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This paper is dedicated to Professor Krzysztof Birkenmajer on his 85-th birthday

New perspectives on the Late Triassic vertebrates of East Greenland: preliminary results of a Polish-Danish palaeontological expedition

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Abstract: The Fleming Fjord Formation (Jameson Land, East Greenland) documents a diverse assemblage of terrestrial vertebrates of Late Triassic age. Expeditions from the turn of the 21st century have discovered many important fossils that form the basis of our current knowledge of Late Triassic Greenlandic faunas. However, due to the scarcity and incompleteness of the fossils and their insufficient study, our understanding of the taxonomic diversity of the Fleming Fjord Formation is hindered. Here, we report the preliminary findings of a Polish-Danish expedition to the Fleming Fjord Formation that took place in 2014. Three areas were visited – the fairly well known MacKnight Bjerg and Wood Bjerg and the virtually unexplored Liasryggen. MacKnigth Bjerg and Liasryggen yielded fossils which promise to significantly broaden our knowledge of vertebrate evolution in the Late Triassic. Stem-mammal remains were discovered at Liasryggen. Other fossils found at both sites include remains of actinopterygians, sarcopterygians, temnospondyl amphibians and various archosaurs (including early dinosaurs). Numerous vertebrate trace fossils, including coprolites, pseudosuchian footprints, theropod and sauropodomorph dinosaur tracks, were also discovered. Newly discovered skeletal remains as well as abundant trace fossils indicate higher tetrapod diversity in the Late Triassic of Greenland than previously thought. Trace fossils also allow inferences of early theropod and sauropodomorph dinosaur behaviour.

Key words: Arctic, Greenland, stem-mammals, dinosaurs, footprints, Fleming Fjord Formation, Late Triassic.

Introduction

The Upper Triassic Fleming Fjord Formation stretches along the north-eastern coast of Jameson Land, East Greenland between latitudes 71°N and 72°N and forms part of the southern sector of a bigger Triassic sequence (Clemmensen 1979; Jenkins *et al.* 1994; Clemmensen *et al.* 1998). The whole formation is of continental origin and is subdivided into the basalmost Edderfugledar Member (?Carnian–Norian), the middle Malmros Klint Member (Norian) and the uppermost Ørsted Dal Member (Norian–Rhaetian), see Jenkins *et al.* (1994) and Clemmensen *et al.* (1998). Although the Fleming Fjord Formation was the subject of sedimentological work since the early 20th century, very few fossils have been identified and described from this region. The first vertebrate fossils from the formation were reported by Grasmück and Trümpy (1969) in the form of a fossiliferous zone from the Ørsted Dal Member. This is a bonebed, which was described as containing fragmentary bones, fish scales and "reptilian"-like teeth. In subsequent years other workers also came across this fossil-rich layer as well as other fragmentary or isolated vertebrate remains in the Malmros Klint and Ørsted Dal members (Perch-Nielsen *et al.* 1972, 1974; Clemmensen 1979, 1980b). All of the reported fossils lacked a detailed description and represented a very narrow array of organisms – temnospondyl amphibians, actinopterygian fish and "reptiles". The lack of fossils of other terrestrial vertebrates was somewhat surprising, especially after sedimentological work by Bromley and Asgaard (1979) and Clemmensen (1980a, b) provided evidence for the similarity of sedimentary environments of the Fleming Fjord and other formations bearing fossil vertebrate remains.

The limited knowledge on the faunal diversity of the Fleming Fjord Formation changed dramatically after a series of expeditions led by the late Farish A. Jenkins of Harvard University (Jenkins *et al.* 1994). During seven field seasons (1988 to 2001) Jenkins' team excavated a diversity of fossils from the Malmros Klint and Ørsted Dal members of the Fleming Fjord Formation. They include dipnoan and actinopterygian fish (Jenkins *et al.* 1994), temnospondyl amphibians *Gerrothorax pulcherrimus* and *Cyclotosaurus* cf. *posthumus* (Jenkins *et al.* 1994, 2008), the turtle cf. *Proganochelys* (Jenkins *et al.* 1994), the aetosaurs *Aetosaurus ferratus* and *Paratypothorax andressi* (Jenkins *et al.* 1994), the pterosaur *Eudimorphodon cromptonellus* (Jenkins *et al.* 2001), unidentified theropod dinosaur and sauropodomorph dinosaur *Plateosaurus engelhardti* (Jenkins *et al.* 1994), the cynodont *Mitredon cromptoni* (Shapiro and Jenkins 2001) and the stem-mammals *Haramiyavia clemmenseni*, *Kuehneotherium* sp. and ?*Brachyzostrodon* (Jenkins *et al.* 1994, 1997), as well as fragmentary remains of other tetrapod taxa (Jenkins *et al.* 1994). Vertebrate trace fossils were also unearthed, including an extensively studied dinosaur footprint assemblage (Jenkins *et al.* 1994; Gatesy *et al.* 1999, 2005; Gatesy 2001, 2003; Milàn *et al.* 2004, 2006). Jenkins *et al.* (1994) concluded that the Late Triassic fauna of the Fleming Fjord Formation belongs to the European-type, as many of the recognised taxa seemed to resemble those form Late Triassic European formations, such as the Knollenmergel and Stubensandstein of Germany.

Although some of the taxa discovered by Jenkins' team became the subject of detailed investigation (the plagiosaurid *Gerrothorax*, the pterosaur *Eudimorphodon*, the cynodont *Mitredon* and other stem-mammals) many of the fossils are still awaiting further study. Representatives of important Late Triassic lineages, such as the cyclotosaur, turtle, aetosaurs, dinosaurs and stem-mammals, are known only from partial remains. Because of this, preliminary identification of these taxa should be treated with caution, as many important anatomical information crucial for establishing the exact phylogenetic identity of these fossils is still missing. As a result, the actual diversity of the Fleming Fjord Formation, as well as its resemblance to European faunas cannot be determined with confidence. Furthermore, fragmentary fossils of uncertain affinity discovered by Jenkins' team suggest that the Late Triassic vertebrate diversity of the Fleming Fjord Formation might be higher than currently known.

In recent years, the discovery of new Late Triassic sites in Poland has provided new important information about the evolution, biogeography and taxonomic turnover in the Late Triassic. These sites have yielded the fossils of previously unknown taxa, including basal dinosauromorphs (Dzik 2003; Dzik and Sulej 2007), the youngest dicynodonts and giant, predatory archosaurs (Dzik *et al.* 2008; Sulej *et al.* 2010), some of the earliest turtles (Sulej *et al.* 2012); stem mammal remains (Świło *et al.* 2014) and unexptected spatial and chronological occurrences of some dinosaur lineages (Niedźwiedzki *et al.* 2014). Furthermore, a recent international expedition revisited some of the fossil bearing sites in the Fleming Fjord Formation (Milàn *et al.* 2012; Mateus *et al.* 2014) and found material belonging not only to known taxa, but discovered fossils belonging to vertebrates previously undescribed from the Fleming Fjord Formation such as phytosaurs (Mateus *et al.* 2014). The partial nature of previous vertebrate discoveries, as well as the new findings from Poland and Greenland have convinced us that further field studies in the Fleming Fjord Formation could broaden our understanding about geographic and chronological distribution of Late Triassic lineages, helping us to fill gaps in our knowledge of Late Triassic ecosystems and vertebrate evolution. The somewhat unexpected findings of the synapsid lineage representatives in southern Poland have sparked T. Sulej's interest in reassessing the evolution of the mammalian body plan based on fossils from new localities. When N. Bonde learnt of these ideas during his visit to the Institute of Palaeobiology, Polish Academy of Sciences, in 2013, he suggested organising an expedition to the Fleming Fjord Formation in pursuit of stem-mammal remains.

Here, we report the results of this Polish-Danish expedition to the Fleming Fjord Formation which took place from 15 July – 8 August 2014. This was the fourth project of exploration of Greenland led by Polish scientists. The first Polish expedition to Greenland was organized by geographers from Lwów Uniwersity in 1934, and explored its western regions. This expedition was followed by expeditions orga-

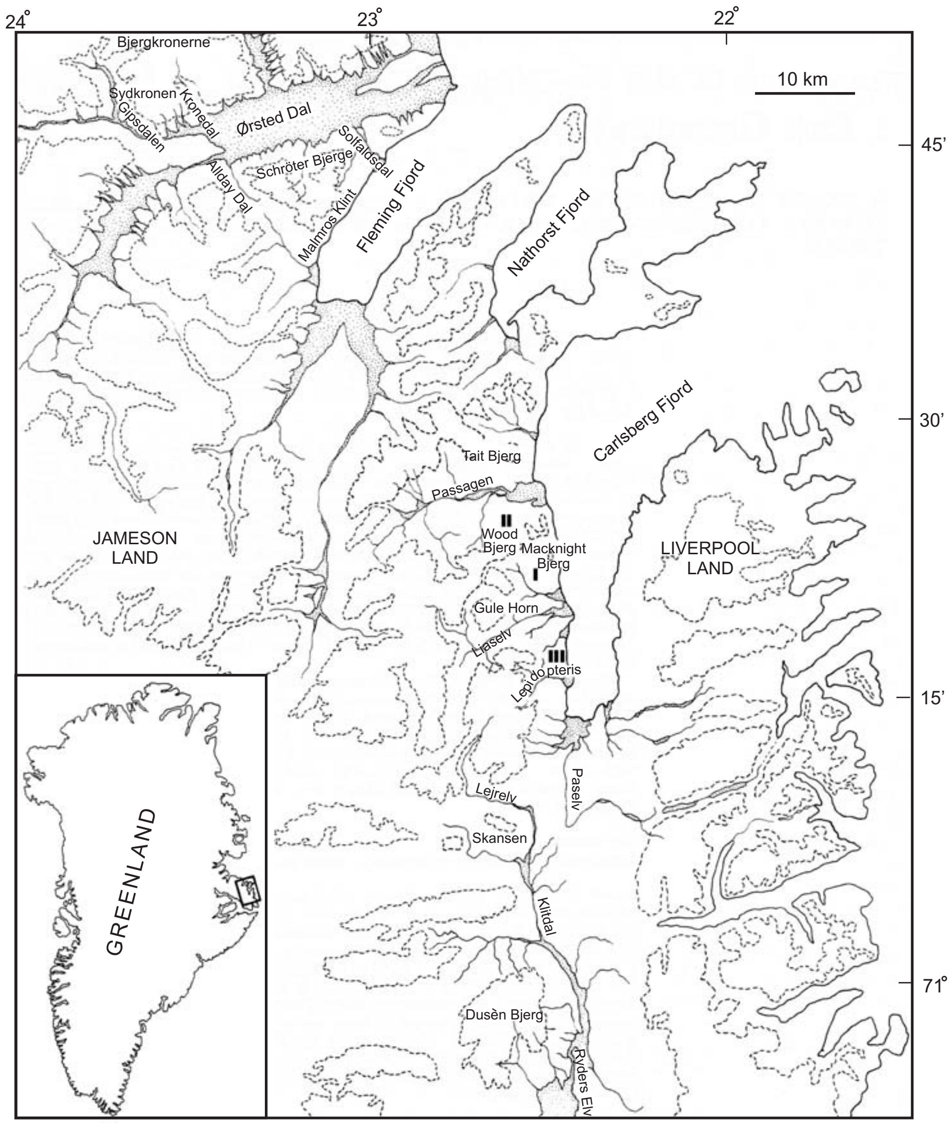

Fig. 1. Map of Jameson Land, East Greenland, with areas surveyed during this expedition highlighted (MacKnight Bjerg – I, Wood Bjerg – II, Liasryggen – III; modified from Jenkins *et al.* 1994).

nized by the Polish Geographic Society in Lwów and the Military Geographic Institute in Warsaw in 1937 and by a group from Wrocław University in 1973. The first Polish geologist to conduct research in East Greenland was Krzysztof Birkenmajer, who took part in Danish expeditions in 1971 and 1976, followed by Birkenmajer (Perch-Nielsen *et al.* 1972, 1974; Birkenmajer 1977, 2013). The locations surveyed during this expedition were the relatively well known MacKnight Bjerg and Wood Bjerg and the virtually unexplored Liasryggen located on the western coast of

Carlsberg Fjord (Fig. 1). Although the collected material is awaiting extensive, detailed studies, preliminary investigation shows that the faunal diversity of the Fleming Fjord Formation is higher than previously thought. Furthermore, both body and trace fossils provide us with new information about the evolution and behaviour of Late Triassic Greenlandic vertebrates.

Geological setting

The expedition focused on prospecting for fossils in three areas on the western coast of Carlsberg Fjord (Fig. 1). These localities were MacKnight Bjerg (base camp at 71°22'14.5" N; 22°34'56.7" W), Wood Bjerg (71°24'88" N; 22°33'17" W; after Jenkins *et al.* [1994]) and Liasryggen (base camp at 71°17'53.2" N; 22°30'53.4" W). Whilst MacKnight Bjerg and Wood Bjerg are well known localities that have been explored by previous palaeontological expeditions to the Fleming Fjord Formation (Jenkins *et al.* 1994; Milàn *et al.* 2012), Liasrygeen was virtually unexplored, only briefly mentioned by Jenkins *et al.* (1994) as a largely unproductive area. A total of 18 days was spent in the field – 10 days at MacKnight Bjerg, 1 day at Wood Bjerg and 7 days at Liasryggen.

In all three localities the Malmros Klint and Ørsted Dal members of the Fleming Fjord Formation were surveyed for fossils. The Malmros Klint Member consists of lake deposits more than 100 m thick (Fig. 2) and is composed of conglomerates, fine-grained sandstones, red siltstones and palaeosols (Clemmensen *et al.* 1998). The Ørsted Dal Member can be further subdivided into the lower Carlsberg Beds and the upper Tait Bjerg Beds. The Carlsberg Beds are 80–115 m thick deposits composed of layers of structureless red mudstones and grey siltstones (Clemmensen *et al.* 1998). The upper Tait Bjerg Beds, 50–65 m thick, can be further subdivided into a lower unit with intraformational conglomerates or thin sandstones, red mudstones, greenish mudstones and yellowish marlstones and an upper unit with greyish mudstones and yellowish marlstones (Clemmensen *et al.* 1998). The sedimentological features of the Fleming Fjord Formation show evidence of cyclicity and seasonal and long-term climate change. The sedimentology of the Malmros Klint Member suggests deposition in a climate fluctuating between very dry and moderately dry. In the Ørsted Dal Member, the Carlsberg Beds were probably deposited in constant, dry climatic conditions, while the Tait Bjerg Beds sedimentology suggests a shift from a dry to more humid conditions during sediment deposition (Clemmensen *et al.* 1998).

Some vertebrate trace fossils were found on the surface of sedimentary rock slabs at the base of the Fleming Fjord Formation in a valley between MacKnight Bjerg and Wood Bjerg. Although this might suggest their association with the basal Edderfugledal Member, the sedimentology of these slabs indicates affiliation with higher strata of the Fleming Fjord Formation.

Review of vertebrate groups and their trace fossils

The majority of the material collected during the expedition still awaits preparation and detailed investigation, but a preliminary account of the findings demonstrates the diversity of fossil taxa in the Fleming Fjord Formation and its potential on broadening our knowledge about the biogeography, taxonomy and evolution of Late Triassic faunas.

Fishes. — Remains of fishes belonging to different taxonomic units have been found at multiple sites within the MacKnight Bjerg and Liasryggen areas. Actinopterygian fossils have been found in both the Malmros Klint and Ørsted Dal members. The majority of the collected material is of poor quality and consists of scales or fragmentary bones. However, one site located within the Malmros Klint Member of MacKnight Bjerg (71°22'58.2" N; 22°33'25.8" W) was of particular interest, as it yielded the partial remains of a few individuals. This bonebed contained many dipnoan tooth plates and cranial elements of differing sizes. These remains occurred in the bonebed in association with actinopterygian remains and chondrichthyan (shark) teeth, as well as temnospondyl amphibian bones. Sarcopterygian remains have also been found in both members. It will be of interest comparing this material with the fishes found by Jenkins' group, especially at their locality 2 (Jenkins *et al.* 1994), where dipnoan teeth of *Ptychoceratodus* type were found associated with skull elements; and they also found a partial coelacanth skull, but very worn.

Temnospondyl amphibians. — The remains of the plagiosaurid *Gerrothorax pulcherrimus* were the most commonly occurring vertebrate fossils in the Malmros Klint and Ørsted Dal members of MacKnight Bjerg and Liasryggen. Although common, most of the remains consisted of isolated and fragmentary bones and parts of the dermal armour. The most complete remains, including fairly complete skulls and whole specimens came from the quarry located in the lower part of the Ørsted Dal Member at MacKnight Bjerg. This site was originally discovered and exploited by the initial Harvard expeditions and produced many complete specimens, representing different ontogenetic stages (Jenkins *et al.* 1994, 2008).

Another taxon of temnospondyl amphibian, the capitosaurid *Cyclotosaurus* cf. *posthumus* was much less common than *Gerrothorax*, with isolated and partial remains collected from only a few localities. A complete lower jaw of this taxon was found in the same quarry that yielded multiple *Gerrothorax* specimens in the lower Ørsted Dal Member of MacKnight Bjerg and a complete but heavily eroded skull was found in sediments corresponding to the uppermost Ørsted Dal Member of MacKnight Bjerg, on its southern peak. Incomplete remains, including skull and pectoral girdle elements, were also collected from the Malmros Klint Member of the Liasryggen area. As far as we know, the collected lower jaw is the only known

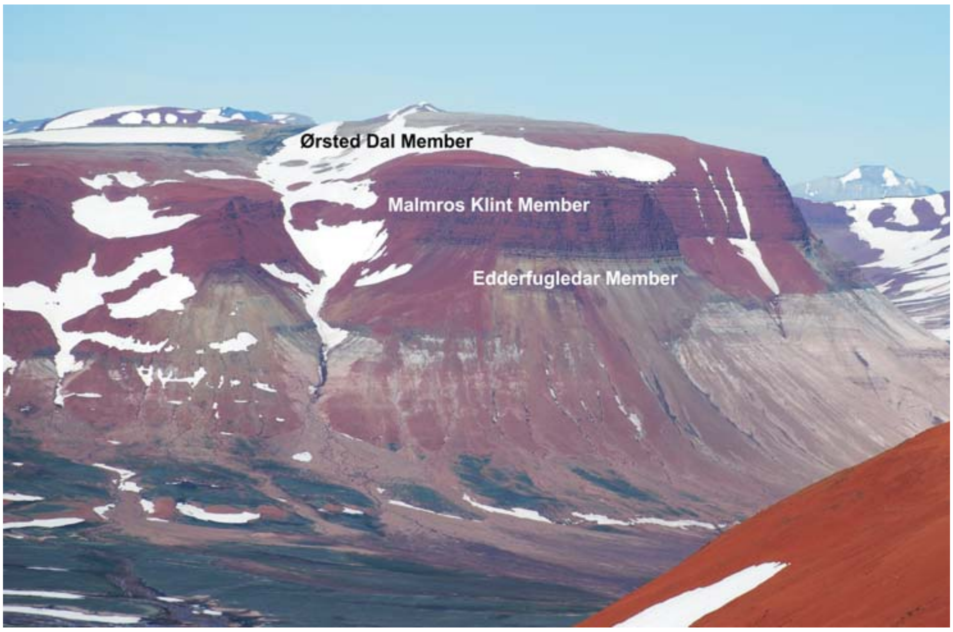

Fig. 2. Outcrops of the Fleming Fjord Formation. Tait Bjerg as seen from the Wood Bjerg summit. A formation is divided into three members. Photo by T. Sulej.

Fig. 3. Footprint of theropod dinosaur from the Malmros Klint Member of Liasryggen. Photo by G. Niedźwiedzki.

lower jaw of the Greenlandic capitosaurid and, since the taxon has been only preliminarily studied, might provide useful information for establishing its exact taxonomic position.

Archosaurs. — Archosaur remains occurred at both MacKnight Bjerg and Liasryggen and were collected from both the Malmros Klint and the Ørsted Dal members. Archosaur occurrences were fairly common but the majority of the collected remains were very fragmentary and included partially preserved vertebrae, fragments of limb and pelvic bones and isolated serrated teeth. However, a few sites produced material of better quality, including a site with limb bones associated with parts of the vertebral column found in the Ørsted Dal Member of Liasryggen and a site in the Malmros Klint Member of MacKnight Bjerg, which yielded a partial skeleton comprising the posterior part of one individual. At this stage it is difficult to determine the exact taxonomic identity of the collected archosaurian remains, but some material is probably referable to sauropodomorph dinosaurs. Jenkins *et al.* (1994) stated that the sauropodomorph remains from the Fleming Fjord Formation are referable to *Plateosaurus engelhardti* and they found a nearly complete skeleton, at present on exhibit in Geocenter Möns Klint, Mön, Denmark. However, because the sauropodomorph material from the Fleming Fjord Formation has been studied only preliminarily, assigning all the sauropodomorph material to that taxon should be treated with caution. However, the most interesting archosaur findings are some fragmentary bones of the limbs and pelvis, collected from various sites. These bones seem to preserve synapomorphies which allow us to confidently place them within basal dinosauriforms and theropod dinosaurs. Further work on the collected material might provide new and important information on the taxonomy, diversity, biogeography and evolution of Late Triassic archosaurs.

Stem-mammals. — Fossil material from a representative of the stem-mammal lineage was uncovered in the Liasryggen area. This material, comprising an incomplete mandible and associated dentition, is currently the subject of detailed study, but will undoubtedly provide new information on the evolution of the stem-mammalian lineage in the Late Triassic.

Other taxa. — Fossils representing other lineages of terrestrial vertebrates, such as turtles, and perhaps pterosaurs were also collected by our team from various sites within the explored areas. These fossils are however very fragmentary. A few bonebed layers were also identified from a couple of sites; their future investigations might increase the known fossil record of lineages poorly represented in the Fleming Fjord Formation.

It is also interesting to note that our team collected remains of invertebrates, such as freshwater bivalves and conchostracans. As well as providing new information on the evolution of these groups, they might help us to better constrain the age estimates proposed for the particular members of the Fleming Fjord Formation.

Fig. 4. Part of the team examining vertebrate footprints in transitional beds between the Malmros Klint Member and the Ørsted Dal Member at Liasryggen. From left: G. Niedźwiedzki, N. Bonde, B. Błażejowski, A. Wolniewicz and M. Tałanda. Photo by T. Sulej.

Fig. 5. Sauropodomorph trackway from the Malmros Klint Member of MacKnight Bjerg. Photo by G. Niedźwiedzki.

Tetrapod trace fossils. — More than 300 tetrapod tracks and traces (manus and pes imprints, swim traces) were recovered from different beds of the Fleming Fjord Formation (Figs 3–5). Traces are preserved mostly as natural prints or casts on the large and naturally exposed surfaces, but numerous natural casts preserved on isolated slabs were also collected from the lower and middle part of the profile. Seven distinct track-bearing intervals were identified, numerous although poorly preserved tracks were also found on mountain slopes. The most common imprints represent tridactyl traces of supposed dinosauriformes, basal dinosaurs or basal theropods (*Anchisauripus* isp.) but isolated footprints and short trackways of other archosaurs and early dinosaurs (cf. *Brachychirotherium* isp., cf. *Apatopus* isp., cf. *Atreipus* isp., Chirotheriidae indet., *Grallator* isp., *Eubrontes* isp., cf. *Evazoum* isp., *Eosauropus* isp., cf. *Tetrasauropus* isp.) were also found. Very enigmatic pentadactyl tracks, possibly of stem-mammal affinity, and traces made by swimming tetrapods are also discovered. The provisionally identified ichnotaxa represent at least nine different kinds of trace makers. Newly discovered material requires more detailed study. For example, further study of the large and oval-shaped tracks could provide new information about the morphology of the manus and pes of Late Triassic sauropodomorphs, as well as information about the size and behaviour of these dinosaurs (Niedźwiedzki *et al.* 2014). The preliminary data suggest that the Late Triassic tracksites of the Fleming Fjord Formation include a truly great ichnotaxonomic diversity of tetrapod trace fossils and preserve many large oval-shaped tetrapod tracks that appear different than these from Late Triassic sites.

Conclusions

This initial look on our survey of the Fleming Fjord Formation provides new perspectives in studies of the Late Triassic of East Greenland. New material of previously discovered, but poorly studied, taxa might be useful in determining their exact taxonomic position. Material representing new archosaur and stem-mammal taxa provides additional information on the evolution of these two important lineages and increases the known diversity of the Fleming Fjord Formation vertebrates. Rich and well preserved vertebrate trace fossils also indicate that the diversity of the Fleming Fjord Formation tetrapod faunas is even greater than previously thought, and will perhaps provide additional information about locomotion and behaviour of Late Triassic vertebrates. Our findings, which are subject of ongoing study, demonstrate the need for further fieldwork in the Fleming Fjord Formation and other Late Triassic sites in order to get a full understanding of the faunal compositions in ecosystems of the Late Triassic Northern Pangaea.

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