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# Who ate whom? Paleoecology revealed through synchrotron microtomography of coprolites (fossil feces)

MARTIN QVARNSTRÖM



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### Abstract

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Fossil droppings, known as coprolites, are being increasingly recognized as a valuable source of paleoecological information with special regard to diets, parasitism, and physiology of extinct taxa. Here, it is suggested that the excellent preservation and amount of inclusions in the coprolites (e.g. food residues and parasites) qualifies them as *Lagerstätten* – deposits with exceptional paleontological information. However, two interlinked problems commonly arise when they are studied. Firstly, it is often difficult to tie coprolites to producers and, secondly, it is challenging to recognize the fragmented and randomly distributed inclusions in their matrix. Here I use propagation phase-contrast synchrotron microtomography (PPC-SR $\mu$ CT) in combination with other techniques to solve these problems. As a result, the oldest known example of archosaurian osteophagy is uncovered based on *inter alia* the occurrence of serrated teeth and many crushed bones in coprolites assigned to the Late Triassic theropod-like archosaur *Smok wawelski*. Osteophagy has previously been thought to be rare among extinct archosaurs with the exception of Late Cretaceous tyrannosaurids. This suggests some degree of ecological convergence between the tyrannosaurids and *S. wawelski*. Furthermore, exceptionally-preserved beetle remains are discovered in coprolites tentatively assigned to the Triassic dinosauriform *Silesaurus opolensis*, which had a specialized dentition and possessed beak-shaped jaws that were likely used to peck insects off the ground. Moreover, pterosaur coprolites are shown to contain similar food residues as found in droppings of recent flamingos, implying that some Late Jurassic pterosaurs were filter feeders. I argue that such paleoecological studies have a large impact on our understanding of ancient animals, and that studies of coprolites can unravel parts of ancient food webs in unprecedented ways. Information on past food webs may, in turn, be used to analyze trophic changes through time, which could cast new light on big evolutionary events. This is demonstrated by reconstructing trophic structures in early Mesozoic assemblages that represent snapshots of three stages of early dinosaur evolution.

*Keywords:* coprolites, paleoecology, synchrotron microtomography, taphonomy, Triassic

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*Till Mormor*



# List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I **Qvarnström, M.**, Niedźwiedzki, G., Žigaitė, Ž. (2016) Vertebrate coprolites (fossil faeces): an underexplored *Konservat-Lagerstätte*. *Earth-Science Reviews*, 162:44–57. doi: 10.1016/j.earscirev.2016.08.014
- II **Qvarnström, M.**, Niedźwiedzki, G., Tafforeau, P., Žigaitė, Ž., Ahlberg, P.E. (2017) Synchrotron phase-contrast microtomography of coprolites generates novel palaeobiological data. *Scientific Reports*, 7:2723. doi: 10.1038/s41598-017-02893-9
- III **Qvarnström, M.**, Niedźwiedzki, G., Ahlberg, P.E. (2019) Tyrannosaurid-like osteophagy by a Triassic archosaur. *Scientific Reports*, 9:925. doi: 10.1038/s41598-018-37540-4
- IV **Qvarnström, M.**, Vikberg Wernström, J., Piechowski, R., Tałanda, M., Ahlberg, P.E., Niedźwiedzki, G. (2019) Beetle-bearing coprolites possibly reveal the diet of a Late Triassic dinosauriform. *Royal Society open science*, 6:181042. doi: 10.1098/rsos.181042
- V **Qvarnström, M.**, Elgh, E., Owocki, K., Ahlberg, P.E., Niedźwiedzki, G. (2019) Filter feeding in Late Jurassic pterosaurs supported by coprolite contents. *PeerJ*, 7:e7375. doi: 10.7717/peerj.7375
- VI **Qvarnström, M.**, Vikberg Wernström, K., Wawrzyniak, Z., Barbacka, M., Pacyna, G., Owocki, K., Sulej, T., Huld, S., Doring, M.A.D., Žigaitė, Ž., Ahlberg, P.E., Niedźwiedzki, G. Food web analysis of early Mesozoic ecosystems shed new light on early dinosaur evolution. (Manuscript)

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Published articles on coprolites which are not included in the thesis:

Niedźwiedzki, G., Bajdek, P., **Qvarnström, M.**, Sulej, T., Sennikov, A., Golubev, V.K. (2016) Reduction of vertebrate coprolite diversity in association to the end-Permian extinction event in Vyazniki, Russia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 450:77–90.

Bajdek, P., **Qvarnström, M.**, Owocki, K., Sulej, T., Sennikov, A.G., Golubev, V.K., Niedźwiedzki, G. (2016) Microbiota and food residues including possible evidence of pre-mammalian hair in Upper Permian coprolites from Russia. *Lethaia*, 49:455–477.

Zatoń, M., Broda, K., **Qvarnström, M.**, Niedźwiedzki, G., Ahlberg, P.E. (2017) The first direct evidence of a Late Devonian coelacanth fish feeding on conodont animals. *The Science of Nature*, 104:26.

**Qvarnström, M.**, Anagnostakis, S., Lindskog, A., Scheer, U., Vajda, V., Rasmussen, B.W., Lindgren, J., Eriksson, M.E. (2019) Multi-proxy analyses of Late Cretaceous coprolites from Germany. *Lethaia*, 52:550–569.

# Contents

|  |    |
|--|----|
| Introduction.....  | 11 |
| Coprolites.....  | 12 |
| A (very) brief historical résumé .....                             | 12 |
| How can a dropping become a fossil?.....                           | 13 |
| Coprolites as <i>Lagerstätten</i> .....                            | 14 |
| A quick guide to finding the perpetrator .....                     | 16 |
| Opaque treasure chests and how to open them.....                   | 18 |
| Aims.....  | 20 |
| Methods .....  | 21 |
| Localities .....   | 21 |
| Krasiejów .....  | 21 |
| Lisowice .....   | 21 |
| Wierzbica .....  | 22 |
| Sołtyków .....   | 22 |
| Imaging techniques .....   | 23 |
| “Conventional” imaging techniques .....                            | 23 |
| Synchrotron microtomography .....                                  | 24 |
| Geochemical methods .....  | 25 |
| Energy-dispersive X-ray spectroscopy .....                         | 25 |
| Time-of-flight secondary ion mass spectroscopy.....                | 25 |
| Main findings.....   | 27 |
| Results and discussion.....  | 27 |
| Setting the stage – papers I & II.....                             | 27 |
| A bone-crushing archosaur from the Late Triassic – paper III ..... | 27 |
| A Carnian dinosauriform that ate beetles – paper IV.....           | 28 |
| The flamingos of the Late Jurassic – paper V.....                  | 29 |
| Putting the puzzle together – paper VI.....                        | 31 |
| Limitations .....  | 32 |
| Coprolite producers.....   | 32 |
| What can we expect to find in the coprolites? .....                | 33 |
| Conclusions .....  | 35 |
| Future perspectives .....  | 36 |
| Svensk sammanfattning .....  | 37 |
| Acknowledgements.....  | 41 |
| References.....  | 43 |



# Abbreviations

|                 |  |
|-----------------|--|
| PPC-SR $\mu$ CT | Propagation phase-contrast synchrotron microtomography |
| SEM             | Scanning electron microscopy                           |
| EDS             | Energy-dispersive X-ray spectroscopy                   |
| ToF-SIMS        | Time-of-flight secondary ion mass spectrometry         |



# Introduction

The general public would probably associate paleontology with findings of *skeletal fossils* of extinct animals, and maybe particularly those of big dinosaurs. This is perhaps not too surprising as skeletons of extinct animals are indeed astonishing and informative when it comes to several evolutionary questions. However, there is a limit to the information that most body fossils can yield on extinct taxa. For instance, they typically do not provide any *direct* evidence for ecology and behavior, although it may be possible to infer such information based on comparative anatomy, functional morphology and co-occurrences of fossils (e.g. Farlow and Holtz, 2002; Meloro and Elton, 2012; Bestwick et al., 2018).

Thankfully, other fossils can answer some of the paleoecological questions that body fossils alone cannot. Trace fossils – or ichnofossils – represent fossilized traces of organisms’ *activity*, i.e. the living beings doing their “every-day thing”, in contrast to the often fragmented and transported biomineralized parts of a dead organism. As a result, trace fossils can provide direct evidence on locomotion, behavior, and ecology of the producer. Trace fossils related to food processing are called bromalites and include fossilized regurgitates, food remains preserved within the body cavity of an animal (e.g. gut contents), and feces (Fig. 1; Hunt, 1992). The latter – termed coprolites – constitute the subject of this thesis. A particular focus lies in the paleoecological information that vertebrate coprolites contain and that can be retrieved using synchrotron microtomography.

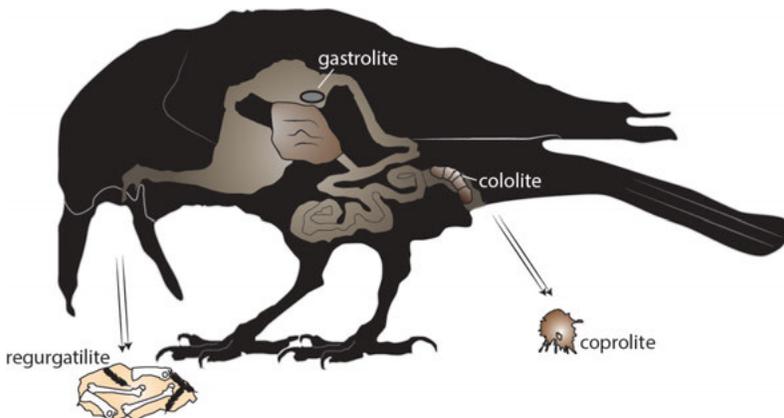


Figure 1. The origin of a few common types of bromalites.

# Coprolites

## A (very) brief historical résumé

A coprolite is a fossilized dropping of an animal, or at least a desiccated one following the archeological definition. The fecal origin of coprolites has been known since the first half of the 19<sup>th</sup> century and the studies of William Buckland (1784-1856). Buckland introduced the term “coprolite” in a presentation in 1829, a series of short subsequent papers, and finally in a publication in the *Transactions of the Geological Society of London* (Buckland, 1835). In this paper, Buckland described how he compiled evidence for a fecal origin of coprolites based on specimens from the Kirkdale Cave (Quaternary cave deposits) and subsequently the Jurassic coast of Lyme Regis (Buckland, 1835). He compared the shapes of the Jurassic specimens to remains in the “abdominal region” of ichthyosaur skeletons (note that Buckland initially referred to both fossil droppings and gut contents as coprolites) showed to him by the famous fossil collector Mary Anning. This was the final piece of evidence he needed to conclude that coprolites were indeed fossilized remnants of food processing. As a side note, Buckland is not only known as the father of “paleocoprology”, but also for earlier having erected the first dinosaur genus, *Megalosaurus* (Buckland, 1824).

The first illustrations of coprolites, however, date as far back as the turn of the 18<sup>th</sup> century (Duffin, 2009, 2012). At this time, coprolites were seen as curiosities and sometimes thought to be fossil larch cones, nuts, or Bezoar stones (i.e. a “stone” formed in the gastrointestinal tract of an animal and often used in ancient medicine). Immediately following the discoveries of Buckland, some naturalists (particularly those from England) became very enthusiastic about studying and discussing this new fossil material, something which is referred by Duffin (2012) as the period of “copromania”. Coprolites and other phosphatic nodules were even commercially excavated and used as agricultural fertilizers in England during the 19<sup>th</sup> century because of their high phosphate concentrations (O’Connor and Ford, 2001; Ford and Connor, 2009). However, with a few exceptions (e.g. Bertrand, 1903; Neumayer, 1904), coprolites were quite seldom studied in detail during the last half of the 19<sup>th</sup> century and major part of the 20<sup>th</sup> century. In general, coprolites (especially pre-Quaternary specimens) and their contents have not acquired the sci-

entific attention they deserve, leading to coprolites being a largely understudied part of the fossil record. In the last decades, however, coprolite research has had quite of an upswing, so it appears that the times are changing!

## How can a dropping become a fossil?

It is often resistant, biomineralized parts such as shells, bones, and teeth that preserve as fossils. So how can feces become fossilized? Assume an individual of a dinosaur. After its death it would leave nothing but a single skeleton that may, against all odds, become preserved as a fossil. However, it probably produced thousands of droppings – and millions of footprints – during its lifetime. So even if the potential of a single dropping (or footprint) to preserve as a fossil is exceedingly small, the likelihood of some of them becoming preserved rises given the large numbers. In fact, coprolites are quite abundant fossils; rocks rich in fossil bones commonly contain coprolites as well. Some deposits that have poorly preserved or no bones may have a large abundance of 3D-preserved coprolites, which are frequently overlooked. It is also likely that many isolated and fragmentary fossils represent food residues from re-worked bromalites.

The exact requirements for the preservation of droppings and their contents are not particularly well understood as very little experimental work has been done on the topic. However, it is possible to infer some important factors from archaeological and paleontological specimens. Most researchers agree that rapid permineralization involving bacteria is a crucial factor for preservation of droppings and that burial environments, climatic variables, and contents likely play important roles also (**paper 1**; Lamboy et al., 1994; Hollocher et al., 2001; Seilacher et al., 2001; Chin et al., 2003; Godbois et al., 2005; Kuehl et al., 2007; Hollocher and Hollocher, 2012). The bacterial influence is evidenced by secondarily mineralized gas bubbles from microbial activity and by replicas of bacteria in the form of micrometer-sized pseudomorphs often being visible in the coprolite matrices (Lamboy et al., 1994; Hollocher et al., 2001; Hollocher and Hollocher, 2012; Owocki et al., 2012).

Another important factor that likely facilitates the preservation of droppings (and their contents) from carnivores is their chemical composition. They are commonly enriched in calcium phosphate, derived from the ingested flesh and bones of prey. Phosphate is one of the most common diagenetic minerals that is associated with exceptional preservation (Allison, 1988). The phosphatic composition of carnivore droppings may trigger microbial-induced permineralization during early diagenesis and thereby explain why they appear to be more common than those from herbivores. Another explanation is that they are simply much easier to identify than coprolites from herbivores.

## Coprolites as *Lagerstätten*

The inclusions (e.g. food remains) in the coprolites are typically also well preserved; often much better preserved than fossils found in sedimentary rocks. Some authors have even drawn the conclusion that coprolites constitute a kind of *Lagerstätte* (**paper 1**; Seilacher et al., 2001); a deposit with extraordinary paleontological information. A deposit is considered a *Lagerstätte* either because it contains an abundance of fossils, termed *Konzentrat-Lagerstätten*, or extraordinarily preserved ones, *Konservat-Lagerstätten* (Seilacher et al., 1985). The latter include deposits with fully articulated skeletons or rarely preserved structures, such as soft tissues and biomolecules, which can provide important paleobiological data on physiological and molecular characters (Sansom et al., 2010, Schweitzer, 2011, Lindgren et al., 2012, 2014; Sansom and Wills, 2013; Moyer et al., 2014). This exceptional information increases our general understanding of the ecology of extinct organisms and the study of paleomolecules represents a relatively new but very exciting area of research.

Given that coprolites still represent an understudied part of the fossil record, there are already surprisingly many findings of different non-mineralized tissues derived from their contents (Fig. 2; **paper I**). Obviously, these delicate tissues must not only get fossilized in an early state to get preserved, but they must initially also have survived the digestive tract of the producer. A few examples of such findings are listed below, but for a more in-depth discussion on the soft tissue record from coprolites of the entire Phanerozoic, the reader is referred to **paper I** and references therein.

There are so far a few known cases of hair preserved in coprolites. One example is from prey animals (Taru and Backwell, 2013), including probable human hair (Backwell et al., 2009), retrieved from hyena-produced coprolites found in Quaternary cave deposits in South Africa. Other examples include the only known occurrence of multituberculate hair in the fossil record (Meng and Wyss, 1997), and possible pre-mammalian (synapsid) hair from continental Permian deposits in South Africa (Smith and Botha-Brink, 2011) and Russia (Bajdek et al., 2016).

Incorporation in coprolites is suggested as one of five possibilities leading to the preservation of feathers (Davis and Briggs, 1995). However, up until recently, there was only a single example known: Wetmore (1943) described detailed impressions of feathers from a Miocene coprolite and suggested them to have been contour feathers of an aquatic bird that got eaten by a crocodylian or fish predator. A more recently discovered example that is not yet fully described comes from the Upper Cretaceous Hell Creek Formation and consists of a coprolite that contains an accumulation of feathers, including flight feathers (Carroll et al., 2019).

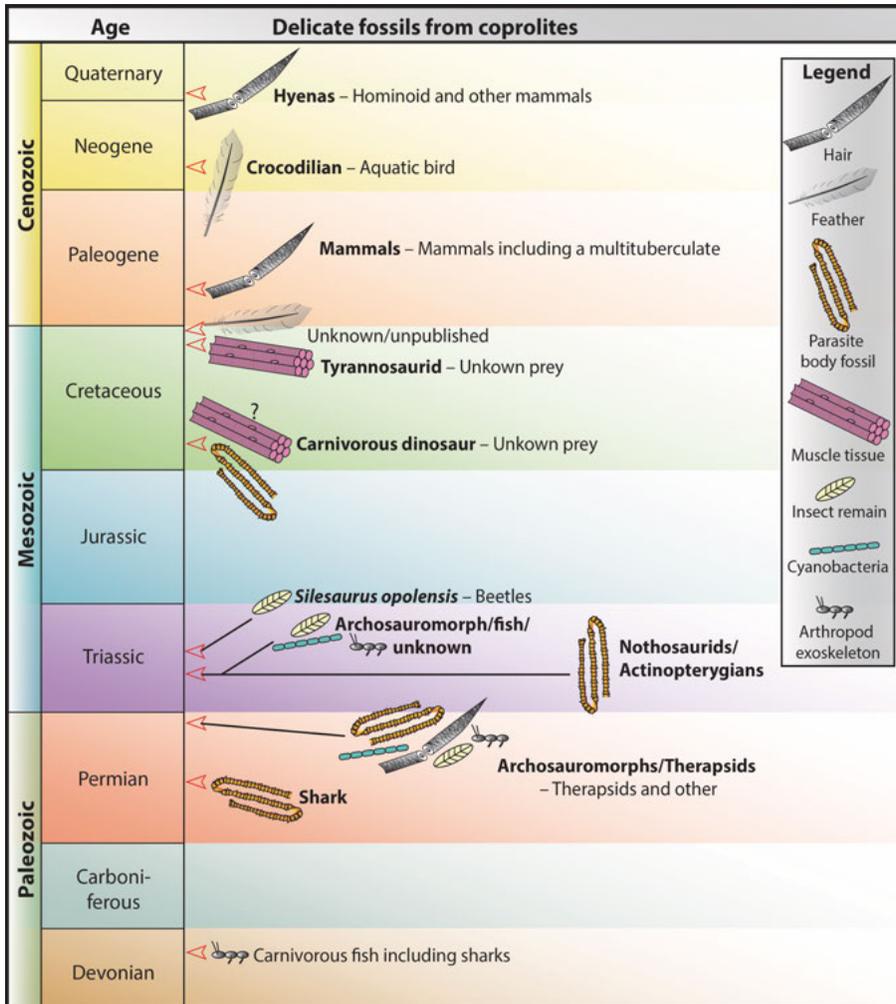


Figure 2. Delicate fossils found in vertebrate coprolites of different age (the time scale ranges from the Upper Devonian to recent). Supposed coprolite producers are indicated in bold, and the affinity of the delicate fossils themselves in regular font. The figure is modified from **Paper I** and based on references therein, **Paper IV**, and Carroll et al. (2019).

Fossilized muscle tissue has been described in coprolites from two localities. Chin et al. (2003) demonstrated evidence of undigested muscle tissue in a big tyrannosaurid coprolite from the Late Cretaceous Dinosaur Park Formation in Canada. The other example originates from the Early Cretaceous Bernissart Iguanodon shaft in Belgium (Bertrand 1903, pl. XIII). The coprolites, containing bones and striated muscles, were assigned to carnivorous dinosaurs by Bertrand (1903), who pointed out *Megalosaurus dunkeri* as a likely producer.

Other delicate remains that have been described from coprolites include remains of various insects and parasites (**paper II**; **paper IV**; **paper VI**;

Northwood, 2005; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013; Brachaniec et al., 2015). Fossil parasites in the form of eggs and/or other life stages have been found in coprolites from various ages and producers (Ferreira et al., 1993; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013; De Baets and Littlewood, 2015). Such parasite records derived from coprolites of different animals (such as synapsids, dinosaurs, and sharks) are remarkable as they extend the record of parasite-host interactions and coevolution to new minimum ages. Coprolites are invaluable in this respect as they preserve rare parasites better than most other environments and represent direct evidence of host-parasite interactions. Other types of paleoecological inferences from coprolites include opportunistic colonization of ancient dung by terrestrial snails (Chin et al., 2009) and early animal-plant interactions (Scott, 1977; Edwards et al., 1995; Hagström and Mehlqvist, 2012).

In a way, coprolites represent both *Konzentrat-Lagerstätten*, since fossils are ‘bioaccumulated’ in coprolites (and thereby enriched in relation to the host sediment), and *Konservat-Lagerstätten*, as the inclusions are often well preserved in three dimensions within them (cf. amber). The importance here does not lie in whether to call them *Lagerstätten* or not, but in highlighting the fact that coprolites contain numerous well-preserved organic inclusions and represent a largely untapped source of paleontological information.

## A quick guide to finding the perpetrator

An obvious challenge for any paleontologist is to link newly discovered fossil remains to the animal to which they belonged. In the case of ichnofossils, this commonly relates to the *maker* of the trace. Some bromalites such as cololites (fossil intestinal contents) are often found in direct association to the organism, making such connection easy. However, the term “coprolite” is most often used to describe fossil droppings that were excreted from their producer, meaning that it is highly unlikely to find them in conjunction with skeletal remains. Consequently, a coprolite detective must use his or her entire toolbox to be able to reconstruct this link to the furthestmost extent. Luckily, there are usually several tools and clues at hand.

Droppings are often used to provide information on diet and population densities in modern studies of wildlife conservation and ecology. In order to do so, the droppings from different animals must be discriminated from each other. The shape and size can sometimes be sufficient to establish schemes to distinguish fecal remains from different animals. There are several guidebooks to the identification of various recent droppings through typical morphologies, sizes and contents (e.g. Stuart and Stuart, 1998; Pagett, 2007). For example, droppings from different canids can to some degree be separated from one another by their diameters (Green and Flinders, 1981; Dellinger et al., 2011).

Similarly, coprolites are often classified by shape and size into so-called morphotypes (which is to be preferred over ichnotaxonomy since coprolites show high variability and provide little information on physiology) (Fig. 3).

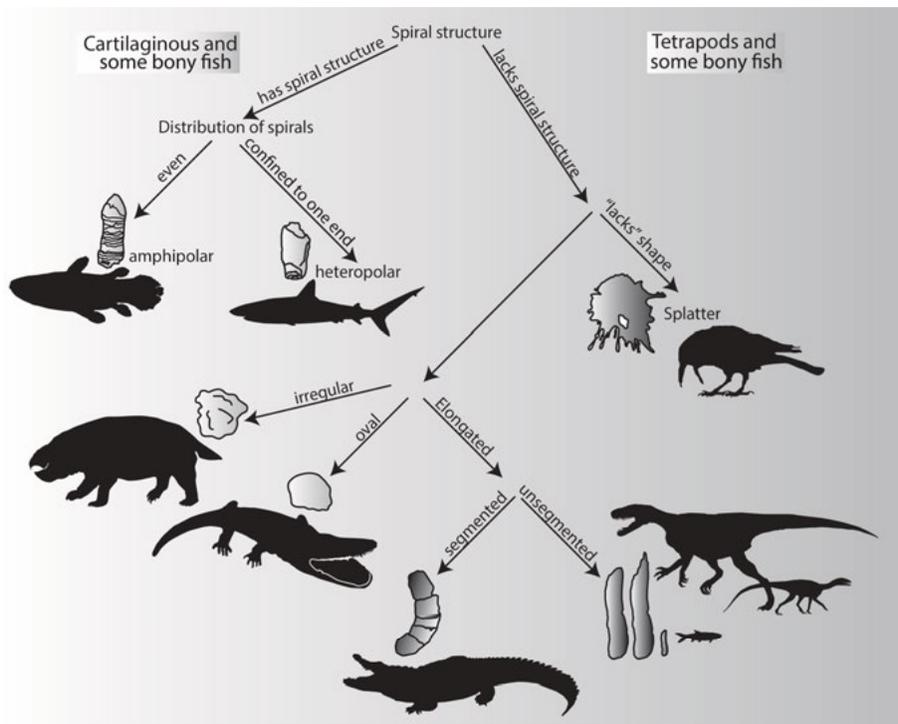


Figure 3. Schematic figure of some common shapes of droppings and the extinct and extant animals they have been linked to. Note that some features may be present/absent due to state of preservation (e.g. Qvarnström et al., 2019). Animal silhouettes are not to scale and represent clockwise from the top left: lobe-finned fish (coelacanth), shark, bird, theropod, dinosauriform, actinopterygian fish, crocodile, temnospondyl, dicynodont. Based on Hunt and Lucas (2012), Milàn (2012), and **papers III, IV, and VI.**

Some characters of shape are in some cases easily distinguished, such as the presence or absence of a spiral structure. Spiral-shaped coprolites are produced by animals with spiral gut valves. Cartilaginous fish, lobe-finned fish, and some ray-finned fish have spiral guts, whereas tetrapods do not. Other characters of shape include terminations of the coprolites, segmentation, and overall shape (e.g. Häntzschel et al., 1968; Hunt and Lucas, 2012). Size alone can in some cases be helpful. For example, tyrannosaurid coprolites have been described from Upper Cretaceous deposits of USA and this identification was done largely on the basis of their large size and stratigraphical age, i.e. there were no other plausible producers (Chin et al., 1998, 2003). However, certain caution should be implemented when using size as an indicator of the producer. Crocodylian scatology suggests that there is weak to no correlation of

scat-to-body length, and only a slight correlation between the scat diameter and the producer's body length (Milàn, 2012).

In contrast, the contents of coprolites reflect paleodiets quite well and can be used to differentiate between herbivorous, omnivorous, carnivorous, insectivorous or piscivorous producers. For example, a carnivore diet consisting of flesh and bones will result in a phosphatic composition of the feces. In addition, the level of degradation of coprolite inclusions (for example bones) may provide clues to the efficiency of the producer's gut system and food retention time (e.g. Bajdek et al., 2016; Barrios-de Pedro and Buscalioni, 2018).

In some situations, it is speculative or near impossible to make an adequate assumption of the coprolite's producer, and thus it could only be possible to link coprolites to more inclusive groups of potential producers (Eriksson et al., 2011; e.g. Northwood, 2005).

## Opaque treasure chests and how to open them

Coprolites contain plenty of well-preserved inclusions that can reflect the paleoecology of the producer. However, to deduce paleoecological relations, we must not only attribute the coprolites to their producers but also characterize the full contents of the coprolites. Needless to say, it is quite a difficult task since the food remains have gone through the entire digestive tract of the animal, meaning that they are potentially broken, and partly digested. Also, there is often no particular organization of inclusions within the coprolites so we cannot predict where in the coprolites we should look for inclusions. So how are coprolite contents analyzed?

Traditionally, the two most common methods to probe the interior of coprolites have been 1) to make longitudinal or transversal thin sections of the coprolites and analyze these under an optical microscope and 2) to mount pieces of coprolites onto stubs and image them with a scanning electron microscopy (SEM). These two imaging techniques yield high-resolution images of the interior of the coprolites and can provide much information on the contents. However, these methods suffer from some serious drawbacks: only parts of the coprolites are imaged, they are spatially restricted to two dimensions and they are destructive. To overcome these problems, a few coprolites have been scanned using X-ray tomography (Milàn et al., 2012; Holgado et al., 2015; Qvarnström et al., 2019). Although X-ray tomographs are non-destructive and potentially enable 3D-imaging, the contrast between the phases within fossils are generally too low. This results in difficulties in interpreting the inclusions in coprolites and to turn them into 3D models. Another method which should also be mentioned, is to dissolve coprolites and study the organic residues. This is commonly done to study the organic remains of parasites, plant cuticles, and palynomorphs (**paper VI**; Poinar and Boucot 2006; Bajdek et al., 2014; Vajda et al., 2016).

This thesis comprises the first study to apply propagation phase-contrast synchrotron microtomography (PPC-SR $\mu$ CT) to coprolites. It is demonstrated that that PPC-SR $\mu$ CT permits non-destructive, high-quality virtual 3D-reconstruction of coprolite inclusions.

# Aims

The novelty of the work presented in this thesis lies in the approach of studying coprolites with synchrotron microtomography, and especially in the resulting paleoecological discoveries. I focused on studying the early evolution of dinosaurs by looking at snapshots of different stages of their evolution. To reach these overall aims, I scanned numerous coprolites (and reconstructed their contents) from a few rich and well-known localities.

The aim of **paper I** was to summarize main findings, current progress and the analytical constraints of detecting fossilized soft tissues in coprolites from mainly freshwater and terrestrial carnivorous vertebrates. In **paper II**, we used two examples to demonstrate the advantages of using PPC-SR $\mu$ CT on coprolite material. In **paper III**, we set out to analyze the diet and behavior of the Upper Triassic theropod-like archosaur *Smok wawelski* by analyzing coprolites, regurgitalites and bite marks. The aim of **paper IV** was to study insect-rich specimens from Upper Triassic locality Krasiejów to infer likely coprolite producers and their diet. In **paper V** we aimed to explore the diet of producers of the coprolites found on a paleosurface with pterosaur tracks. In the last paper of this thesis, **paper VI**, we aimed to reconstruct food webs of three different vertebrate faunas that represent three stages of early dinosaur evolution.

# Methods

## Localities

### Krasiejów

The material that was studied in **papers II, IV and VI** derives from an abandoned clay pit at Krasiejów, located some 30 km east of Opole in southern Poland. The roughly 30-meter thick deposits in Krasiejów contain a rich record of fossils. These are mainly found in two fossil-bearing intervals, both approximately 1–1.5 m thick (Fig. 4). The lack of radiometric dates and diagnostic palynomorphs make an exact dating of the deposits difficult. However, the vertebrate fauna, some invertebrates (conchostracans and charophytes), and plant fossils are compatible with a late Carnian age of the assemblage (Zatoń et al., 2005; Dzik and Sulej, 2007; Lucas, 2015). Coprolites occur in great numbers in both fossil-bearing intervals in Krasiejów.

The vertebrate freshwater fauna consists of the phytosaur *Parasuchus* sp., two temnospondyls (*Metoposaurus krasiejovens* and *Cyclotosaurus intermedius*), dipnoans (including the large lungfish *Ptychoceratodus roemeri*) and various actinopterygian fish. Terrestrial vertebrates include small diapsids (e.g. sphenodonts), the gliding archosauromorph *Ozimek volans*, the dinosauriform *Silesaurus opolensis*, the large carnivorous ‘rauisuchid’ *Polonosuchus silesiacus* and the aetosaur *Stagonolepis olenkae*. Moreover, the site also contains other components of a seemingly complex ecosystem including charophyte gyrogonites, cycloid crustaceans, conchostracans, ostracods, beetles, unionid bivalves and gastropods (Zatoń et al., 2005; Dzik and Sulej, 2007).

### Lisowice

Coprolites from the Lipie Śląskie clay-pit at Lisowice village near the town of Lubliniec (S Poland) were studied in **papers III and VI**. The site contains a 12-meter thick succession with well-preserved vertebrate bones and footprints found in several intervals (Fig. 4). Most bones derive from the so-called “upper interval”, and are usually found in lenticular bodies of carbonate-rich siltstones and mudstones. The vertebrate assemblage includes many terrestrial, and a few aquatic/amphibious, tetrapods (Dzik et al., 2008; Niedźwiedzki et al., 2012; Niedźwiedzki, 2013; Pieńkowski et al., 2014).

The terrestrial fauna was composed of the giant dicynodont *Lisowicia bojani*, the big archosaur *Smok wawelski*, small theropods, early ornithischian-

like dinosaurs, and mammaliaforms (Dzik et al., 2008; Niedźwiedzki et al., 2012; Niedźwiedzki et al., 2015; Sulej and Niedźwiedzki, 2019). The temnospondyls *Cyclotosaurus* sp. and *Gerrothorax* sp. are known from various isolated bones and the fish fauna is inferred from macroremains of coelacanths, lungfish (mainly bones and tooth plates of *Ptychoceratodus* sp.) and actinopterygians. Vertebrate microfossils are dominated by actinopterygian remains and shark denticles, but archosaur teeth, postcranial elements of early anurans and teeth of mammaliaforms also occur (Niedźwiedzki et al., 2015).

### **Wierzbica**

Around 60 meters of early Kimmeridgian (Upper Jurassic) carbonates outcrop in the abandoned Wierzbica Quarry (Fig. 4), which is located 20 km south of the town Radom on the Mesozoic margin of the Holy Cross Mountains (S Poland). The carbonates display a shallowing-upward cycle with open shelf facies that pass into intertidal facies, and was assigned by Gutowski (2004) to the Wierzbica Oolite and the Platy Limestone. Five facies/environmental units have been identified in the succession by Pieńkowski and Niedźwiedzki (2005): (1) grey laminated marls representing lagoonal/lower tidal flat facies; (2) white/grey heteroliths composed of micritic limestone and marls, which are attributed to a mixed tidal flat/intertidal environment; (3) laminated clay-rich marls with a strongly impoverished microfauna recognized as representing an upper tidal flat; (4) cross-bedded grainstones containing glauconite and redeposited shells attributed to a tidal channel; and (5) pelitic limestones/marls with disturbed bedding and numerous trace fossils representing an upper tidal flat deposit.

A large number of pterosaur tracks (which do not form any trackways) occur in two layers, one within facies unit (2) and the second in the interface of facies (3) and (4) (Pieńkowski and Niedźwiedzki, 2005). The coprolites studied in **paper V** were collected from the latter. The pterosaur footprints have been assigned to the ichnogenus *Pteraichnus*, and the most likely trackmakers are thought to have been ctenochasmatoids, or possibly non-pterydactyloid monofenestratans or rhamphorhynchids (Elgh et al., 2019).

### **Sołtyków**

Sołtyków is an outcrop located on the margin of the Holy Cross Mountains in southern Poland with alluvial-plain deposits that were formed in the lower Hettangian (Fig. 4; Pieńkowski et al., 2014). The dinosaur-dominated fauna known from the locality is largely inferred from a rich ichnological record, as bones are rare. It consisted of theropods of various sizes, ornithischians, large sauropods, a small crocodylomorph, palaeonisciform fish and a mammaliaform (Pieńkowski et al., 2014). Coprolites from Sołtyków were studied in **paper VI**.

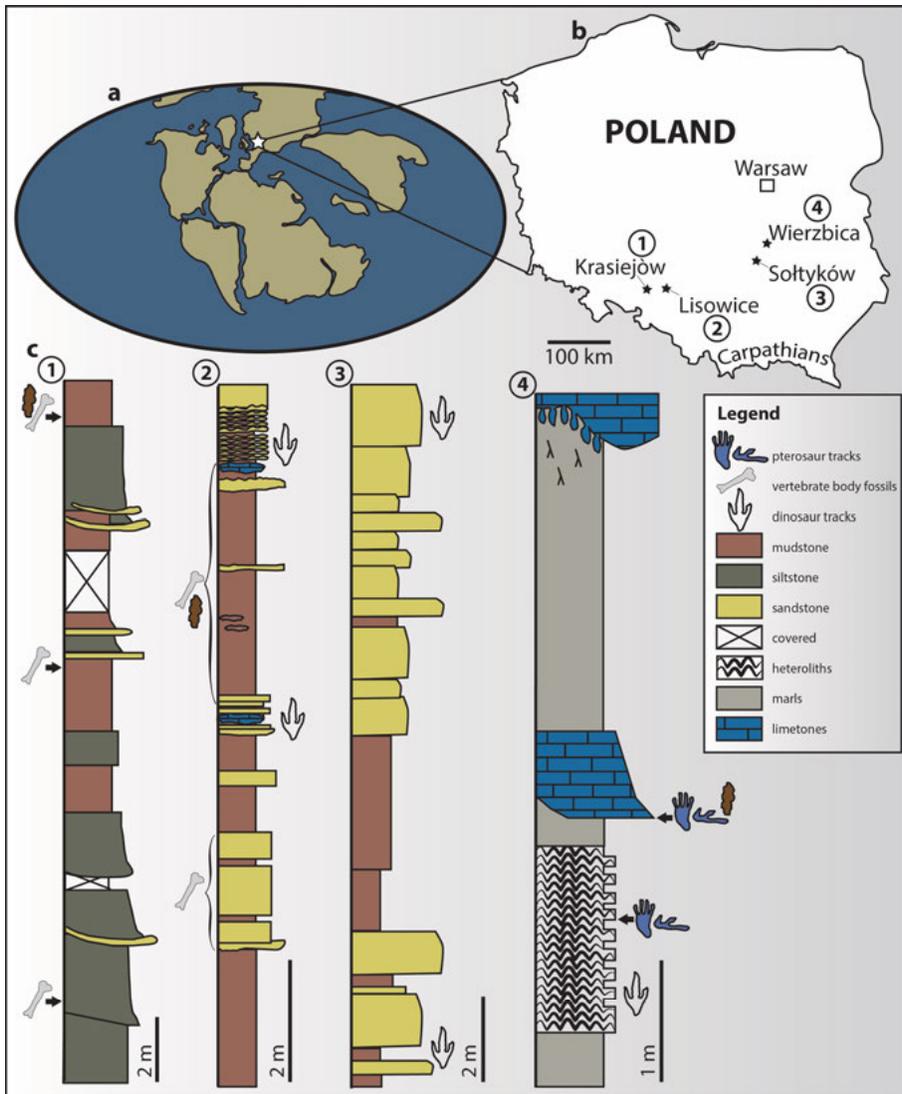


Figure 4. Details of the study area. (a) The location of Poland in the Late Triassic. (b) Map of Poland with the positions of the coprolite-yielding localities. (c) Simplified sedimentary profiles of the localities. The figure is based on **papers III-VI**; Gruszka and Zieliński (2008); Pieńkowski et al. (2014); Pieńkowski and Niedźwiedzki (2005).

## Imaging techniques

### “Conventional” imaging techniques

Optical microscopy of thin sections is by far the most commonly used technique to study coprolite contents (Chin, 2007). A coprolite is sectioned, glued

onto a glass slide, and ground down to an appropriate thickness to allow light to be partially transmitted through the specimen. This makes it possible to study the sections in high resolution and take photographs of the sections (given that the microscope is equipped with a camera). Thin sections were studied using optical microscopy for **papers I, III and VI**.

SEM produces images of even higher resolution and can be used to study the fine details of coprolites. Fragments of coprolite specimens are removed, glued onto stubs and coated (e.g. with platinum or gold) to enhance imaging. SEM analyses were carried out for **papers I, III, V and VI**.

### **Synchrotron microtomography**

Data collected for **papers II-VI** was generated using synchrotron microtomography, which produces stacks of images that can be used to trace internal structures in three dimensions (Fig. 5). This method has previously been shown to be outstanding in imaging internal structures of various fossils with great quality and sensitivity (Tafforeau et al., 2006; Smith et al., 2009; Carlson et al., 2011; Sanchez et al., 2012, 2016).

Microtomography based on synchrotron radiation makes use of high beam energies, and the propagation phase contrast effect can reveal structures that are completely invisible using X-ray tomography. The phase contrast effect derives from the detection of phase shifts of the beam emerging through the sample (Wilkins et al., 1996), in contrast to X-ray absorption in which only decreased beam intensities when passing through a sample are recorded. This results in a much higher sensitivity, which becomes useful in paleontology as mineralized fossils exhibit low absorption contrasts (Tafforeau et al., 2006).

The studied material was scanned as part of project ES145 at beamline ID19 of the European Synchrotron Radiation Facility (ESRF) in Grenoble, France. Different scan settings were applied to the coprolites depending on the size of the specimens to maximize resolution but maintaining a field of view that would capture the entire specimens. The coprolites were scanned in two sessions, with four different voxel sizes (6.36, 6.54, 13.4 and 13.83  $\mu\text{m}$  respectively) depending on the size of the specimens. For all scans, the propagation distance (the distance between the sample on the rotation stage and the camera) was 2,800 mm and the camera was a sCMOS PCO edge 5.5 detector.

Reconstructions of the scanned data were based on a phase retrieval approach (Paganin et al., 2002; Sanchez et al., 2012) and ring artefacts were corrected by using an in-house correction tool (Lyckegaard et al., 2011). Binned versions (bin factor of 2) were calculated for fast processing and screening of the samples, and most segmentation was done on the binned data. The final volumes consist of JPEG2000 image stacks that were imported and segmented in several versions of the software VGStudio MAX (Volume Graphics Inc., Heidelberg, Germany).

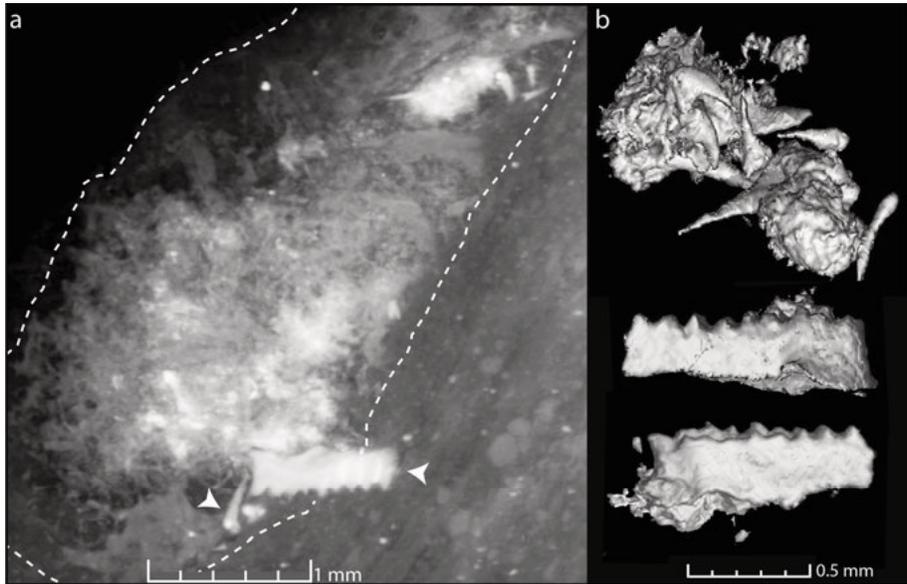


Figure 5. Synchrotron microtomography of coprolites permit to analyze the interior of coprolites in three dimensions, to produce virtual thin sections (a), and to render objects in 3D (b). This example derives from a coprolite that was produced by a coelacanth and contain pectiniform and coniform conodont elements (arrows in a, and 3D models in b). The figure is modified from Zatoń et al. (2017).

## Geochemical methods

### Energy-dispersive X-ray spectroscopy

For **papers III, V, VI** we used SEM coupled with EDS. In EDS, an X-ray spectrum (from which specific elements can be identified) is calculated based on the energies released when a solid sample is bombarded by an electron beam. EDS can be used to get an overall idea of the geochemical signature of a specimen. For example, the calcium phosphatic composition of coprolites can be analyzed as well as minor chemical components (e.g. siliciclastic grains). Specific inclusions can also be geochemically characterized.

### Time-of-flight secondary ion mass spectroscopy

ToF-SIMS permits to analyze the elemental composition of surfaces with very high mass and spatial resolution. This technique uses a pulsed ion beam which removes molecules of the topmost part of the surface of the analyzed specimen. These molecules are accelerated and their time to reach the detector, which is specific to a certain particle, is measured. This permits surface spectroscopy, surface elemental imaging, and to some degree depth profiling. For paleontological samples in which organics are preserved, ToF-SIMS can be

used to characterize the composition of a given structure, which can then be compared to reference spectra of a known organic compound.

Fragments of two coprolites were analyzed using ToF-SIMS for **paper VI**. The ToF-SIMS analysis was carried out using a TOF.SIMS 5 instrument (ION-TOF GmbH, Germany), at the University of Sciences and Technologies of Lille. The analyses were performed using the 2D-imaging mode and composition maps were retrieved using both positive and negative polarity filters. Pulsed  $\text{Bi}^{3+}$  primary ions were predominantly used for the analyses (25 keV, 0.3 pA), which were performed semi-quantitatively using the ‘mapping mode’ setting (500 x 500- $\mu\text{m}^2$  grids, and the acquired images were 512 x 512 pixels). The acquisition was performed in a high-current bunched mode. In the mapping-mode experimental conditions, we obtained a lateral resolution of c. 1  $\mu\text{m}$ . Spectra were produced from selected 2D spots.

# Main findings

## Results and discussion

### Setting the stage – papers I & II

The first two papers in this thesis set the framework for the following paleoecological studies (papers III-VI). **Paper I** summarizes findings of delicate fossils in coprolites and highlights the untapped potential of coprolites as loci for exceptional preservation. **Paper II** is by and large a methodological paper highlighting the benefits of applying synchrotron microtomography to coprolite material. Two coprolites from the late Carnian locality Krasiejów were used as examples in that study. The first specimen contains various insect remains, notably elytra and appendages of beetles, and the other one contains a semi-articulated redfieldiid fish and crushed bivalves. A synopsis of these two papers has substantially already been presented in the background and methods sections above.

### A bone-crushing archosaur from the Late Triassic – paper III

Three big elongated coprolites from an Upper Triassic locality in Lisowice, Poland were synchrotron scanned, and the data from these specimens constitute the core for **paper III**. The association to the body and footprint record at the site, as well as the morphology and size of the coprolites suggests that the most likely producer was *Smok wawelski* – a 5 to 6-meter long predatory theropod-like archosaur. Skeletal fossils of *S. wawelski* are mostly from subadult individuals, but a larger, isolated tooth suggests that adult individuals could grow at least 30 percent larger.

The coprolites were shown to be comprised of up to 50 percent by volume of bones, and fragments of in total three crushed serrated teeth (Fig. 6). Most bones were difficult to identify due to their fragmented and sometimes much-digested state. However, others were identifiable enabling us to conclude that temnospondyls, dicynodonts and other archosaurs were on the menu of *S. wawelski*. The crushed serrated teeth match those of *Smok wawelski* and probably belonged to the coprolite producer itself. Most likely, the teeth were repeatedly crushed against hard food items (bones), involuntarily ingested, and replaced by new.

These facts suggest that *Smok wawelski* was osteophagous, i.e. ingested and processed bones voluntarily. Further evidence for a bone-crushing behavior can also be found in other fossils from the same bone beds. These include wear

on isolated teeth, bone-rich fossil regurgitates, and bones with bite marks, which are all attributable to activities of *Smok wawelski*.

Many modern mammals are osteophagous (Biknevičius and Ruff, 1992; Palmqvist et al., 2011; Hutson et al., 2013) but such behavior, with a few exceptions, e.g. vultures (Houston and Copsey, 1994), is usually not associated with archosaurs in general or specifically with dinosaurs. One counterexample of the latter is represented by the Late Cretaceous tyrannosaurids of North America, which are thought to have crushed bones by repeated biting with high forces as evidenced by coprolite contents, worn teeth, bite marks and kinetic modeling (Erickson and Olson 1996; Chin et al., 1998, 2003; Jacobsen 1998; Gignac and Erickson 2017).

Several of the anatomical characters related to osteophagy, such as a massive head and robust body, seem to be shared by *Smok wawelski* and the tyrannosaurids, despite them being distantly related and living 140 million years apart. These large predators, therefore, seem to provide evidence of similar feeding adaptations being independently acquired at the beginning and end of the age of dinosaurs.

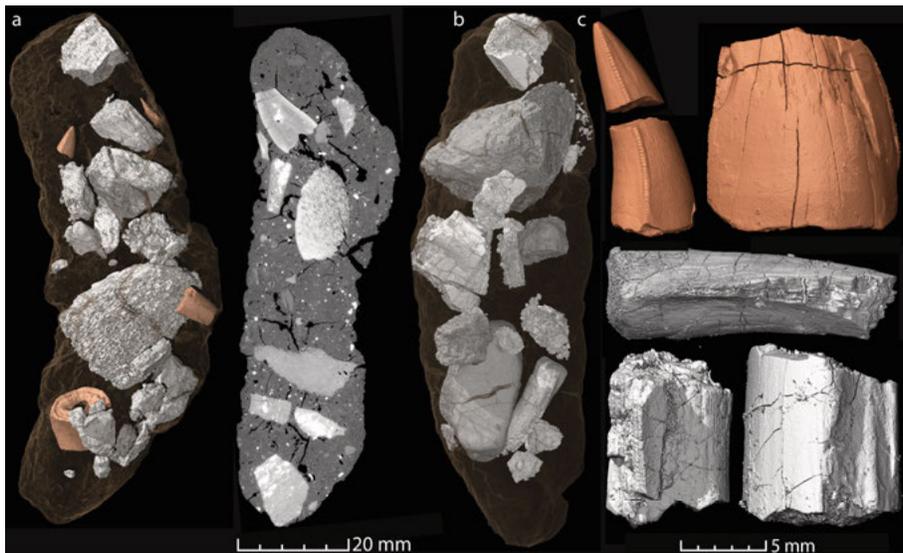


Figure 6. Some of the contents of the coprolites assigned to *Smok wawelski*. (a) Virtual reconstruction of the contents, and a virtual thin section (right), from specimen ZPAL V.33/344. (b) Virtual reconstruction of the contents of specimen ZPAL V.33/345. (c) Examples of bone fragments (white) and serrated teeth (orange) from the coprolites from *S. wawelski*.

#### **A Carnian dinosauriform that ate beetles – paper IV**

**Paper IV** deals with five coprolites that belong to the same morphotype (i.e. a group of coprolites of similar shape and appearance). These are elongated

and non-spiral specimens with a characteristic outer coating. One of the coprolites, specimen ZPAL AbIII/3402, contains lots of beetle remains including many small elytra (i.e. the second wing pair in beetles which cover the actual flight wings), two large ones, and a few appendages (Fig. 7). Small elytra and partial beetle bodies were found in the other coprolites of the same morphotype, altogether indicating that the coprolite producers voluntarily ingested these relatively small insects as a part of their diet. The size of the coprolites ranges from 16 to 22 mm in maximum diameter, suggesting that the producer itself was not a small animal. The best candidate from the body fossil record of the same site, the Carnian locality Krasiejów, is the dinosauriform *Silesaurus opolensis*. *S. opolensis* displays some interesting feeding adaptations, including a specialized dentition and protrusions of the dentary (and probably premaxilla) that formed a beak (Dzik, 2003). We hypothesize that the beak was used to peck insects of the ground and/or to root in the litter much like modern birds. An insect diet has previously been hypothesized for non-dinosaurian dinosaurimorphs, but not silesaurids (Langer et al., 2013).

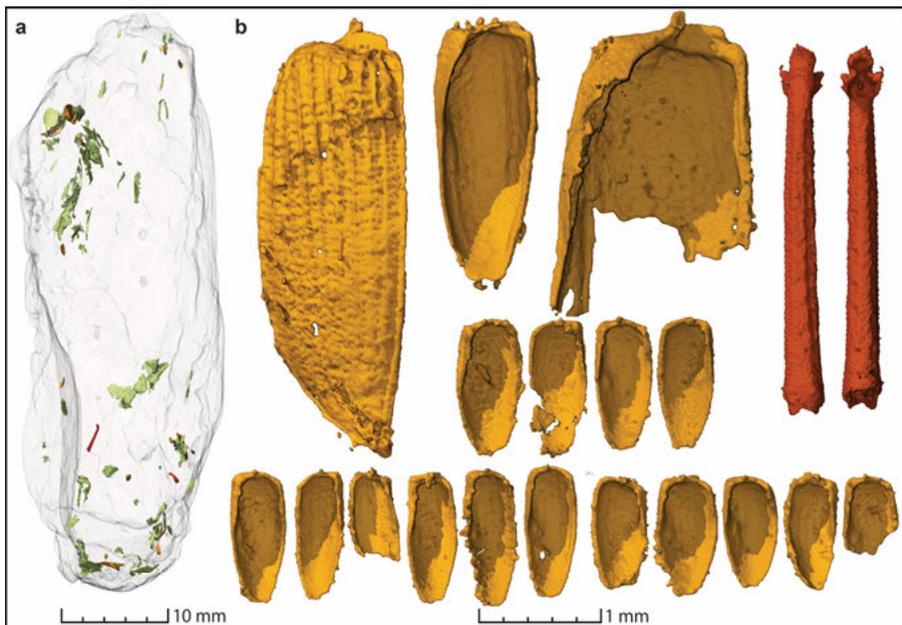


Figure 7. One of the coprolite specimens (ZPAL AbIII/3402) assigned to *Silesaurus opolensis*. (a) Coprolite in semi-transparency with inclusions visible. (b) Elytra (orange) and a tibia (red) from beetles.

### The flamingos of the Late Jurassic – paper V

In **paper V**, we analyze three coprolites from Kimmeridgian (Upper Jurassic) intertidal deposits found in the Wierzbica Quarry in Poland. The coprolites were found on a paleosurface covered with pterosaur tracks, which have been studied and assigned to the ichnogenus *Pteraichnus* (Pieńkowski and

Niedzwiedzki, 2005; Elgh et al., 2019). The coprolites' size, shape, and association to the tracks suggest that they were produced by pterosaurs. The synchrotron scans of the coprolites revealed an abundance of microscopic food remains including foraminifera, small shells of marine invertebrates and possible remains of polychaete worms (Fig. 8). The most probable explanation for how a pterosaur, big enough to have produced the droppings, ingested such small prey is through filter feeding.

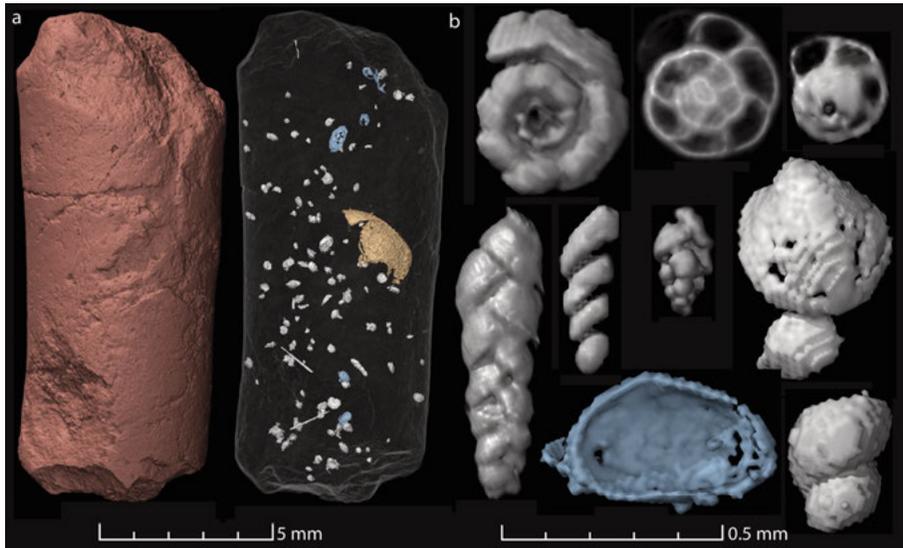


Figure 8. One of the pterosaur coprolites (MUZ PGI 1663.II.15a) and examples of the contents. (a) The coprolite rendered in 3D, along with the coprolite semi-transparent (right) to highlight the inclusions. (b) Various foraminifera and small shells of a bivalve, ostracod, and gastropod.

Modern flamingos employ filter-feeding and their feces are consequently rich in remains of microscopically small aquatic prey. Droppings of the Chilean Flamingo have been shown to contain mostly remains of foraminifers, copepods, and polychaetes when feeding in coastal wetlands (Tobar et al., 2014). The similar contents of the flamingo droppings and the pterosaur coprolites can be explained by a few factors. Likely, the targeted prey was similar due to a similar mesh size produced by the filter-feeding apparatus in the animals. The functional sieve in the Chilean flamingo ranges from 80 to 959  $\mu\text{m}$  across the beak (Mascitti and Kravetz, 2002). Most of the inclusions from the pterosaur droppings are around 300  $\mu\text{m}$  in size and thus fall in the same size range. Furthermore, similar contents also imply a similar feeding environment.

But were there any potential filter-feeding pterosaur taxa which could have produced such droppings around at this time? The short answer is yes. Pterosaurs were a diverse, long-lived and successful group of archosaurs that had many different sizes, life strategies and diets (Unwin, 2003; Henderson, 2010;

Prentice et al., 2011; Bestwick et al., 2018). All pterosaurs that have been linked to a filter-feeding habit belong to a group of pterosaurs known as the Ctenochasmatidae. The most obvious filter feeder in this group is *Pterodaustro*, which is known from the Cretaceous of South America. *Pterodaustro* had a very specialized feeding apparatus; the two up-curved dentaries housed a large number of teeth that formed a filter-feeding basket (Chiappe and Chinsamy, 1996; Chiappe et al., 2000). Ctenochasmatid ancestors of *Pterodaustro* were around during the Late Jurassic. These include taxa such as *Ctenochasma* and *Gnathosaurus*, which display elongated rostra with numerous teeth, and have also been assigned as filter feeders (Wellnhofer, 1970; Bennett, 2007; Zhou et al., 2017; Henderson, 2018), although some authors have claimed that they were not (Sanderson and Wassersug, 1993; Witton, 2013). Our results strongly favor that they were filter feeders, and represent the first retrieved food remains for the group.

The mode of filter-feeding in these Jurassic pterosaurs is still not particularly well understood. It likely differed a lot from that of modern flamingos, which is very specialized and involves turning their heads up-side-down and actively pumping water across their lamellar meshes during feeding (Jenkin, 1957; Zweers et al., 1995).

The three pterosaur coprolites differ in size, with one having a significantly larger diameter than the other two. The diameter of droppings correlates somewhat with the size of the producer (Milàn, 2012), suggesting different sizes of the coprolite producers. The larger specimen contains more of the small inclusions, whereas polychaete bristles are more common in at least one of the other two specimens. This is interesting as the ontogenetic series of *Ctenochasma* shows that the rostrum becomes more elongated through ontogeny, as does the number of teeth. It might be the case, consequently, that more adult individuals were specialized for filter-feeding whereas younger individuals relied more on eating soft-bodied animals as well. Alternatively, this area was occupied by a flock of pterosaurs of conspecific species, or differently sized animals visited the area during a very limited period of time (the droppings and footprints were likely buried in the following tide).

### **Putting the puzzle together – paper VI**

In **paper VI**, which is a manuscript that still is in a provisional state, we unravel diets and interactions in vertebrate assemblages from three sites in Poland: the late Carnian locality Krasiejów (with inferences from the mid-late Carnian site Woźniki), the late Norian/early Rhaetian locality Lisowice, and the early Hettangian locality Sołtyków (Fig. 4). These sites represent snapshots of three stages of early dinosaur evolution and can be described as assemblages in which dinosauriforms/dinosaurs (1) played a minor ecological role (Krasiejów), (2) a moderate role (Lisowice) and (3) completely dominated the terrestrial fauna (Sołtyków).

Over 80 coprolites are analyzed by synchrotron microtomography and matched to the fossil record of the sites to infer producers, diets, and behaviors. Plant cuticles from coprolites of all three sites are also studied. Food webs are reconstructed based on the coprolite data combined with other evidence on feeding (regurgitalites, bite marks and functional morphology). Data from the Carnian locality Krasiejów show that the large rauisuchian *Polonosuchus* fed on the herbivorous aetosaur *Stagonolepis*, several animals (actinopterygians, lungfishes, temnospondyls, and phytosaurs) fed on fish, and the dinosauriform *Silesaurus opolensis* likely ate insects. The assemblage from the Norian/early Rhaetian locality Lisowice was characterized by the youngest and largest known dicynodont *Lisowicia bojani* and other herbivores feeding on a variety of plants, numerous aquatic and terrestrial piscivores (hybodont sharks, dipnoans and dinosaurs), and the osteophagous top predator *Smok wawelski* that fed on *L. bojani*, temnospondyls, fish and other archosaurs. The basal Jurassic Sołtyków locality, by contrast, bears evidence of an ecosystem dominated by dinosaurs, including a high diversity of herbivores and carnivores.

Based on our model in a restricted geographical setting in northern Pangea, we propose that the dinosaurs' rise to ecological dominance can be described in three steps. The first two steps represent a gradual replacement of niches previously occupied by other tetrapods with (1) the appearance of omnivorous dinosauriforms, followed by (2) small to medium-sized carnivorous theropods, small omnivorous/herbivorous ornithischian-like dinosaurs and herbivorous sauropodomorphs, and finally (3) an expansion of ecospace marked by the appearance of very large predators and a diverse herbivore fauna in the earliest Jurassic. The latter was likely a result of new dietary key adaptations and large-scale climatic changes (more primary food resources). The disappearance of other Triassic tetrapods in the late Norian to Rhaetian interval seems to have been gradual and it remains unclear how much of this can be attributed to climate changes/fluctuations and how much to interspecific competition with early dinosaurs.

## Limitations

### **Coprolite producers**

It is often stated that it is problematic and sometimes purely speculative to assign coprolites to specific producers (Chin, 2002; Eriksson et al., 2011; Qvarnström et al., 2019), which is true; even after using all available clues from the coprolites and the associated fossil record (as outlined in the background), it is difficult to have a good idea about who produced the coprolite(s). Skeletal material from producers might not be known and coprolite morphotypes can be hard to distinguish.

None of the papers herein present *proof* that any particular coprolite was produced by a certain taxon. We use all possible evidence to deduce *the most probable producer* based on the simplest explanation of the data. What we can be sure about through coprolites analysis is that a certain type of animal was present. Let us take the coprolites from **paper III** as an example. We know that a coprolite producer existed that fed on the animals to whom the bones in the coprolites belong. We also know that the large quantities of bones in the fossilized droppings mean that the producer ingested and processed bone material. The serrated teeth in the coprolites are similar to those of *Smok wawelski* – the only known animal from the vertebrate assemblage big enough to have produced the droppings. None of these points prove that *S. wawelski* was the producer of the coprolites, but it is surely the most parsimonious and probable explanation.

In cases when it is much harder to find producers of coprolites, studying them may still provide clues about prey selection patterns, digestive strategies, and the occurrence of previously unknown taxa in a paleoecosystem (e.g. Chin, 2002).

### **What can we expect to find in the coprolites?**

It is becoming increasingly clear that an exceptional preservation of fossil inclusions occurs in coprolites. However, the fossils that will potentially be well preserved must have been ingested by the coprolite producer, lived inside the digestive tract (e.g. parasites), or ended up in the dung after deposition. If ingested, they must also have survived the digestive tract of the producer. Fossils in coprolites can often constitute unknown parts of the assemblages, but a complete representation of the ecosystem is not to be expected. When it comes to insect remains, there is probably also a bias related to size for the very well-preserved specimens. For example, remains from large beetles in **paper IV** are generally fragmentary due to disarticulation and fragmentation in the alimentary tract of the producer. Small insect remains, on the other hand, have a greater potential to end up intact in the feces. All near-complete insects so far discovered in coprolites are very small (**papers IV and VI**; Northwood, 2005).

To study inclusions by the means of synchrotron microtomography is a time-consuming task, at least at the moment. In the near future, however, it could be possible with faster scanning times to screen a plethora of coprolites, make fast reconstructions, and rescan promising specimens in better resolution. Moreover, machine learning could also assist in the segmentation work in the relatively near future. However, a difficulty when working with coprolites is that one is never completely sure what to expect to find in them.

To sum up, there are many new interesting questions to be solved by studying coprolites. It is not straightforward, but nevertheless sometimes possible, to assign them to known producers. The inclusions must have been selected by the producer (or ended up there by some other means) and survived their

alimentary tract and diagenesis to be available for study. But the fossil record is heavily biased in general, and that does not mean that any inferences based on it are useless. On the contrary, all new discoveries provide us with new clues about evolution and past life on our planet. The same goes for coprolites, so when all things come around it is hard to study coprolites but it is definitely worth the effort!

## Conclusions

Many coprolites carry fundamentally important paleoecological information, including unusually high accumulations of delicate fossil food remains (**paper I**). Given these statements, coprolites are per definition qualified as fossil *Lagerstätten*. By using synchrotron microtomography, we were able to visualize the contents of coprolites, as well as the organization and internal structure of the inclusions (**paper II**), thereby elucidating parts of food webs that date back hundreds of millions of years. Interesting feeding strategies were discovered such as durophagous lungfish eating clams and fish (**paper II**), a beetle-eating dinosauriform (**papers II and IV**), an osteophagous archosaur predator (**paper III**) and a filter-feeding pterosaur (**paper V**). The osteophagous top predator *Smok wawelski* occupied a similar ecological niche as the tyrannosaurids of the Late Cretaceous, despite having a much smaller body size. Osteophagy may consequently not have been as rare in the Mesozoic as previously thought (**paper III**). Similarly, we believe filter-feeding behaviors may have evolved several times in the history of life, with the Late Jurassic pterosaurs being one example (**paper V**). All in all, this thesis suggests that coprolites represent good targets for further analyses of ancient diet and food web relationships. In fact, this was partly shown in the last paper analyzing a large number of coprolites (80 specimens by PPC-SR $\mu$ CT) and other fossils from three sites, suggesting both similarities and dissimilarities in food web structures. Such large-scale analyses have the potential to cast new light on old classic evolutionary questions such as the origin of dinosaurs and their rise to ecological dominance (**paper VI**).

## Future perspectives

In the light of the new findings presented herein, and elsewhere by fellow researchers, it appears evident that coprolites represent an untapped source of paleontological information that deserves much attention in the future. It is indeed both a difficult and time-consuming job to reconstruct paleoecological relations based on coprolites, but the possible payoff merits the effort. Hopefully, machine learning and artificial intelligence can be of use in the future in order to speed up the time-consuming search for inclusions in coprolites.

There are many interesting directives for future work on coprolites. These include further studies of predator-prey relations based on identification of coprolite inclusions and producers; parasite-host relations based on a similar strategy; metabolism of extinct animals based on comparisons of the preservation (e.g. degree of etching on bone) of fossil and recent fecal contents; as well as behavior and feeding strategies/modes, as exemplified by **papers III, IV, V, and VI**. I believe that many more exciting findings of predator-prey relations similar to the ones described herein will be revealed in the future. Moreover, large-scale analyses of the kind presented in **paper VI** have the potential to cast new light on many important evolutionary questions. This requires, however, a very good understanding of the context in which the coprolites are found.

Another intriguing, and largely unexplored aspect, is the taphonomy of coprolites. We currently know very little about how, where, and when coprolites become preserved, but we do know that some remains preserve generally better within coprolites *versus* in the sedimentary rocks that house them. An increased understanding of coprolite taphonomy would require a large-scale comparison of coprolites from different depositional environments and an in-depth study of the geochemical composition of these (including organics). A bridging between recent coprology, archaeology, and paleontology is probably the best direction in order to solve such questions. Also, paleomolecules of producers, prey, parasites, and bacteria are likely preserved in coprolites.

I would also like to mention that there are still very interesting unpublished data from the scan sessions at ESRF (Grenoble, France) that were done for this project (proposal ES145). Some of these data require more segmentation work. From preliminary studies, it is evident that the coprolites include a plethora of food remains including exceptionally well-preserved insect remains. These data are currently being studied and will hopefully be published in the near future.

# Svensk sammanfattning

Sannolikheten att en enskild bajskorv ska bli till ett fossil är svindlande låg. Ändå är koproliter, det vill säga fossila bajskorvar, relativt vanliga fossil. En förklaring till det är att dynga helt enkelt produceras i sådan mängd att det kompenserar för den låga bevarandepotentialen. Föreställ dig till exempel att du är ute och vandrar i en skog. Förmodligen kommer du stöta på betydligt fler äglortar än ben från döda älgar. På samma vis lämnade varje utdött ryggradsdjur bara ett skelett efter sig när det dog (som förmodligen aldrig fossiliserades), men producerade potentiellt tusentals bajskorvar, och miljontals fotspår, under sin livstid.

En annan förklaring har med kemi att göra. Ur en kemisk synvinkel utgör nämligen bajs, och tillika koproliter, en unik mikromiljö rik på kalcium och fosfat (likt bajs har faktiskt koproliter utvunnits och använts under tidigt 1900-tal som gödningsmedel!). Den kemiska mikromiljön attraherar vissa bakterier, som inte nödvändigtvis bara bryter ned det biologiska materialet utan också kan mineralisera det i en upplösning av bakteriernas egen storlek (ofta cirka en mikrometer). Bakterierna livnar sig alltså på det organiska materialet och mineraliserar bajset på samma gång. Bajset börjar bli till en koprolit!

I den mineraliserade koprolitmassan går det att finna matrester och parasitägg, som kan användas för att återskapa olika djurs samspel med varandra (ekologi). Det går till exempel att ta reda på vem som åt vem. Fossil bevarade inuti koproliterna är likt i bärnsten ofta mycket välbevarade just tack vare den kemiska sammansättningen och bakteriernas hjälp. Det kan till och med gå att hitta rester av fossila mjukvävnader såsom hår och muskelceller, vilka annars är väldigt ovanliga fossil. Detta till trots är koproliter inte alls särskilt välstuderade. **Artikel I** i den här avhandlingen handlar om den här typen av mjukvävnadsbevaring i koproliter och i artikeln dras slutsatsen att koproliter förtjänar större uppmärksamhet. Här har paleontologin något att lära från arkeologin där koproliter ofta studeras mycket noga med fascinerande upptäckter som följd.

I det här arbetet avhandlas sedan framförallt den ekologiska informationen koproliter bär på och jag försöker framförallt svara på vem som ätit vem, och hur. De två huvudsakliga utmaningarna har varit att ta reda på vilka djur spillningen tillhörde och att identifiera de kaotiskt organiserade matresterna däri (till skillnad från bärnsten är inte koproliter genomskinliga). Ett sätt att ta reda på vad som finns i koproliterna, och samtidigt få information om den som

har producerat dem, är att använda synkrotröntomografi. Det är en sorts skikt-röntgenteknik som liknar den som används vid sjukhus med skillnaden att energin i röntgenstrålarna är tusentals gånger starkare. Fördelarna med att studera koproliter med hjälp av synkrotröntomografi är att det går att: visualisera matresterna i 3D, se deras inbördes organisering (delar av ett skelett kan fortfarande sitta ihop), studera interna strukturer i inklusionerna, finna helt nya typer av fossil, och studera paleoekologi. Dessutom är metoden icke-destruktiv vilket innebär att koproliterna inte behöver sågas sönder. Efter att ha presenterat fördelarna med metoden i **artikel II**, ges flera exempel på vad för typ av information vi kan få ut av att använda den.

I **artikel III** presenteras data från tio relativt stora koproliter från *Smok wawelski*, en 5 till 6 meter stor arkosaurie (härskarödla) som upptäckts i 210 miljoner år gamla sediment i Polen. Den tvåbenta härskarödlan såg i grova drag ut som en dinosaurie, även om det inte är helt klart om det faktiskt var en dinosaurie eller en föregångare till dessa. Över hälften av innehållet i koproliterna består av ben, bland annat från stora amfibier och dicynodont-ungar (en grupp växtätare). Flertalet krossade sågtänder fanns också i koproliterna. Dessa tillhörde förmodligen djuret som lade spillningen och krossades mot hårda födoämnen, svaldes och ersattes sedan av nya. Det hela tyder på att *Smok wawelski* tuggade i sig ben för att få i sig salter och märke, ett beteende som ofta förknippas med däggdjur men inte så ofta med reptiler. Ett undantag är de tyrannosaurider som härskade i Nordamerika mot slutet av dinosauriernas herravälde (*Tyrannosaurus rex* och dess närmaste släktingar). *Smok* verkar ha haft flera anatomiska drag relaterade till att krossa ben gemensamt med tyrannosaurierna, såsom ett massivt huvud och en kraftig kropp. Detta trots att de inte var särskilt närbesläktade med varandra och levde mer än 140 miljoner år isär. De liknande födoanpassningarna hos dessa stora köttätare verkar alltså ha uppkommit oberoende av varandra i början respektive slutet av dinosauriernas herravälde.

I **artikel IV** beskrivs fem koproliter från 230 miljoner år gamla sedimentära bergarter från Polen. Alla fem utgör tillsammans en morfotyp – koproliter av samma form och utseende – och visade sig innehålla rikligt med insektsdelar, speciellt från skalbaggar. I en koprolit fanns det fler än 20 täckvingar från skalbaggar. Alla insektsrester tyder på att koproliterna kommer från en insektsätare som livnärde sig på små byten. Däremot var inte själva insektsätaren särskilt liten. Storleken av den största koproliten är snarare jämförbar med bajs från en prärievarg än ett litet insektsätande däggdjur. Den troligaste kandidaten till att ha lämnat den insektsrika spillningen efter sig är den tidiga dinosaurien (eller i alla fall dinosaurieföregångaren) *Silesaurus opolensis* som är känd från samma avlagringar som koproliterna hittades i. *Silesaurus* hade en egendomlig näbb som vi förmodar användes för att plocka i sig insekter från marken som vissa fåglar gör idag. För 230 miljoner år sedan, då *Silesaurus* levde, fanns en hel del dinosaurier, men de hade ännu inte blivit den dominerande djurgruppen på land. Att ta reda på så mycket som möjligt om dessa

tidiga dinosaurier (inklusive deras diet) är nödvändigt om vi ska kunna förstå varför just dinosaurier tog över som den dominerande gruppen landdjur i slutet av trias för att sedan härska på jorden, uppnå hiskliga storlekar och (med undantag för fåglar) försvinna i utdöendet i krita.

I **Artikel V** beskriver vi 150-miljoner-år-gamla koproliter från sen jura, vilka kommer från en yta med flygödlafotspår i ett kalkbrott i Polen. Koproliternas form, storlek och association till fotspåren tyder på att de kommer från pterosaurier, mest troligt från en grupp som kallas Ctenochasmatidae. Pterosaurier var en mångfaldig grupp arkosaurier som härskade i skyarna under mesozoikum. Skelettfossil vittnar om att de precis som dagens fåglar var anpassade till en rad olika levnadsmiljöer och födostrategier. Direkta födobevis såsom tarminnehåll är däremot ovanliga och endast känt från ett fåtal arter. Nya fynd är därmed viktiga för att lära oss mer om dessa fascinerande djur.

Bilderna från synkrotronmikrotomografin avslöjade att koproliterna innehåller många små matrester inklusive foraminiferer (små skalförsedda amöbor), möjliga borst från havsborstmaskar och små skal från andra havslevande ryggradslösa djur. En möjlig förklaring till att en flygödlas stor nog för att producera bajset fick i sig så små byten är att den filtrerade ut sin föda från havsvatten. Vissa ctenochasmatida flygödlor tros faktiskt ha varit filtrerare. *Pterodaustro*, som kommer från krita och därmed är något yngre än de polska koproliterna, hade en väldigt specialiserad ”siktorg” bestående av många små tunna tänder i underkäken och var säkerligen en filtrerare. Äldre ctenochasmatider hade inte en lika specialiserad siktorg, men deras långa käkar med många tänder har också tolkas som anpassningar för att filtrera. Dessa flygödlor fanns både i Europa och i resten av världen under samma tid som kalkstenen med det fossila bajset avsattes i Wierzbica. Förmodligen kommer både spillningen och fotspåren från dessa typer av flygödlor.

Chileflamingon är en filtrerare vars bajs har visat sig innehålla många foraminiferer då den söker efter föda i våtmarker nära kusten. Likheten mellan innehållet i chileflamingons bajs och flygödlekoproliterna tyder på att flygödlorna sökte föda i samma typ av miljö, filtrerade ut sin föda från vattnet och hade samma typ av såll som dessa flamingor. Man kan med andra ord säga att flygödlorna som lämnat spår efter sig i kalkbrottet Wierzbica i Polen var dåtidens flamingor!

I det sista manuskriptet i avhandlingen beskrivs näringskedjor i ekosystem från tre utgrävningsplatser från slutet av trias och början av jura. De tre ekosystemen representerar olika stadier av tidig dinosaurieutveckling och kan beskrivas som ekosystem där dinosaurier/dinosaurieföregångare (1) spelade en mindre ekologisk roll (Krasiejów), (2) en måttlig roll (Lisowice) och (3) helt dominerade den terrestra faunan (Sołtyków).

Över 80 koproliter analyseras genom synkrotronmikrotomografi och koproliterna jämförs med skelettfossil och fossila fotspår för att ta reda på vilka

djur koproliterna kommer ifrån samt dessa djurs föda och beteende. Näringskedjorna är baserade på koprolitdatan i kombination med direkta (fossila spyor, bitmärken) och indirekta (funktionell morfologi) födobevis. Data från utgrävningsplatsen Krasiejów (yngre trias) visar att den stora krokodilföregångaren *Polonosuchus* livnärde sig på den växtätande aetosaurien *Stagonolepis*, att flera andra djur (strålfeniga fiskar, lungfiskar, temnospondyler och fytosaurier) åt fisk och dinosaurien *Silesaurus opolensis* troligen insekter. Utgrävningsplatsen i Lisowice kännetecknades av den yngsta och största kända dicynodonten *Lisowicia bojani* och andra växtätare som livnärde sig på en lång rad olika växter, många akvatiska och terrestra djur som åt fiskar (hybodonthajar, lungfiskar och dinosaurier), och den benkrossande topppredatorn *Smok wawelski* som jagade *L. bojani*, temnospondyler, fiskar och andra archosaurier. Fossil från den jurassiska lokaliteten Sołtyków vittnar om ett ekosystem som helt domineras av dinosaurier, inklusive en mängd växt- och köttätare. Vi demonstrerar att integrerade analyser av skelettfossil, fotavtryck och bromaliter ger robusta bilder av tidigare näringskedjor och kastar nytt ljus på viktiga evolutionära frågor, såsom uppkomsten av dinosaurier och dinosaurie-dominerade ekosystem.

Sammanfattningsvis är huvudslutsatsen i den här avhandlingen att synkrotrantomografi av koproliter är ett effektivt sätt att ta reda på utdöda djurs matvanor och samspel med varandra. Speciellt då metoden används ihop med andra tekniker går det att utröna hela näringskedjor från urtida ekosystem.

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