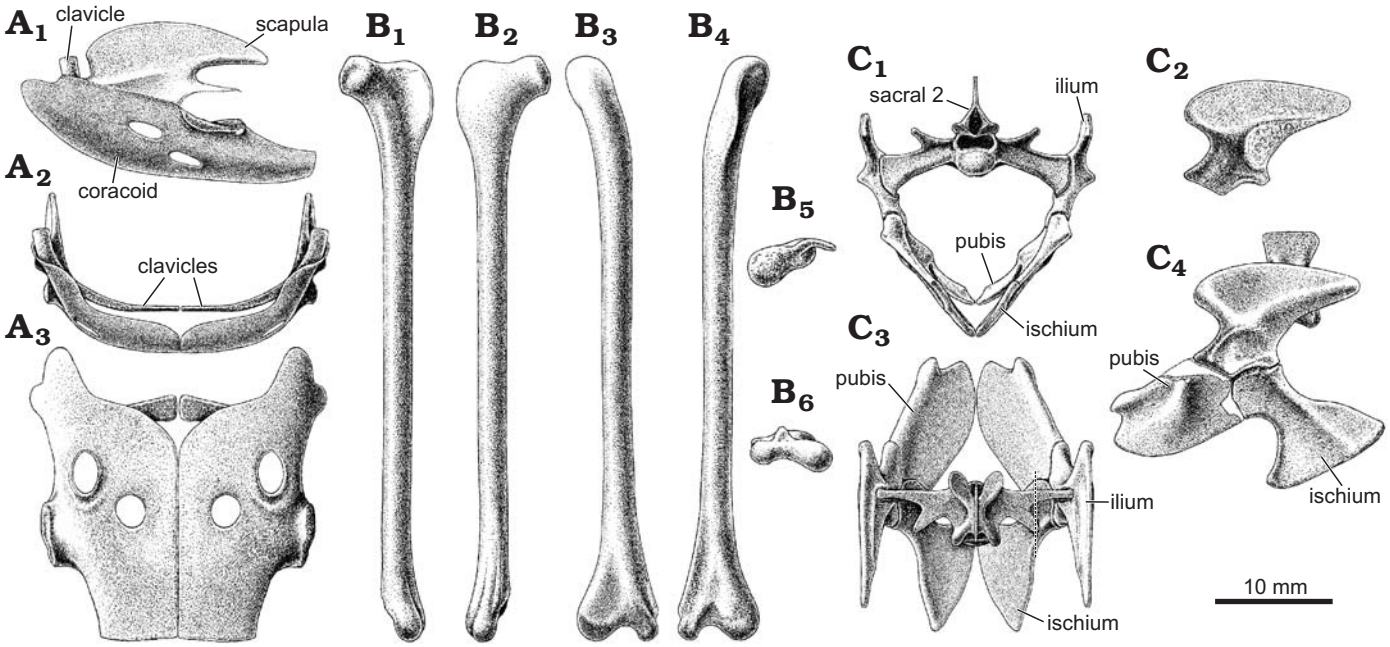


Fig. 11. Restoration of pectoral and pelvic girdle elements of long-necked reptile *Ozimek volans* gen. et sp. nov. **A**. Scapulocoracoid and clavicles in left lateral (A_1), anterior (A_2), and ventral (A_3) views, based on ZPAL AbIII/2512. **B**. Right humerus in proximal (B_1), medial (B_2), external (B_3), distal (B_4), anterior (B_5), and posterior (B_6) views, based on a juvenile ZPAL AbIII/2512. **C**. Pelvis with sacral 2 in posterior (C_1) and dorsal (C_3) views, ilium in medial view (C_2), pelvis in left lateral view (C_4), based on ZPAL AbIII/2511.

teroposteriorly but very thin, connecting medially with each other for all their length with a straight suture. The ventral surface of the coracoids is gently convex. There are two large fenestrae in each coracoid separating it from the part probably representing the ossified sternum. The posterior one, of an homology we are unable to determine, penetrates the centre of the bone, which is very thin. A similar anteriorly located fenestra seems to be developed between the coracoid and scapula, which are fused anteriorly. Possibly this is an enlarged ancestral coracoid foramen.

The clavicles are gently arched and parallel the anterior margin of the coracoids (Fig. 7H), being partially hidden beneath them. The medial part of the clavicle is ventrally flat and expands into a narrow triangle. The dorsal tip of the clavicle is almost circular in section, with an empty interior. No remnant of the interclavicle has been identified and there is apparently no space left for it between the clavicles and coracoids.

Humeri are completely preserved and in articulation only in ZPAL AbIII/2512 (Figs. 7, 11B). They are tightly pressed to the body and oriented forward. Left humerus is 45.5 mm and the right 46.7 mm long (SOM 1). This difference probably resulted from diagenetic distortion, or perhaps also from different degree of calcification of cartilaginous heads. Such a probable deformational disparity in length is also expressed in ZPAL AbIII/2511 (Figs. 5, 6). Here one humerus is 59.0 mm and the other is 61.0 mm long (with parts somewhat displaced). Both bones are crushed in their proximal regions but the distal heads are well preserved owing to their strong calcification. The morphology of the distal head is ginglymoid, which apparently restricted movement in its articulation to one plane. The proximal head is spherical in juvenile specimens and with prominent dorsal crest (probably deltopectoral crest). In mature individuals (preserved well enough only in ZPAL AbIII/2529 of 74.4 mm length) the proximal head was probably poorly calcified and the crest was low and extended distally over a larger distance. The crest was apparently rather wide in crushed specimen ZPAL AbIII/ 2459 of length 60.2 mm. Apparently, proportions of humeri changed allometrically in their growth and the shaft diameter changed more than the bone length: in ZPAL AbIII/2511 (Fig. 6) its diameter was 3.2–3.5 mm whereas in ZPAL AbIII/2512 (Fig. 3) it is only 2.0 mm. The ratios of shaft diameter to humerus length are 0.057 and 0.043, respectively. Specimen UOPB 1148 is of a size that is similar to ZPAL AbIII/2512 but the distal head of the humerus is a little more advanced in calcification and of a more symmetrical appearance. The proximal head, although poorly preserved in UOPB 1148, is also of similar shape in these specimens.

Both sets of radius with ulna are preserved in ZPAL AbIII/2511 (Figs. 4, 12A), but their distal ends are poorly preserved as imprints. The ulna is flat and proximally extends somewhat more posteriorly to the radius. The estimated length is 87.0 mm; and the isolated probable radius ZPAL AbIII/2527 is 81.3 mm long. The proximal head of the radius is triangular in outline but there seems to be much shape variation in its development, both in growth and within population. It is difficult to distinguish isolated radii from tibiae.

The manus (Fig. 12B) is preserved in partial articulation in ZPAL AbIII/2511. There are four metacarpals in a parallel arrangement probably reflecting their original disposi-

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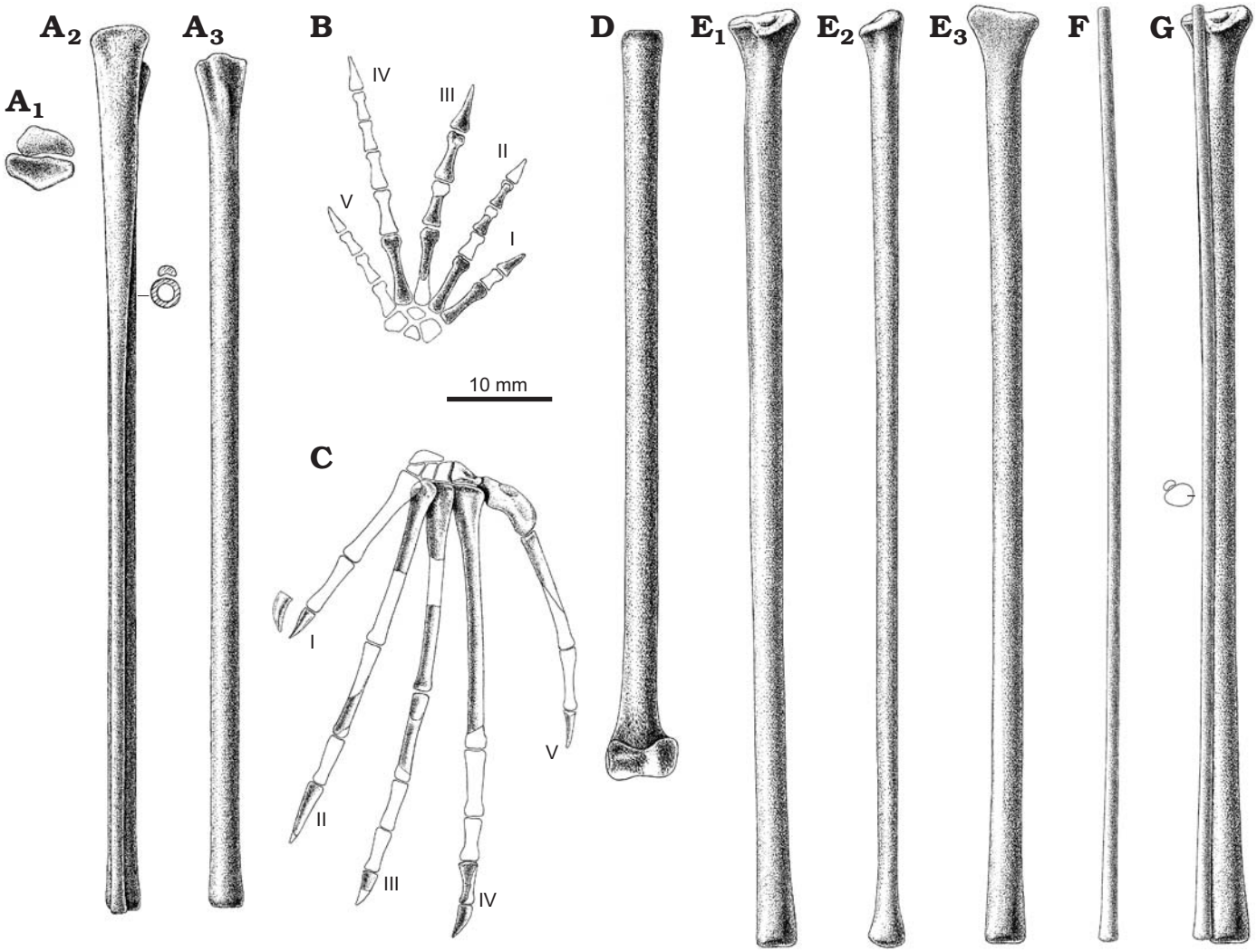


Fig. 12. Restoration of long bones, manus, and pes of long-necked reptile *Ozimek volans* gen. et sp. nov. **A**. Right ulna and radius in proximal (A_1) and posterior (A_2) views, radius in anterior view (A_3), based on ZPAL AbIII/2452, /2511. **B**. Manus, based on ZPAL AbIII/2511. **C**. Pes, based on UOPB 1148, ZPAL AbIII/3198, /2511. **D**. Right femur in anterior view, based on UOPB 1148 and ZPAL AbIII/3191. **E**. Tibia in anterior (E_1), lateral (E_2), and posterior (E_3) views, based on ZPAL AbIII/2526, /2527, /2512. **F**. Fibula, based on ZPAL AbIII/2512, /2525, /3191. **G**. Tibia and fibula in anterior view, based on ZPAL AbIII/2512.

tion, and six phalanges (two of them being terminal claws) displaced in a way that prevents the identification of their location in the manus. The morphology of all identified elements is rather indifferent. Apparently, the manus lacked any specializations and was of a generalized protorosaurian morphology (Rieppel et al. 2003).

Pelvic girdle: A complete set of pelvic bones (Fig. 11C) is preserved in ZPAL AbIII/2511. The two preserved ilia are incomplete and visible only from the inner side, and their attachment to the anterior sacral ribs is well seen. Supplementary information is offered by the two ilia in ZPAL AbIII/2512, which is visible from their external surface and with posterior tips of the blades preserved. These are missing in the former specimen. The ilium has convex dorsal edge (in lateral view) and rather shallow glenoid with slightly prominent its anterodorsal edge. The posterior part of blade is twice longer than anterior. In each of the specimens single pubes are represented, both incomplete in a similar way, so only the anterior margin of the bone is well documented. It shows an indentation near its distal end. The bone is rather flat and without any apparent concavity supporting viscera. An almost complete ischium is preserved in ZPAL AbIII/2511, and its probable external surface exposed. The bone outline is ax-like, with a wide foot (ventral base of the ischium) and the deep anterior indentation. It is also possible that the posterior indentation in the pubis and the anterior indentation in the ischium were confluent in the *Ozimek* gen. et sp. nov. pelvis, forming a single thyroid fenestra, but material is too badly preserved to determine the real condition. In general, the pelvis was of generalized protorosaurian morphology and is similar to that of *Prolacerta*, *Malerisaurus* (Chatterjee 1986) and *Pamelaria* (Sen 2003).

Although specimens ZPAL AbIII/2511 and ZPAL AbIII/2512 do not differ much in the size of the axial skeleton, the proportions of their appendages are dramatically different. This most probably is a result of ontogenetic change, as

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is indicated by incompletely calcified heads in the smaller specimen. The front appendages were much smaller in respect to the hind legs in the juvenile ontogenetic stage. Although the femur is only partially preserved in the juvenile specimen ZPAL AbIII/2512, its shaft is thicker than in the mature ZPAL AbIII/2511, in which their latero-medial and cranio-caudal diameters are 2.8 mm × 3.4 mm, respectively. The preserved femora of ZPAL AbIII/2512 were >45.5 mm and 48.7 mm long; tibia and fibula >63.5 mm and 67.5 mm; in ZPAL AbIII/2511 the femur is 70.5 mm long.

Both sets of tibia and fibula (Fig. 12D–G) are preserved in ZPAL AbIII/2511 but incompletely. The left set is preserved proximally but without the head of the tibia. The fibula is proximally flat, and with a crescent cross section. In the right set the tibia is represented at its complete length of 90.0 mm, but the heads are crushed and represented partially only by imprints. A probable distal portion of the fibula is preserved in the rock matrix below the manus. The narrower of its preserved ends is oval, and the other is circular. That this is undoubtedly a fibula (no alternative interpretation can be offered) is supported by the morphology of its distal end in specimen ZPAL AbIII/2526. It is 75.2 mm long, thus younger, and showing clearly a circular cross section. In ZPAL AbIII/2525 (preserved length 46.5 mm, certainly incomplete), the fibula is oval at its distal tip and somewhat shorter than the tibia. Presumably, in ontogeny the fibula became more robust. In the largest known tibia ZPAL AbIII/2452, 106.0 mm long, there is a distinct furrow, in which the fibula was located at most of its proximal part. It appears thus that generally the fibula was much like the ulna, flat and in close contact with the tibia in its proximal half, but rather free in the remaining distal portion.

The foot (Fig. 12C) was large, with elongated metatarsals and phalanges. Disassociated elements preserved in ZPAL AbIII/2511 (Fig. 4) show that it was more than two times larger than the manus. It is preserved almost completely in articulation in UOPB 1148, and four metatarsals occur in their original position in ZPAL AbIII/2526. Except for a problematic triangular bone in UOPB 1148, tarsals are missing in both specimens, which may mean that they were poorly ossified. The most characteristic element of the pes is the metatarsal of the fifth digit, curved, with a robust appearance.

"*Pneumaticity*" *of bones*: Vertebral centra and appendage bones of *Ozimek volans* gen. et sp. nov. were empty inside, usually filled with calcitic sparite that preserves as smooth cylinders wherever the bone is exfoliated. Such bone structure is usually referred to as pneumatic but there are no openings for possible airs sac entrances and the presence of calcite instead of clay shows that the bone interior was completely closed. Presumably, they were filled with fat, forming a kind of bone marrow. Regardless as to whether there was fat or air inside, the adaptive value of such structure was probably to make the skeleton lighter.

Remarks.—Fossils of *Ozimek volans* gen. et sp. nov. are easily recognizable owing to elongation of vertebrae and appendage bones, both of which have a large medullary cavity with smooth walls. They are similar in this respect to bones of *Tanystropheus* and this is why a cervical of *Ozimek* gen. nov. was originally captioned by Dzik and Sulej (2007: fig. 9A) as the caudal vertebra of a pterosaur or cervical vertebra of *Tanystropheus*.

No other reptile described in the literature shows a pectoral girdle of pectoral girdle of Ozimek-like morphology. Possibly, ossified sterna of the kind known in the tanystropheid protorosaurian *Tanytrachelos* (Olsen and Johannson 1994) are homologous to the posterior part of the extremely large coracoids, which would then be a composite of various ossifications. This suggestion is based on the preservation of an accessory foramen between the primordial coracoid and primordial sternum. Protorosaurian *Tanytrachelos* also had a similarly short scapulae (Smith 2011) but it lacks elongation of the appendages and the neck, which refers also to *Langobardisaurus* and *Macrocnemus*. Elongation of vertebrae and a large medullary cavity with smooth walls in both vertebrae and long bones make *Ozimek* gen. nov. similar to advanced Tanystropheidae (e.g., *Tanystropheus*) and this makes likely its protorosaurian affinity. These features also characterize the poorly known *Sharovipteryx* and other early archosauromorphs (e.g., *Trilophosaurus*, Azendohsauridae). Incomplete preservation of its thorax prevents a closer comparison with *Ozimek* gen. nov., but the hind limbs were definitely much longer in respect to the thorax seen in *Sharovipteryx*, which if not deformed had a ratio of 2.1 compared to *Ozimek* gen. nov., which had a ratio of 1.2. The robust hind limbs of *Tanytrachelos* were of a length similar to the thorax (ratio about 1.0). *Ozimek* gen. nov. had appendages incomparably more elongated than any other protorosaurian. The ratio of femoral length to the diameter of its proximal head is about 18.0, being 14.5 in *Sharovipteryx*, but only 7.6 in *Langobardisaurus* and 7.1 in *Macrocnemus obristi* (Fraser and Furrer 2013).

Stratigraphic and geographic range.—Type locality and horizon only.

Concluding remarks

Ozimek volans gen. et sp. nov. is medium and anatomically generalized (especially in the morphology of its pelvic girdle and probably also the skull; Fig. 11), except for a few advanced traits. Among these features of specialization, the elongated neck is most similar to protorosaurian (Sues and Fraser 2010). The robust metatarsal of the fifth digit makes it similar to *Azendohsaurus* (Nesbitt et al. 2015: fig. 65) and the Early Triassic *Prolacerta* (Camp 1945), and its more advanced relatives (Colbert 1987). The hooked fifth metatarsal forms part of a third-order lever in diapsids operated by the gastrocnemius, owing to functional consolidation of all the pedal elements distal to the mesotarsal joint into a relatively rigid unit (Lee 1997). This means that the Krasiejów reptile

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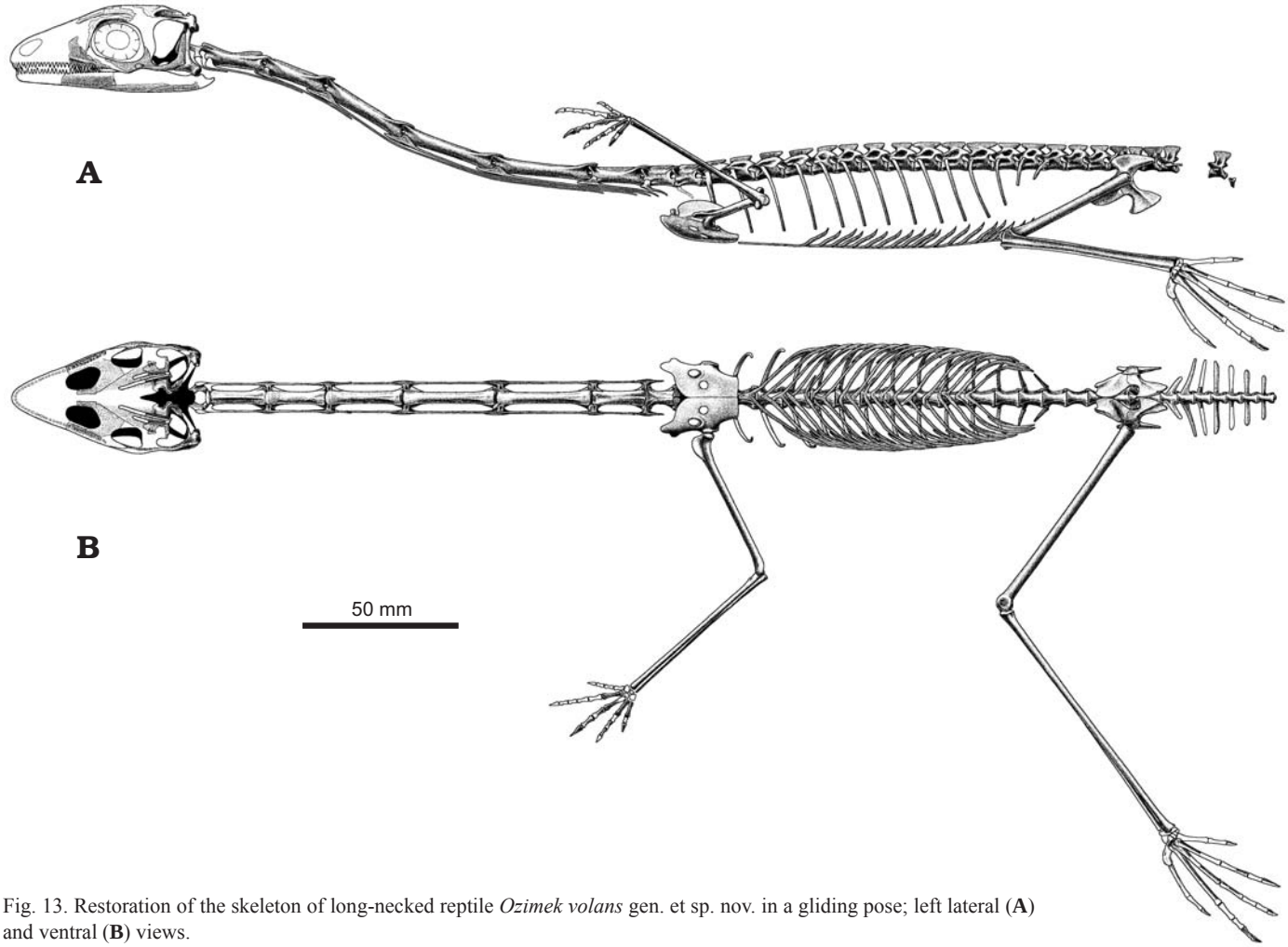


Fig. 13. Restoration of the skeleton of long-necked reptile *Ozimek volans* gen. et sp. nov. in a gliding pose; left lateral (**A**) and ventral (**B**) views.

was probably rather efficient in elevating its body and accelerated locomotion.

Scleromochlus, a roughly coeval late Carnian small reptile from the Lossiemouth Sandstone of Scotland, had similarly elongated appendages but differs in several other aspects of the skeleton. Its cervicals are not elongated, the foot lacks the specialized metatarsal of the first digit, and the skull has well developed antorbital fenestrae (Benton 1999).

The long-necked protorosaurians had a long evolutionary history (Benton and Allen 1997; Jalil 1997; Borsuk-Białynicka and Evans 2009), their oldest known member being the Late Permian *Protorosaurus* (Gottmann-Quesada and Sander 2009). This early form had a rather robust appearance, with strong appendages and elongated skull, features that are not similar to *Ozimek* gen. et sp. nov. Also, members of the Tanystropheidae, as well as *Langobardisaurus* and *Macrocnemus*, have relatively short appendages (Wild 1973, 1980a, b; Rieppel 1989; Renesto 2005; Renesto and Dalla Vecchia 2007; Renesto et al. 2002; Pritchard et al. 2015).

Unfortunately, the skull of *Ozimek* gen. nov. remains incompletely known. Until more complete fossils are found, the available material can hardly be compared with that of other protorosaurians. The extremely elongated appendages make *Ozimek volans* gen. et sp. nov. comparable to *Sharovipteryx mirabilis*. It is known to have had a flight membrane extending to the tips of its hind appendages, which is consistent with the aerodynamic needs of a reptile with most of its muscles located in the pelvic girdle (Sharov 1971; Gans et al. 1987; Unwin et al. 2000). Such was probably the situation in the ancestor of the pterosaurs, whatever was its exact affinity, before they changed from gliding to active flight supported by the pectoral girdle musculature. Only after the pectoral muscles increased their size (and weight) did the center of gravity move forward. To retain stability in flight, the center of lift had to move forward as well. Unwin et al. (2000) questioned identification of the forelimb by previous authors (Sharov 1971; Gans et al. 1987; Peters 2000), and proposed that they were mistaken about the ribs. He also suggested that actual forelimbs are hidden under the sediment. The front limbs are preserved in *Ozimek* gen. nov. showing elongation comparable to that of hind limbs. However, the peculiar structure of the pectoral girdle of *Ozimek* gen. et sp. nov. makes active flight an impossibility. If the elongated appendages are truly flight adaptations, they served at the best to glide between trees (Fig. 13).

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Unwin et al. (2000) diagnosed the monotypic family Sharovipterygidae, in which *Sharovipteryx* is classified, based on pronounced caudal elongation of hyoids, anterior development of preacetabular process of ilium, pulley-like process on distal end of femur, elongation of tibia, which is longer than the trunk. Those of the listed characters, which can be confidently recognized in the crushed only specimen of *Sharovipteryx*, are also present in the Krasiejów reptile. The skull of *Sharovipteryx* was interpreted as narrow and thus apparently deep, with a large orbit and both upper and lower temporal openings. However, the proportions of possible frontals and parietals are not significantly different from those observed in the Krasiejów material. According to Unwin et al. (2000), the *Sharovipteryx* sacrum was composed of at least four, and possibly as many as six vertebrae. The poor state of preservation prevents close comparison with the Krasiejów reptile, but it is a possibility that there were two or three sacrals, only two of them firmly joined with ilia.

The peculiar thin-walled long bones and vertebrae, with a thin layer of compacta without any trace of spongiosa, is known not only in *Sharovipteryx* (Unwin et al. 2000) but also in several protorosaurians with relatively short appendages and no adaptations to flight or gliding (e.g., Saller et al. 2013). This has little to do with the true pneumatization (no traces of pneumatic foramina have been detected). However, only an arboreal adaptation, hunting for insects with its elongated neck and gliding makes sense of the peculiar appearance of this animal and the common occurrence of its skeletons in lacustrine strata.

Probably the most unusual aspect of the new Krasiejów reptile is its very low scapula and extremely large coracoid with two fenestrae. One may guess that such a coracoid originated by fusion of the coracoid proper with ossified sterna of the kind known, among others, in the tanystropheid protorosaurian *Tanytrachelos* from the latest Triassic Lockatong Formation of Pennsylvania (Olsen 1979; Olsen and Johansson 1994; Smith 2011; Casey et al. 2007). It had posteriorly curved relatively short scapulae and large coracoids associated with very large quadrangular sterna (Olsen and Johansson 1994). This makes *Tanytrachelos* similar to *Ozimek* gen. nov., but it lacks an elongation of the appendages and the neck, having instead a highly derived skull and vertebrae (Pritchard et al. 2015). Twelve cervical and 13 dorsal vertebrae make *Tanytrachelos* similar to *Tanystropheus* and distant from *Sharovipteryx*.

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