The Triassic world of Krasiejów

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Krasiejów is a small village some 20 kilometres east of Opole. In recent years, it has rapidly become a mecca for lovers of palaeontology from all over the world. The prime reason is the sheer abundance of accumulated fossil vertebrates on the grounds of old brickworks for which claystones were excavated in an open-cast mine (Dzik and Sulej, 2007). The age of these rocks and the fossils that they contain is Late Triassic, but a more precise dating (*i.e.*, either Carnian, Norian or Rhaetian) still is ambiguous. Generally, the view is that the claystones at Krasiejów were not laid down earlier than latest Carnian (230-225 million years ago, Ma) and no later than middle Norian (220-210 Ma) (Gruszka and Zieliński, 2008). As far as the geological time scale is concerned, this is merely a narrow age range difference, but from the point of view of the evolution of terrestrial Triassic vertebrates it does make quite a difference!

Locality and geological setting

What did present-day Silesia look like during the Late Triassic? The wider surroundings of Krasiejów area were quite flat, except for the southwestern edges of Poland (Fig. 1), where elevated terrain remained, representing remains of deeply eroded Variscan rock formations. Mainly from there, rivers proceeded and formed more or less extensive backwaters and swamps, separating islands from the dry mainland. This area was situated much further south on the globe during the Triassic, under warm, subtropical climatic conditions and the impact of monsoon rains.

Because of these circumstances air temperatures were very similar to those of the present-day Mediterranean basin, with merely two seasons; a rainy (summer) and dry (winter) one. Under such conditions, rivers swelled during summer and extended far beyond their beds, whereas in winter they almost disappeared and marsh and swamp areas decreased in size. Occasionally, rainfall was very intense which locally led to flooding. Just as a result of one of such floods, the extensive accumulation of fossil bones came into being in what is now Krasiejów (Gruszka and Zieliński, 2008). The rapid rise of flood waters washed out skeletal remains from neighbouring areas, and transported them to their final site of burial (Fig. 2).

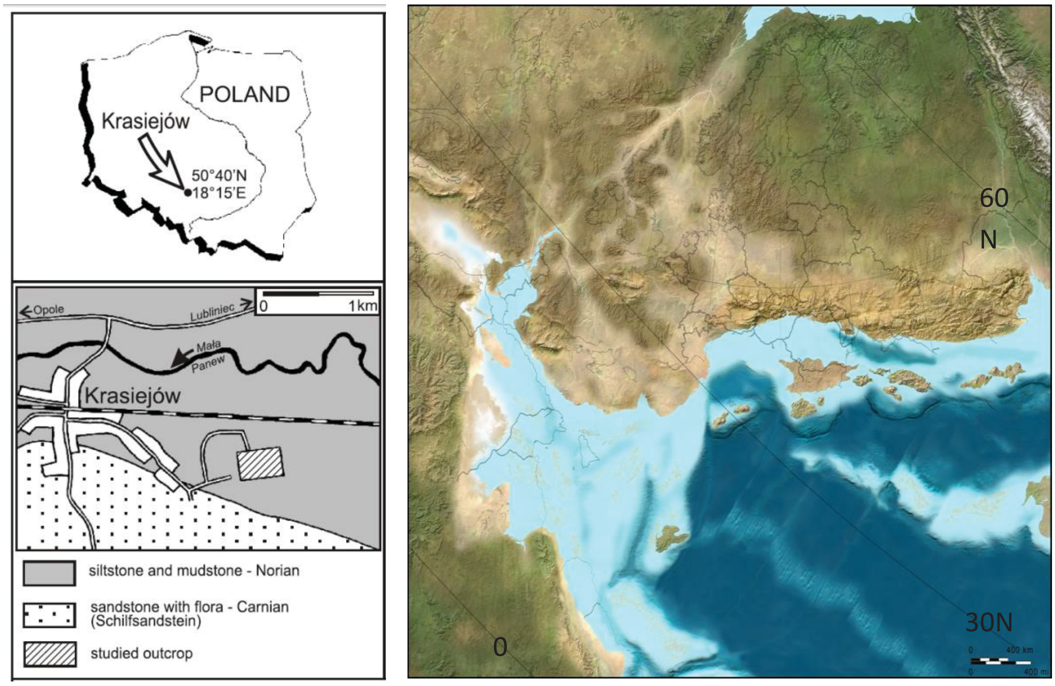
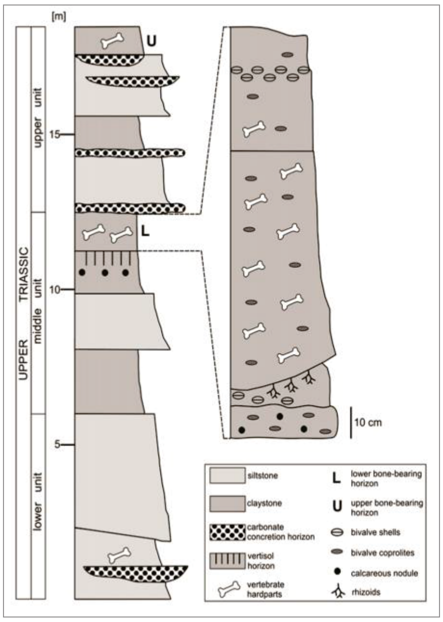


Fig. 1. Position of the Krasiejów site within Poland (left; from Gruszka and Zieliński, 2008) and location of Europe during the latest Triassic (right: ©Ron Blakey, Colorado Plateau Geosystems, Inc., courtesy by Dr Ron Blakey).

During transportation and prior to deposition, material was segregated, intermingled and often damaged as well (Bodzioch and Kowal-Linka, 2012). This explains why entire skeletons with proper anatomical arrangement of all elements are rare at Krasiejów. However, the rapid process of bone bed accumulation meant that interspersed bones of various animal species are now very numerous. Remains of large-sized vertebrates are present in both upper and lower claystone horizons (bone beds). These two levels are separated by a several layers of claystones and siltstones with a thin veins of carbonate concentration (Fig. 3). The lower bone-bearing horizon is situated about 10 metres below ground surface and is still exploited for fossils. This comprises the richest bone accumulation of aquatic (*Metoposaurus* and *Paleorhinus*), semi-aquatic (*Cyclotosaurus*) and terrestrial (*Stagonolepis* and *Polonosuchus*) taxa (Bodzioch and Kowal-Linka, 2012). The upper horizon is at two metres below ground level, and has already been exploited within the limits of the Krasiejów bone bed. The most famous taxon from Krasiejów, the dinosauromorph *Silesaurus opolensis*, stems from this particular horizon.



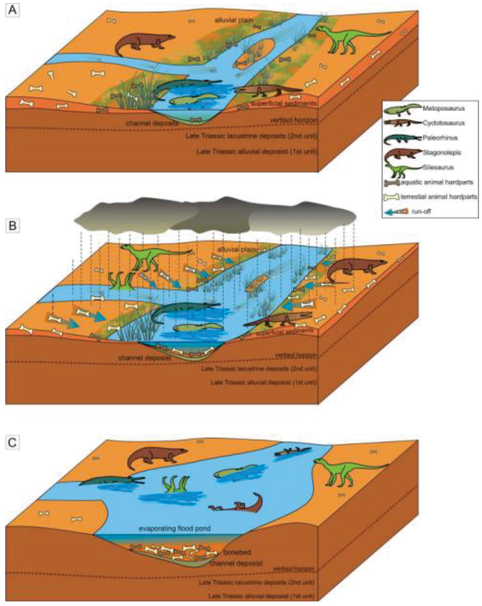


Fig. 2 (left). Schematic lithostratigraphic log of the Krasiejów site.
Fig. 3 (right). Schematic model illustrating how the lower bone-bearing bed might have formed (after Bodzioch and Kowal-Linka, 2012).

Plants, invertebrates and small vertebrates

In general, plant remains are poorly preserved at Krasiejów, but there are sufficient data to provide a landscape characteristic. The large accumulations of oospores (spore cells) indicates that green algae occupied inland waters. The wetlands were covered mostly by large horsetails and ferns, while in drier areas conifers could develop.

The fauna of small aquatic invertebrates was dominated by bivalves. A new genus and species, *Silesunio parvus* Skawina and Dzik, 2011, has recently been described from Krasiejów, on the basis of numerous moulds. Apart from bivalves, fossils of a cycloid, a crab-like crustacean (*Opolanka decorosa*), ostracods and phyllopods were recovered here (Dzik, 2008). Coleoptera (beetles) are on record from sediments formed beyond the aquatic environments.

Remains of ganoid and dipnoan fishes comprise scales, teeth and larger fragments of the skeleton; these are awaiting publication. The same holds true for skeletal material of sphenodonts, pterosaurs and very numerous, tiny bones of unknown animals – perhaps small mammals.

Larger vertebrates

Metoposaurus was the commonest aquatic vertebrate of the Upper Triassic wetlands. Recent microscopic studies of this huge amphibian have focused on long bones and vertebrae (Konietzko-Meier and Sander, 2013; Konietzko-Meier et al., 2013); currently, the skull and mandible bones receive most attention (Fig. 4). Remains of metoposaurids are known also from Morocco, North America, India and Germany. The German species, which was described in 1842 by Hermann von Meyer, is, anatomically speaking, the most closely similar to the Polish taxon. Both of them are considered to belong to the same species, *Metoposaurus diagnosticus*, but small differences in skull anatomy led Sulej to distinguish two subspecies in 2002, namely *Metoposaurus diagnosticus diagnosticus* for older form from Germany and *Metoposaurus diagnosticus krasiejowensis* from Krasiejów. Brusatte et al. (2015) described a new species of *Metoposaurus* from the Algarve, southern Portugal, and raised the Polish *Metoposaurus* to species rank, *Metoposaurus krasiejowensis*.

Metoposaurids were huge, 2-m-long aquatic temnospondyl amphibians with dorso-ventrally flattened bodies (Sulej, 2007). They probably lived at the bottom of shallow-water reservoirs, as ambush predators hunting for fish and other small vertebrates (Fig. 5). For air, they had to resurface regularly and the main mode of locomotion (swimming) was via the long and laterally flattened tail. The most characteristic feature of their skull is the location of the orbits; these did not lie on the top posterior parts of the skull, like in extant crocodiles, but were located in the anterior skull region, near the nostrils. Such placement of the orbits helped this aquatic predator in its search for prey and during swimming in the murky waters (Sulej, 2007).

Fig. 4. *Metoposaurus krasiejowensis* – skull and left ramus of mandible.

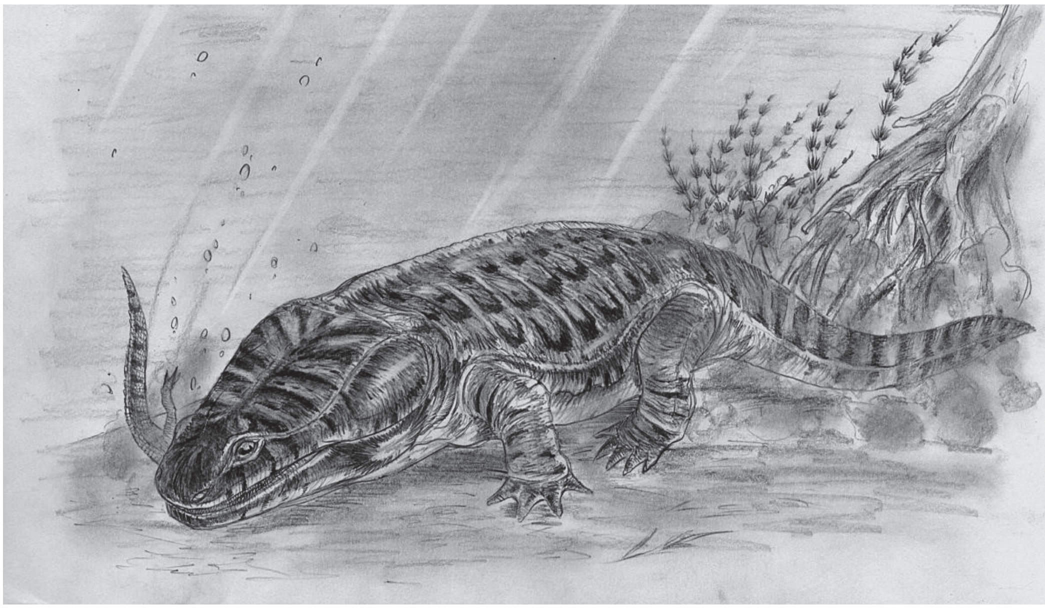


Fig.5. Reconstruction of *Metoposaurus krasiejowensis* during seizure of a small phytosaur.(project Kamil Gruntmejer; drawing by Jakub Kowalski).

Phytosaurs are the second commonest group of large vertebrates at Krasiejów, occurring in the lower bone bed. *Paleorhinus* sp. was a 3,5-m-long, semi-aquatic predator (Fig. 6), closely similar to extant gavials. Its skull was narrow, markedly elongated and possessed numerous, sharply pointed teeth adapted for a piscivorous habit. Features differentiating phytosaurs from Krasiejów from extant crocodylomorphs include the weak construction of the pelvis in the former, and the development of a secondary palate and a shift of the nostrils to the forehead as in extant whales (Dzik, 2001). The long jaws, slender body and extension of epiphyses in caudal vertebrae suggest that *Paleorhinus* was a fast and active predator in the waters at Krasiejów.

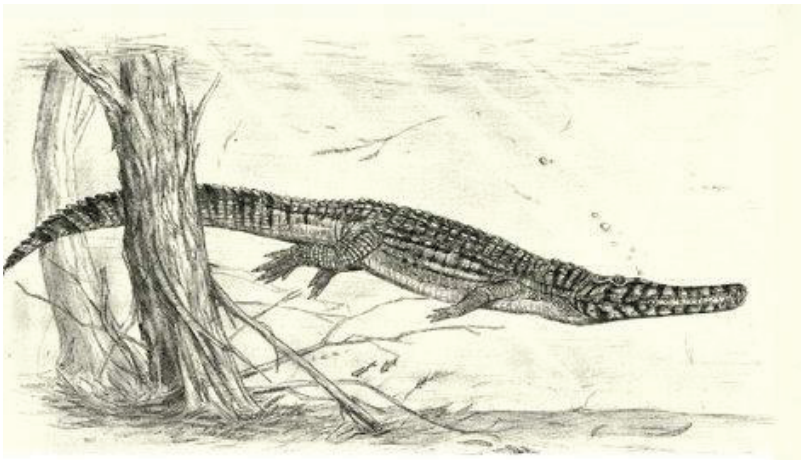


Fig. 6. Reconstruction of *Paleorhinus* sp. (drawing by Jakub Kowalski).

Capitosaurid temnospondyls are represented in Krasiejów by a single species, *Cyclotosaurus intermedius* (Fig. 7). This semi-aquatic, 3,5-m-long amphibian was a larger relative of *Metoposaurus*. Cyclotosaurids were the main predators near the edges of the bodies of water, their behaviour having been similar to extant crocodiles and alligators. The loss of lateral lines on their skull surface indicate that *Cyclotosaurus* was adapted for a predatory life style both in the water and in terrestrial habitats (Sulej and Majer, 2005). The location of the orbits in the posterior part of the skull and closure of the otic notch during evolution made capitosaurids hunt efficiently, from ambush, and exert a strong biting force.

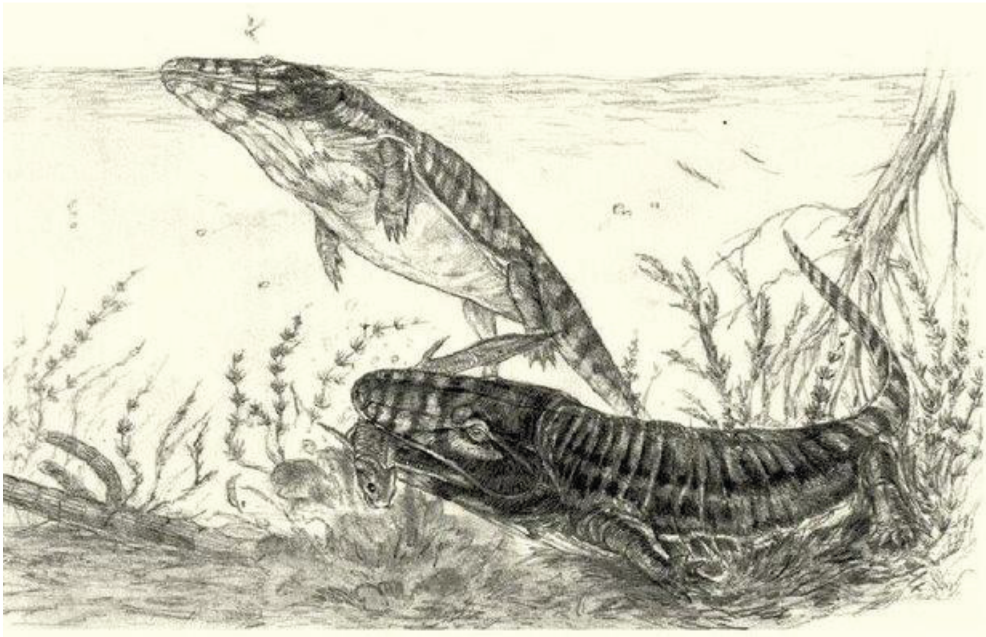


Fig. 7. Reconstruction of *Cyclotosaurus intermedius* (drawing by Jakub Kowalski).

Aetosaur remains (*Stagonolepis olankae*) are known from the lower and upper bone beds at Krasiejów. *Stagonolepis* was a herbivorous, 3,5-m-long archosaur with a heavily armoured body (Fig. 8). This natural armour played a protective role against attacks of large predators. The osteoderms overlapped closely and possessed diagnostic features used to differentiate amongst aetosaur species. Osteoderm morphology of the Polish aetosaur at first appeared to indicate its conspecificity with the Scottish species, *Stagonolepis robertsoni*. Subsequent studies of skull anatomy have shown this conclusion to be erroneous; the Krasiejów aetosaur is now considered a distinct species, *Stagonolepis olankae*. The skull of *Stagonolepis* was small and equipped with conical teeth and a horny beak on the mandible and a fleshy snout on the upper jaw (Sulej, 2010). Jaw morphology and tooth shape suggest that *Stagonolepis* used its snout to poke around amongst rhizomes and in the muddy bottom, in search of small invertebrate prey.

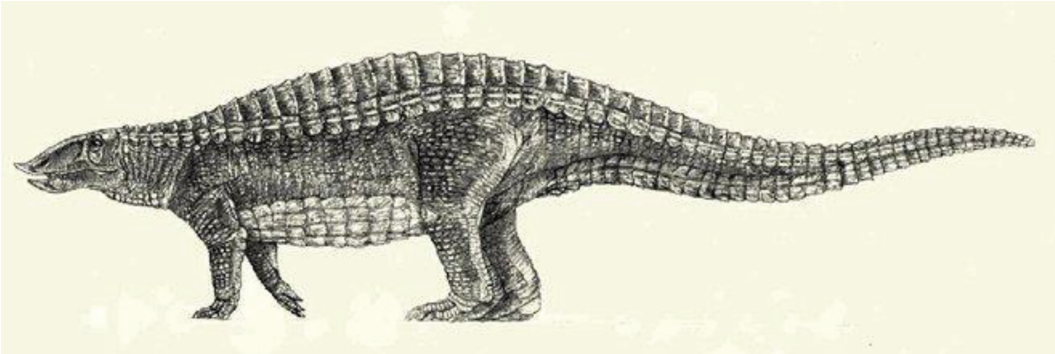


Fig. 8. Reconstruction of *Stagonolepis olankae* (drawing by Jakub Kowalski).

Polonosuchus silesiacus was the largest rauisuchian predator in the terrestrial habitat of Krasiejów. This 4-m-long archosaur was a seasoned hunter, specialising mainly in chasing armoured aetosaurs (Fig. 9). The Polish *Polonosuchus* is a smaller relative of the German genus *Teratosaurus* and the North American *Postosuchus*. At Krasiejów, rauisuchian remains were found in a thin layer of siltstones, between the upper and lower bone beds. All that is known at present are a single, incomplete skull, several vertebrae and isolated teeth. The most specific skull feature is the elastic and mobile connection of adjoining bones in the anterior part (Sulej, 2005). This elasticity of the skull made that teeth slipped from the aetosaur osteoderm surface during biting, to penetrate the soft tissues between these dermal plates. It is also possible that *Polonosuchus* could have been an ambush predator that went for smaller, yet faster animals.

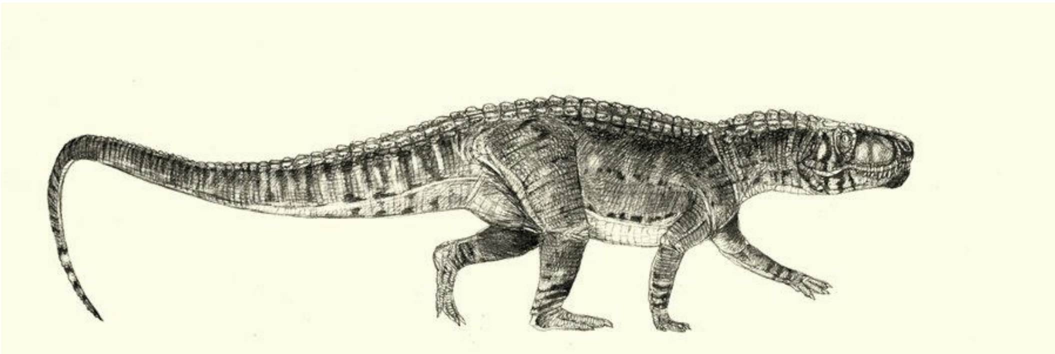


Fig. 9. Reconstruction of *Polonosuchus silesiacus* (drawing by Jakub Kowalski).

Bony remains of *Silesaurus opolensis* illustrate the unique and precious nature of the Krasiejów bone beds. *Silesaurus* was a small, *c.* 2-m-long, herbivorous dinosauromorph, *i.e.,* an intermediate form between archosaurs and dinosaurs (Fig. 10). The construction of its hind legs and pelvis and the open-work structure of the cervical vertebrae constitute features that are typical of the dinosaur lineage. On the other hand, skull morphology and tooth shape are characteristically archosaur. The delicate construction of the skeleton, and the fact that remains of several individuals were found accumulated in a single spot, suggest that *Silesaurus* was an agile, herbivorous animal (Dzik, 2003). During feeding the partially edentulous mandible with a horny beak at its end was used. Both its agility and life in a herd helped in spotting larger, yet slower, predators and in running from them. It is difficult to imagine that this small and inconspicuous species is closely related to the majestic, herbivorous ornithischian dinosaurs from the Jurassic and Cretaceous.

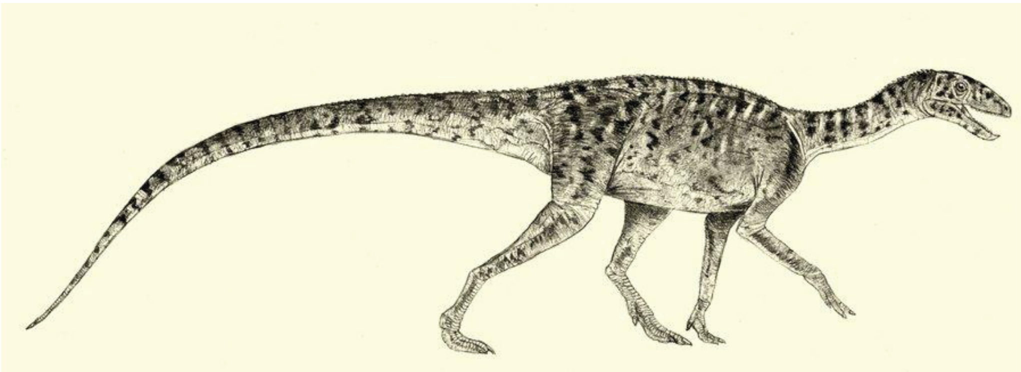


Fig. 10. Reconstruction of *Silesaurus opolensis* (drawing by Jakub Kowalski).

Agrotourism in Krasiejów

In recent years, the area of the former claystone pit at Krasiejów has been developed and in 2010 the 'Jurapark' opened its doors to the public It is the largest European object of science, amusement and agrotourism. Visitors can marvel at life-size models of prehistoric creatures, beginning from the Triassic and extending into the Cretaceous (Fig. 11A). Here also there is a palaeontological museum with exhibits of fossils and skeletal reconstructions of vertebrates from Krasiejów (Fig. 11B). During summer, visitors can experience what makes palaeontologists tick at special digs near the pavilion (Fig. 11C). Moreover, in 2014, just next to 'Jurapark' complex a new facility was opened, 'The Science and Human Evolution Park'. This modern object offers visitors a multimedia exploration of the museum which hosts life-size models of early hominids and illustrates the evolutionary process that led from our ancestors to modern man (Fig. 11D). Due to these tourist attractions and primarily because of the palaeontological excavations, young researchers from around the world visit Krasiejów every year. The sheer number of fossils and their unique nature (on a European scale) have turned Krasiejów into the largest bone bed of the Upper Triassic across Europe and the one that is most valued by research institutes abroad.

Fig. 11A-D. Tourist attractions in the 'Jurapark' complex. **A.** Life-size models of *Tyrannosaurus rex* and *Triceratops horridus*. **B.** Skeletal reconstructions of vertebrates from Krasiejów in the palaeontological pavilion. **C.** Palaeontological excavations in 2014. **D.** Life-size hominid model in the Science and Human Evolution Park.

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