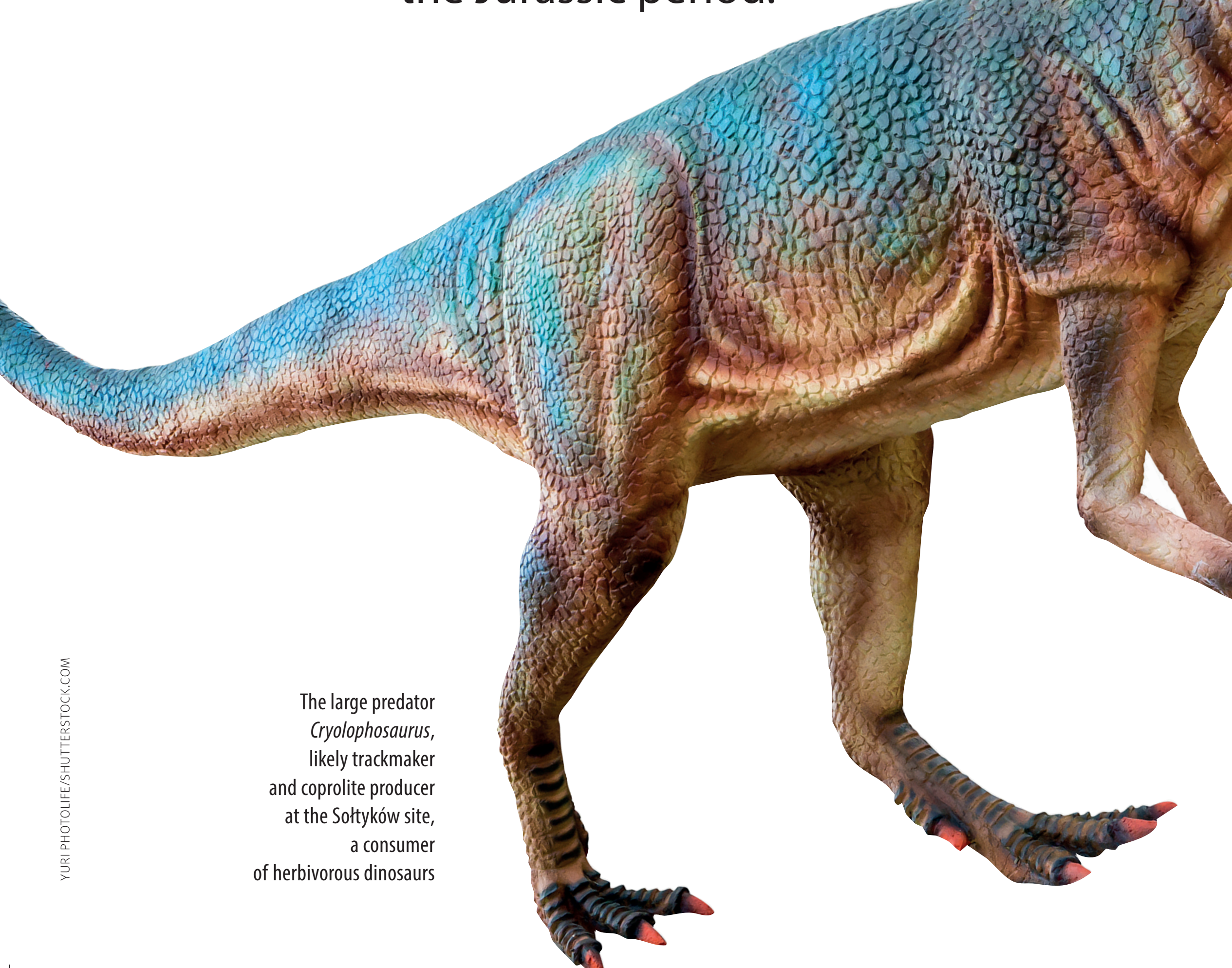
DOI: 10.24425/academiaPAS.138420

What Powered the Dinosaurs?

Maria Barbacka, PhD, DSc
is a paleobotanist specializing in plant fossils from the Mesozoic Era, mainly the Jurassic. She works on sites in Poland, Hungary, Germany, and Alaska. Her research focus is on taxonomy and paleoecology. She uses interdisciplinary methods to reconstruct Jurassic ecosystems.
maria.barbacka@gmail.com

Where did early dinosaurs get their energy from? Studying fossilized feces reveals certain secrets of herbivore evolution during the Jurassic period.

Grzegorz Pacyna, PhD
is a paleobotanist. His current focus is on the taxonomy and evolutionary significance of Silesian conifers from the Upper Triassic and on the taxonomy, evolution, paleoecology, and succession of flora from the Lower Jurassic in Poland's Holy Cross Mountains. He also studies interactions between plants and animals in the fossil record and biostratigraphy using plant fossils.
grzegorz.pacyna@uj.edu.pl



YURI PHOTOLIFE/SHUTTERSTOCK.COM

The large predator *Cryolophosaurus*, likely trackmaker and coprolite producer at the Sołtyków site, a consumer of herbivorous dinosaurs

Maria Barbacka

PAS Władysław Szafer Institute of Botany in Kraków
Botanical Department at the Hungarian Natural History Museum in Budapest

Grzegorz Pacyna

Institute of Botany, Faculty of Biology, Jagiellonian University in Kraków

Jadwiga Ziaja

PAS Władysław Szafer Institute of Botany in Kraków

Grzegorz Niedźwiedzki

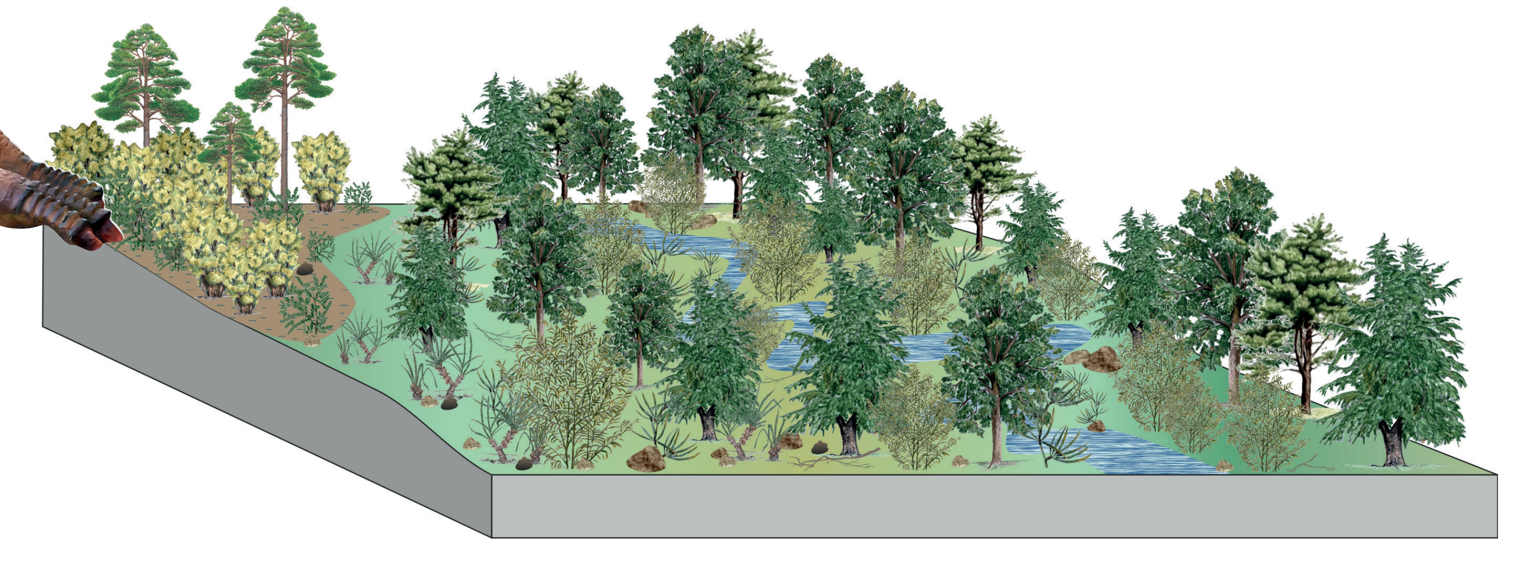
Evolutionary Biology Centre in Uppsala, Sweden

Jadwiga Ziaja, PhD
is a palynologist studying spores and pollen of Mesozoic plants, mainly from the Jurassic. She uses palynological analysis of rocks to trace changes in the climate and environment in certain regions. She identifies and describes spores and pollen grains in situ, which is an important element in determining botanical relationships between fossil plants.
j.ziaja@botany.pl

The study of coprolites (fossilized feces) left behind by Jurassic dinosaurs, both herbivorous and carnivorous, at the Sołtyków site in central Poland reveals fascinating information about their diet and habits and about the flora present in the Holy Cross Mountains some 200 million years ago.

The site

Sołtyków (also known as Odrowąż) is a village in Poland's Holy Cross Mountains region, close to the small town of Końskie. Part of a former open-pit quarry, once producing ceramic clay to make bricks, is currently a geological nature reserve (named Gagaty Sołtykowskie). Numerous dinosaur tracks left behind in the boggy soil of the floodplain 200 million years ago have been preserved in the sandstones of the reserve. The most common are mid-sized footprints, most likely made by theropods (early predatory dinosaurs). The largest, spanning up to 50 cm,



Reconstruction of the flora known from coprolites, in accordance with the plants' environmental preferences and the surroundings as reconstructed based on sedimentology studies

Grzegorz Niedźwiedzki, PhD

is a graduate of the Faculty of Biology at the University of Warsaw. He participates in numerous expeditions studying the Permian-Triassic and Jurassic periods in Poland, Russia, Tunisia, Greenland, and Sweden. He has discovered several sites with preserved tracks and bones of Mesozoic amphibians and reptiles, tracks of early quadrupeds, and dinosaur remains.

grzegorz.niedzwiedzki@ebc.uu.se

are tridactyl tracks believed to have been left by large early therapods, although their fossilized bones have yet to be found.

The tracks known as *Stenonyx* and *Grallator* were likely made by small *Coelophysis* theropods. There are also numerous footprints spanning up to 40 cm made by sauropods, classified to the *Parabrontopodus* ichnotaxon (an "ichnotaxon" being a taxon based on the fossilized traces of animal activity). The small and medium-sized tracks known as *Anomoepus* and *Delatorrichnus* may have been left by early armored dinosaurs or heterodontosaurus. Other tracks offer evidence of the presence of mammal-like reptiles, early mammals or mammaliaforms, lepidosaurs, pterosaurs and early crocodylomorphs.

While very few bones have been found in Sołtyków, dinosaur coprolites are common in the region. Around 300 coprolites have been collected so far, with a handful of them sufficiently well preserved to be suitable for closer study.

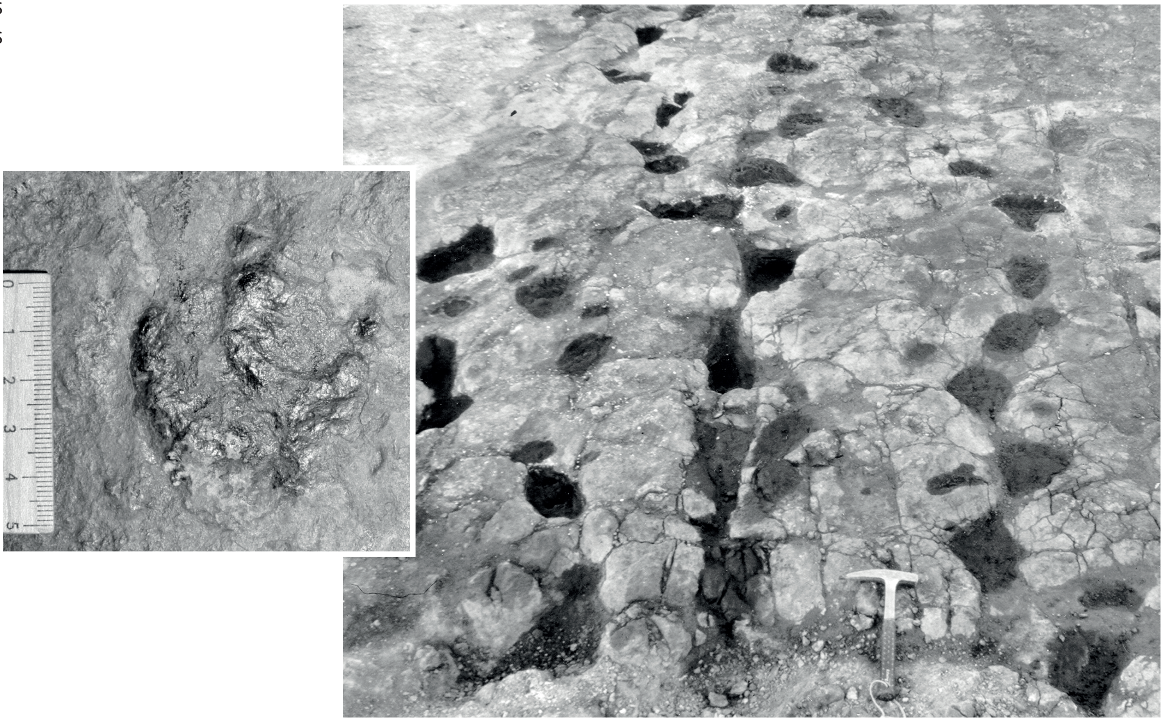
Coprolites

Plant remains may be preserved in the coprolites of both herbivorous (plant-feeding) dinosaurs, as well as carnivores who hunted them. Plant remains and fragments such as bones, insects, shells, etc., also found in coprolites, are an excellent source of information on the real diet of these animals. They also allow us to fill in gaps in our understanding of plants and animals which have not been noted in any other fossil record.

Generally speaking, when the remains of plant cuticles (protective layers made up of lipids, cellulose and pectin on the surface of the epidermis) are found in coprolites, they are present as tiny fragments in digested matter, and are usually identifiable only as plant remains, and more rarely as belonging to a specific group of plants, for example conifers. The coprolites found at the Sołtyków site (both from herbivores and large carnivores) are a unique exception in this regard, in that the leaf fragments are sufficiently large and numerous that some have been successfully assigned to a species, some to a genus, others to a particular systematic group, and in two cases researchers have even been able to describe a new taxon.

We currently do not know why the quality of plant remains is so high in coprolites at this particular site. Early Jurassic sauropods did not have a highly developed mechanism of chewing and masticating food and their teeth only allowed them to tear leaves and perhaps rip branches, so the largely intact food they swallowed was fermented in their stomachs; however, the digestion process was relatively efficient. Some species swallowed rocks (gastrolites) to help break down their food. In carnivores, large plant fragments may have been preserved in feces because they originated from the digestive tracts of their prey at various stages of digestion, and they were not digested further since carnivores lack the appropriate bacterial microflora and enzymes. This means that any plants they ingested were excreted at the same stage of digestion. Large fragments of undigested plant cuticles are highly unusual in herbivore coprolites.

Sołtyków, imprints of tracks left by Sauropodomorphs



Studies

We studied 14 coprolites, seven from large predators and seven from herbivores, most likely Sauropodomorpha. Preliminary treatment involved mechanically breaking down the fossils, dissolving them in hydrochloric acid and soaking in EDTA. After thorough rinsing, organic remains were selected and categorized.

Plant remains extracted from coprolites are preserved in the same condition as those fossilized in sediment: as coalified leaf fragments, or more precisely their cuticles. They are prepared following a classic palaeobotanical method by immersing in Schulze's reagent (concentrated nitric acid and potassium chlorate) and washed in a weak solution of potassium hydroxide. This removes diagenetic carbon, and all that remains is a clean cuticle which is now ready for microscope analysis.

Leaf fragments preserved in coprolites range from a few mm to around 20 mm, with the upper and lower surfaces preserved, allowing us to identify the plants more precisely.

As well as plant cuticles, coprolites may also contain pollen grains and spores, present either in fecal matter (residue) or adhering to cuticles. They also help us identify plants from feeding grounds and to determine the age of research sites.

Interpretation

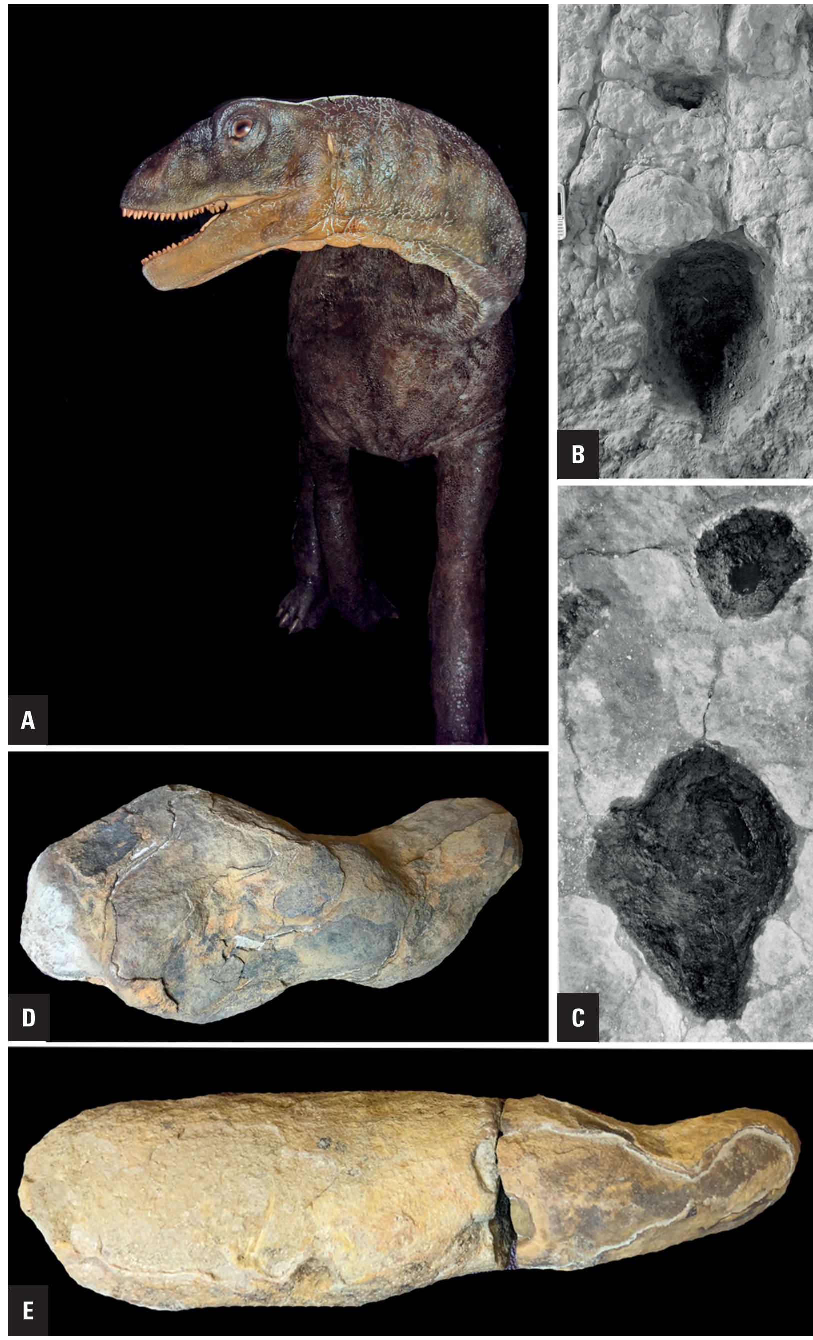
The plant fragments found in the coprolites of predators, as we have noted, mainly originate from the digestive tracts of their prey. But it is also possible that the carnivores ingested plants accidentally, and we also cannot be certain that the animals may not have eaten them on purpose, since our understanding of the physiology of digestion of Mesozoic reptiles is still very poor. We consider it best to examine these cuticles in the botanical context, leaving conclusions about dinosaur feeding habits focused on herbivores.

Analysis of cuticles from both types of coprolites has revealed the presence of 12 plant taxa, of which five have been assigned to a species, five to a genus, and the remaining two to a higher taxonomic category. Four types of cuticles remain unidentified. In addition to cuticles, we also found one fragment of wood a few millimeters long. The coprolite remains represent three species of seed ferns, one species each of cycad, bennettitalean and gingko, four conifer species and two of unknown affinity. Three species had previously been identified near the Holy Cross Mountains, while the others were reported for the first time; thus our knowledge of the local flora has had nine previously unknown taxa added to it.

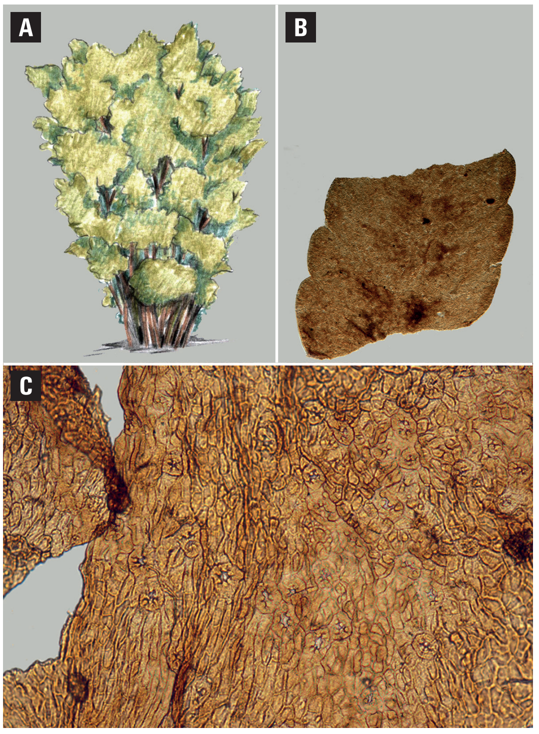
Analysis of spores present in the coprolites (from bryophytes, lycophytes, and ferns) further rounds out our picture of the local flora composition in the dinosaurs' feeding area.

Environmental preferences of plants found in coprolites were determined using methods usually used for fossil plants, on the basis of analysis of sediments containing plant fragments and based on the plants' morphology and structure of their cuticles. The majority of taxa found in coprolites are a close match with the reconstructed ecosystem of the Early Jurassic in the region. They are also found at other sites in Europe, mainly in river and delta deposits.

One of the seed fern species found in coprolites shows xeromorphic characteristics, indicating an arid



A. The herbivorous dinosaur *Vulcanodon*, likely trackmaker and coprolite producer at the Sołtyków site. Reconstruction at the Jan Pazdur Museum of Natural History and Technology, Starachowice.
B, C. Imprints of tracks of smaller and larger individuals, respectively.
D, E. Coprolites likely left by a Sauropodomorph



One of the plants found in the coprolites, the seed fern *Pachypteris papillosa* (Thomas et Bose) Harris.
A. Likely appearance of the plant.
B. Fragment of a leaf found in the coprolite.
C. Enlarged cuticle fragment showing stomata regulated by papillae

or saline environment. This means relatively small leaves (compound pinnate), thick cuticles, and stomata protected by papillae. All these features aim to limit evaporation and thus to protect the plant from drying out. Topographic reconstruction of the site does not indicate exposed arid areas, therefore our search for the reasons for xeromorphism turned to local saline sites. This made sense, since the species in question, *Pachypteris papillosa* (Thomas et Bose) Harris, is known from coastal regions and is interpreted as halophytic (salt-tolerant). However, Sołtyków was situated ~700–800 km from the nearest coastline (in present-day Germany). Which means even a large predator could not have covered such a vast distance between feeding and defecating. However, it turns out that at Miłków-Szewna (70 km from Sołtyków), high boron content was found locally, perhaps indicating an ancient saline environment (this is explained by Permian/Triassic evaporate-bearing deposits, which could have delivered salt to springs and soils in the area). A distance 70 km probably was no problem for large animals and reveals some information about the direction of migration of some individuals.

The question remains whether dinosaurs intentionally fed on halophytes, like some contemporary herbivores do, thereby utilizing of the microelements in salt. We currently have no data on whether dinosaurs ingested salt, but given our understanding of present-day reptiles, intentional feeding on halophytes seems unlikely. Recent reptiles which live in salt water (for example crocodiles) have glands which excrete salt. It appears, therefore, that reptiles do not have a mechanism for utilizing microelements from salt, so feeding on halophytes was most likely incidental.

Judging by the proportion of fragments found in coprolites, the majority of plants eaten by dinosaurs had large leaves and belonged to seed ferns and cycadophytes. Conifers were less numerous, predominantly thuja-like, offering soft, fleshy twigs. Other conifers and gingkoes were found less frequently. All taxa found in coprolites were trees or large shrubs, which indicates that dinosaurs fed at the canopy level – an interesting detail about feeding behavior.

A complete absence of wood in coprolites (the single microscopic fragment being insignificant in this respect) attests to an abundance of easily digestible, high-energy plant material. A large amount of wood in feces would indicate that animals were forced to feed on material harder to digest, suggesting possible famine conditions.

The taxa from the coprolites we studied likely do not represent the entire diet of herbivorous dinosaurs in the Holy Cross Mountains.

It should be noted that cuticles of many plants, for example large-leaf ferns (which also included tree-like forms) are faint and easily-degrading, while seed plants have cuticles resistant to such a degree that they could pass through the digestive tract undigested – and so, the cuticle fragments in coprolites represent just a small proportion of food which had not been digested for certain reasons. Spores and pollen grains are of no help since they are not equivalent to the species which produced them; they may have simply been found in water or on the surface of plants eaten by the animals.

New information

Overall, the results of our studies of plant fragments in dinosaur coprolites have provided valuable palaeoecological information on a new ecological niche, in particular for the *Pachypteris papillosa* species which inhabited salty inland regions, as well as improving our understanding of dinosaur behavior, diet, and feeding habits. The research has revealed new information on Early Jurassic flora from the northern margin of the Holy Cross Mountains and expanded the number of taxa by nine, including two which had not been described previously at all.

The findings presented here represent the newest results of the research done under the project. Although similar studies have been conducted at other sites all over the globe for many years, none of the materials have been so well preserved or provided so many important data in palaeobotany.

The research was funded by Poland's National Science Centre (grant no. 2017/25/B/ST10/01273) and the statutory funds of the PAS Władysław Szafer Institute of Botany.

Further reading:

Dzik J., 2003, Krasiejów – u zarania ery dinozaurów [Kresiejów – At the Dawn of the Era of Dinosaurs], *Ewolucja* 1, 2–13.

Dzik J., Niedźwiedzki G., Sulej T., 2008, Zaskakujące uwieńczenie ery gadów ssakokształtnych [Surprising Pinnacle of the Era of Mammal-Like Reptiles], *Ewolucja* 3, 2–21.

Pacyna G., Zdebska D., Barbacka M., Ziaja J., 2013, Co jadły polskie dinozaury? [What Did Polish Dinosaurs Eat?], *Wszechświat* 114 (7), 250–252.