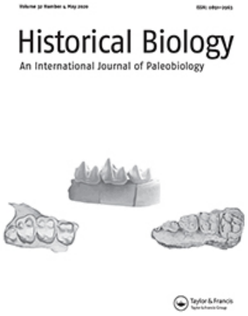

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ARTICLE

# Timing of dicynodont extinction in light of an unusual Late Triassic Polish fauna and Cuvier's approach to extinction

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**ABSTRACT**
Dicynodont therapsids are prominent elements of Triassic continental faunas, but the date of their demise is controversial, linked either to end-Carnian faunal turnover or to end-Triassic mass extinction. The second timing is based on a unique, giant dicynodont-theropod dinosaur fauna from Lipie Śląskie, Poland, thought to be Rhaetian in age, due to conjectural botanical and conchostracan (but not tetrapod) evidence. On the other hand, an age assignment for the Lipie fauna to the mid-Norian (Revueltian) has been demonstrated recently by regional integrative stratigraphic data. To test once more this still debated age assignment, we recall the rationale of Georges Cuvier in the study of the fossil record ('the best documents of Earth's past are fossilized large tetrapods'). This approach was applied successfully 200 years ago to the species extinction dilemma. In light of the worldwide distribution of dicynodonts, the alleged compositional paradox of the 'Rhaetian' fauna from Poland can be significantly reduced by its recognition as a more 'normal' early-middle Norian assemblage. The simple megafaunal correlation appears to be conclusive. Thus, there was a major pulse of dicynodont extinction at the end of the Carnian, with the final extinction of the few remaining species happening in the Norian.

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Upper Triassic; Upper Silesia; vertebrates; dicynodonts; Georges Cuvier; species extinction

## Introduction

Dicynodont therapsids were a characteristic herbivorous element of continental communities from the middle Permian to the Late Triassic, and medium- to large-sized species (about 3 m long) thrived during the Triassic (Tucker & Benton 1982; Benton 1983; Lucas 1994, 2018a; Fröbisch 2008, 2009; Sues and Fraser 2013). The decline of this long-lasting and successful synapsid group, which survived the end-Permian ecosystem apocalypse ('bottleneck'), is differently interpreted, as stressed by Irmis (2011, p. 398). This extinction has been correlated either to the minor end-Carnian faunal turnover (advocated multiple times by Benton 1997, 2006, 2014; among others) or directly to the end-Triassic mass extinction (Pieńkowski et al. 2014). The recently generated mismatch is well expressed in a review paper by Benton et al. (2014), in which the early Norian timing of dicynodont demise is quoted (p. R90, R92), but their temporal range is shown up to the end of the Triassic (their Figure 2).

The second timing was promoted exclusively by an uniquely abundant Rhaetian tetrapod assemblage from Lisowice village (Lipie Śląskie Keuper clay–pit), Upper Silesia, Poland (Figure 1), called a dicynodont–theropod association (Niedźwiedzki and Sulej 2008; Dzik et al. 2008a, 2008b). A peculiar mixture of typically Triassic ('conservative') and advanced, Jurassic biotic types (respectively, giant dicynodonts and capitosaur amphibians versus gymnosperm flora, dinosaurs and pterosaurs; see also Pacyna 2014) was emphasized. Consequently, several groups of the Lipie fauna, including dicynodonts, were described as victims of the broadly-defined end-Triassic mass extinction (Pieńkowski et al. 2014; see also Dzik et al. 2008a, 2008b). These interpretations were proposed by members of a single research group from the Institute of Paleobiology, Polish Academy of Sciences and Warsaw University, named the Warsaw research group in Szulc et al. (2015a).

However, the question of the age of this unique (but tentatively only investigated) Keuper biota as well as the putative Rhaetian stage assignment of the second large-sized dicynodont locality in the region, at Zawiercie (Niedźwiedzki et al. 2014) was, in fact, neither sufficiently documented nor comprehensively discussed by the Warsaw group. On the other hand, integrative stratigraphic study by Szulc et al. (2015b) assigned a Norian age to both dicynodont-bearing successions in a broad regional perspective of the vertebrate-rich Upper Silesian Keuper (Figure 1(b); see review in Szulc et al. 2015a).

The dating of the Lipie succession, however, is still debated (see Brański et al. 2015; Szczygielski and Sulej 2016; Racki 2017; Tałanda et al. 2017; Sulej et al. 2018). In this supplementary note, to test once more the stratigraphic inference, paired with the general disparity concerning the dicynodont demise, we address the rationale of Georges Cuvier in the study of the fossil record (paraphrased as 'fossilized large tetrapods are the best documents of Earth's past'). In this conceptual context, we comprehensively review previously omitted problems of the vertebrate biochronological implications for the age of the Lipie locality (Lucas 2015a). When this seemingly intricate problem is viewed in light of the analytical approach of Georges Cuvier to the tetrapod extinction enigma during the birth of the geosciences (over 200 years ago), the oddity of the

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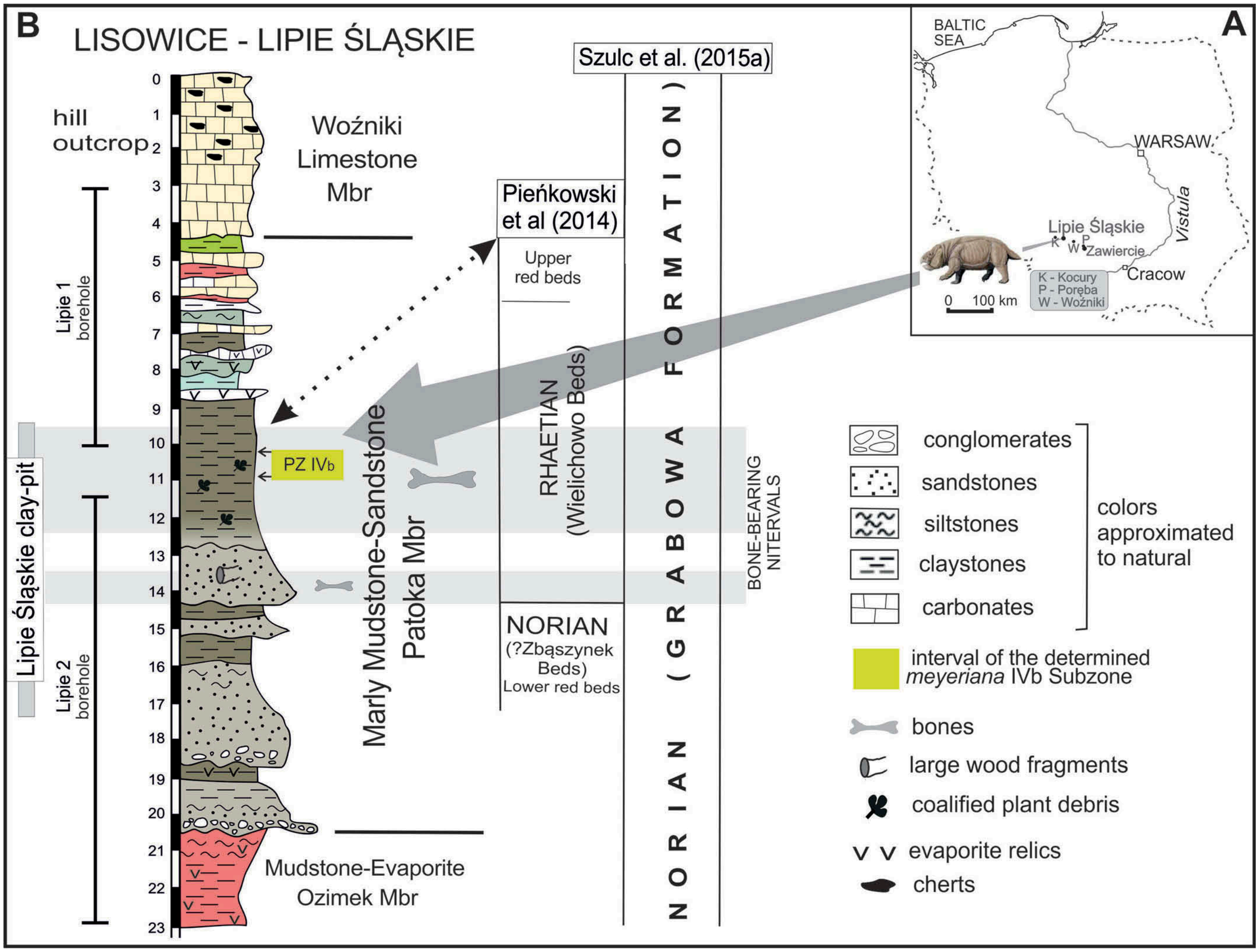


**Figure 1.** Location of two 'Rhaetian' large-sized dicynodont sites and age-related localities of the Lisowice bone-bearing level (Szulc et al. 2015b; Racki 2017; see Figure 5(b)) in Poland (A), and the crucial lithological succession of the clay pit at Lisowice – Lipie Śląskie and nearby drillings (B; adapted from fig. 5 in Szulc et al. 2015a; see also Szulc et al. 2006, fig. 5; Pieńkowski et al. 2014, fig. 4; Tałanda et al. 2017, fig. 2), with updated formal lithostratigraphy after Szulc et al. (2015b), bone-bearing intervals of the Lisowice level, and palynologically-dated interval (Fijałkowska-Mader et al. 2015). The stratigraphic diagnosis of Pieńkowski et al. (2014; fig. 4) is given for comparison; note the seriously over-estimated thickness of the upper part of the Lipie pit section by the Warsaw group (12 m instead of 8 m; marked by arrows).

alleged Rhaetian fauna can be significantly reduced by its confirmation as a more 'normal' Norian assemblage. This confirmed age assignment has serious implications for the recently created puzzle of dicynodont extinction.

## Stratigraphic setting of the last dicynodonts and previous age interpretations

The clay pit in Lipie Śląskie at Lisowice village near Lubliniec was active, with some interruptions, from 1928 to 2013, and was known in the geological literature since 1980. The ca. 8 m thick fluvial succession includes mostly greenish, reddish, and grey claystones and siltstones, interbedded with stratified sandstones and limestone (oncoid-bearing; Tałanda et al. 2017) intercalations (Figure 1(b)). Pieńkowski et al. (2014, p. 272) interpreted the bone-bearing facies of Lipie as: '(…) a mosaic of alluvial-plain environments swamps with ephemeral ponds and laterally shifting river channels'. In a palynofacies context, a lacustrine (or, more accurately, stagnant water) habitat was also proposed by Fijałkowska-Mader et al. (2015).

This excavated Keuper section of man-made exposure was stratigraphically extended by two shallow drillings in its immediate vicinity (Lipie 1 and Lipie 2), studied by Szulc et al. (2006). In lithostratigraphic terms, the fossiliferous series belongs to the Patoka Marly Mudstone-Sandstone Member (= Steinmergelkeuper) of the Grabowa Formation (Szulc et al. 2015b; Racki 2017). As documented in boreholes, these strata at the clay pit are sandwiched between the red-colored Ozimek Mudstone-Evaporite Member (= the Upper Gypsum Keuper) and Woźniki Limestone Member, a marker unit in the local stratigraphy (Szulc et al. 2015b; Figure 1(b)). This locality was thought of as the locus typicus of the Lisowice bone-bearing level, which likely encompasses at least five vertebrate sites, including Zawiercie, widely distributed in the Upper Silesian region (see Figure 1(b); Racki (2017), Tałanda et al. (2017)).

The rich bone material was discovered and has been exploited by the Warsaw research group since 2006, but the collection work became practically stopped after 2013 because of the recently abandoned flooded excavation. The first

**Figure 2.** A. The young Georges Cuvier (1769–1832; portrait by François-André Vincent 1795, https://upload.wikimedia.org/wikipedia/commons/7/78/Georges_Cuvier_3.jpg). B. Plate from Cuvier's (1806, plate 5) in-depth memoir on living and fossil elephants, showing a distinctive morphological separateness of mammoth jaw (fig. 4) as a starting point to the species extinction principle.

papers, already advocating a definite Rhaetian age, were published in 2008 (Niedźwiedzki and Sulej 2008; Dzik et al. 2008a, 2008b). Awkwardly, most of the supporting paleontological evidence, with a focus on well-preserved plant remains, is contained in a popular-science article in Polish only, without individual citation of primary references (Dzik et al. 2008b). Subsequently, Dzik et al. (2008a, p. 737), in a brief report, concluded: 'Taken together, both macrofloral and palynological evidence indicates Rhaetian as the age of the Lisowice site,' supported in addition by 'unusually small-sized' conchostracans. Finally, Pieńkowski et al. (2014, p. 269) clarified the age of the entire succession as 'latest Norian and early (possible also younger) Rhaetian'.

Also, another locality of giant dicynodonts in the Silesian region, at Marciszów in Zawiercie city (Budziszewska-Karwowska et al. 2010; Szulc et al. 2015a), addresses a similar disagreement. When the Norian age was accepted, mostly after palynostratigraphic data, by Szulc et al. (2006), Figure 5; (2015a)), Budziszewska-Karwowska et al. (2010), and Sadlok and Wawrzyniak (2013), a correlation with the Rhaetian Lisowice locality was proposed by Niedźwiedzki et al. (2014). On the other hand, the third dicynodont-bearing locality of the Lisowice level (Woźniki), characterized by a medium-sized (ca. 2 m) kannemeyeriiform species, was assigned to the upper Carnian by Sulej et al. (2011), (2018)), but mostly based on the poorly-documented conchostracan fauna and tetrapod correlations (see critical comments in Szulc et al. 2015a, p. 601).

It is thus surprising that such a poorly supported biostratigraphic conclusion on the Rhaetian age of the Lipie section has been repeated many times without any critical attention. Most recently, authors of the Warsaw research group claim that stage assignment at this site cannot be resolved in the light of available, indecisive data (Brański et al. 2015; Szczygielski and Sulej 2016) or simply quote both dates as equally reliable alternatives (Tałanda et al. 2017; see also Racki 2017; Sulej et al. 2018). Altogether, new arguments are necessary in this ongoing polemical debate, particularly from vertebrate paleontology and biochronology.

## Vertebrate aspects

Significantly, converse to another famous Silesian Keuper Lagerstätten at Krasiejów (Dzik and Sulej 2007; see also Szulc et al. 2017; Sulej et al. 2018), vertebrate evolutionary arguments were never analyzed and explicitly used in their biochronological context in the case of the Lipie assemblage. However, its assignment to the Rhaetian age had some serious implications for the evolutionary picture of the leading Keuper tetrapod groups, as noted by some authors (reviewed in Szulc et al. 2015a). Since the beginning, the unusual character of the 'Rhaetian' Lipie fauna was particularly demonstrated by relic but uniquely large-bodied dicynodonts. Thus, in the interpretation of Pieńkowski et al. (2014), the members of the definitely Rhaetian fauna with large therapsids, temnospondyls and pseudosuchians, were eventually exterminated as late as during the end-Triassic mass extinction. Furthermore, a recognition of such surprising long-term persistence of typically Carnian faunal elements (dicynodonts and capitosaur amphibians) indicates a peculiar zoogeographic character and/or a unique kind of localized taphonomic window in the Polish Keuper strata, which are, in fact, usually marked by very low fossilization potential.

In this dispute context, we draw attention to a fundamental line of reasoning in answer to the species extinction question, introduced conclusively by Georges Cuvier over 200 years ago, with reference to a key paleontological dilemma of that time: the existence or demise of ancient elephants.

## Species extinction and large bones: Cuvier's line of reasoning

The great French naturalist, Georges Cuvier (Figure 2(a)), 'perhaps the finest intellect in nineteenth-century science' (Gould 1987, p. 113), is famous mostly as a founder of vertebrate paleontology and zoological systematics. However, in the context of the recently revived theory of geological catastrophes (Ager 1993), Cuvier, beginning with his first systematic papers on the bones of ancient elephants, had also highlighted an application of the inevitable succession of more and more complex fossils, especially tetrapods, to the understanding of Earth history (Cuvier 1796, 1800, 1806; Cuvier et al. 1807; Figure 2(b)). As summarized by Adams (1938, p. 265):

> A further very important contribution to the progress of science made by Cuvier was the establishment of the fact that these bones were not the remains of animals belonging to species which still survived but that they belonged to allied forms which had now become extinct. He also recognized that certain forms were confined to certain beds or formations. This caused him to seek for the reason why certain animals had been abundant on the earth's surface at one period and had then disappeared.

The idea of species extinction was indeed essential but controversial in the time of the emergence of geology and paleontology as real scientific disciplines (also in the context of forthcoming biostratigraphy; see Rudwick 1997, 2005). This concept, unacceptable even for the leading naturalists of the Enlightenment epoch (see in-depth review in Green 1959; Grayson 1984), was in notable opposition to the sacred dogma of the God-created steady biosphere, containing species that lived forever after their creation.

In the distinguished essay, *Discours Preliminaire*, which opens Cuvier's first great monograph, *Recherches sur les Ossemens Fossiles* (1812), he explicitly expressed the notion that fossilized large-sized tetrapods ('quadrupeds') are the most reliable documents of Earth's past. In the chapter entitled *Of the small probability of discovering new species of the larger quadrupeds*, after an in-depth examination of the literature, Cuvier emphasized that 'all the larger species of quadrupeds, which possess any peculiar or remarkable character (…) at the present day, were known to the ancients' (from the first English translation by Kerr – Cuvier 1813, p. 72). He, in the end, concluded that:

> ….none of the large species of quadrupeds, whose remains are now found imbedded in regular rocky strata, are at all similar to any of the known living species; that this circumstance is by no means the mere effect of chance, or because the species to which these fossil bones have belonged are still concealed in the desert and uninhabited parts of the world and have hitherto escaped the observation of travelers; but, that this astonishing phenomenon has proceeded from general causes (Cuvier 1813, p. 87–88).

Cuvier was well aware of the limitations of negative evidence, so he avoided a strict claim of extinction for ammonites and belemnites due to the scarce information on modern marine fauna then available. However, he maintained that knowledge of large tetrapods, studied so intensively since ancient times, was already sufficient to produce an accurate picture of their temporal distribution. Importantly, Cuvier wrote only about 'small probability' (or, more literally, a 'peu d'espérance' – Cuvier 1812; p. 39; 'little hope' – Rudwick 1997; p. 207), but not about conclusive evidence with regard to the discovery of large-sized species identical to ancient taxa (see also Grayson 1984). The disappearing quadrupeds had been exemplified by him since 1796 by the Siberian mammoth (Figure 2(b)), but, implicitly, he finally recapitulated that:

> we have ascertained and classified the fossil remains of seventy-eight different quadrupeds, in the viviparous and oviparous classes. Of these, forty-nine are distinct species hitherto entirely unknown to naturalists (Cuvier 1813, p. 103),

that is, they likely represent extinct species.

### *Some still-extant implications*

In recent biostratigraphical terms, Cuvier rightly determined the 'last appearance datum' (LAD) of the giant tetrapods, and placed it chronologically ca. 5000–6000 years age, in causal link to the last global revolution on Earth's surface. More exactly, however, the LAD could be considered as located sometime between this 'great and sudden' catastrophe and ancient times (which is to say, between 2000 and 5000 years ago), if the fauna survived locally after this cataclysm. We know today that the latest population of woolly mammoth vanished on Wrangel Island 3700 years ago (Pecnerova et al. 2016), and this matter remains a key element of the polemics of the Pleistocene megafaunal demise (see review in Cohen 2002; Levy 2011) .

The inductive generalization of Cuvier implied that available data were in fact sufficient to claim that 'absence of proof' approximates 'a proof of absence' (compare recent discussion in logic – Holes 2005). 200 years later, uncertainty about whether mammoths are still hiding among the living biota is a relic logical fallacy of 'argumentum ad ignorantiam.' The effective line of reasoning (opening, indeed, the door to the scientific study of mass extinctions) leads us to identify a general 'Cuvier's principle': 'Hard parts of large-sized, characteristic and common organisms, in particular vertebrates, are of primary significance in interpretation of the fossil record, including biochronological inferences.'

Spectacular-sized bone material, in addition to its increased fossilization potential, at all times will be preferentially collected and investigated. The terrestrial record of vertebrate microremains would more likely be primarily a record of collection intensity (in contrast to intensively studied marine microfossils, such as conodonts and planktic foraminifers), due to their less charismatic nature. In fact, the question of negative evidence is *a priori* crucial in biostratigraphy as it is invariably linked to fossil ranges (Salvador 1994), determined by the species non-occurrence below and above the recognized sampling-controlled range (biased also by a physical gap or preservation effect, or a migration event; cf. concept of stratal events of Johnson 1979).

A fundamental weakness still exists with respect to widely used Upper Triassic terrestrial biozonal taxa (see below). In this context, the distribution of the megafauna in space and time is in general well acknowledged, and that can provide important arguments with regard to disputed Keuper correlations and biozonations.

## Application to the Lipie fauna

It is significant that correlation of the Lipie locality has hitherto ignored the vertebrate fossils as a clue to its precise age; only botanical and invertebrate fossil arguments have been directly cited as the basis for a Rhaetian age (see critical review in Szulc et al. 2015a). Indeed, acceptance of a late Norian or, in particular, a Rhaetian age for the Lipie vertebrates disregards the evidence that the vertebrates, themselves, present that suggests the locality is older, mostly likely of early-middle Norian age (= Revueltian sensu Lucas 2010). Vertebrate taxa documented and/or listed from this locality include, among others, amphibians, dinosauromorphs, dinosaurs and poposaurids, the endemic large archosaur *Smok wawelski*, a giant-sized (more than 4 m) dicynodont and the mammaliaform *Hallautherium* (Dzik et al. 2008a, 2008b; Niedźwiedzki et al. 2012; Pieńkowski et al. 2014; Świło et al. 2014).

Looking into the tetrapod assemblage, it is very clear that the various taxa present have different biochronological value in the light of Cuvier's approach, as quoted above (Figure 3). Of course, this is still a provisional interpretation, because only one species of uncertain phylogenetic status has been described, but even taxonomic identification to the level of orders and families permits us to outline a precise age inference. Furthermore, the correlative value of low-level taxa is frequently restricted by endemism.

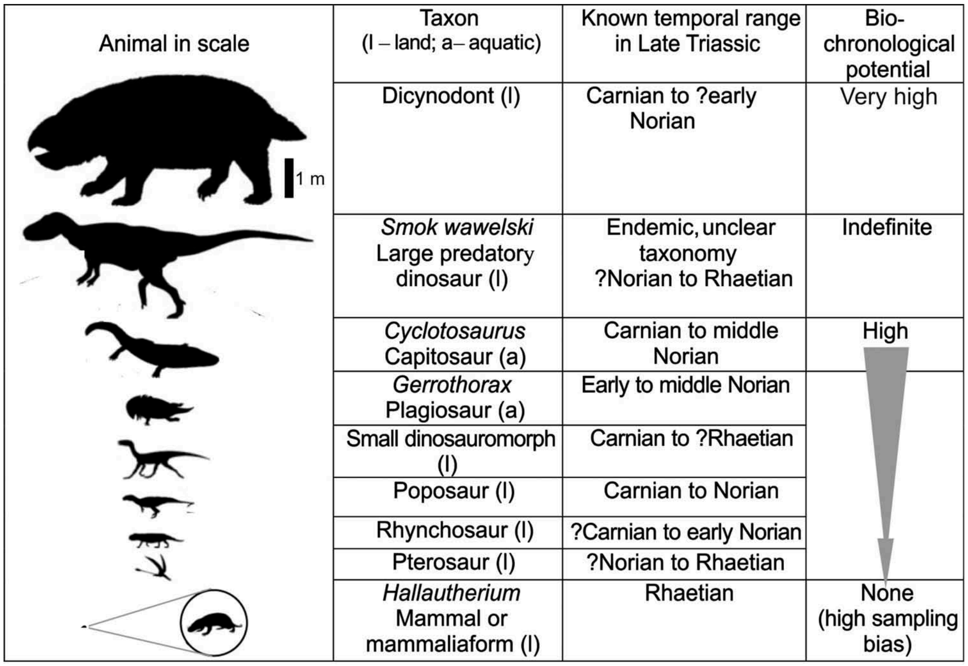
Among three large-sized groups, all Late Triassic dicynodont records, other than at Lipie, are regarded as Carnian, except for one early(?) Norian record from Argentina (Lucas 2010, 2018a), a recently reported early-middle? Norian record from South Africa (Kammerer 2018) and records from Brazil that some workers consider to be Norian (Langer et al. 2018; but see another stage concept in Lucas 2018a).

Note that assigning a Norian (instead of a late Carnian) age to the famous *Placerias* quarry near the base of the Chinle Group in Arizona, USA, an extensive dicynodont bonebed, is based on a questionable detrital zircon age of ~ 219 Ma from that stratigraphic level published by Ramezani et al. (2014). As Lucas (2018b) noted, the *Placerias* quarry is stratigraphically below older detrital zircon ages from the lower-middle part of the Chinle Group published earlier by Ramezani et al. (2011). Furthermore, biostratigraphy based on palynomorphs, conchostracans and tetrapod vertebrates also indicate a late Carnian (Adamanian) age for the *Placerias* quarry, so we do not consider it a Norian dicynodont locality.

The Lisowice level amphibians *Cyclotosaurus* and *Gerrothorax* co-occur in Germany in the Löwenstein Formation (lower Stubensandstein), long regarded as of early Norian age (though most records of *Cyclotosaurus* are older than early Norian, and a few may be as young as middle Norian). This co-occurrence of the two amphibian genera reported from Lipie is in the same broad basin of deposition (Germanic basin), and provides another strong basis for correlating Lipie to a level in the Norian (Lucas 2015a). Despite the low correlation potential of both groups (Figure 3), rhynchosaur records are (notably) no younger than early Norian, and there are important Norian records of pterosaurs (Lucas 2010; Spielmann et al. 2013). The Lisowice level aetosaur is *Paratypothorax*, and the turtle material has been referred to *Proterochersis* (Poręba, likely also at Zawiercie; Szczygielski and Skawiński et al. 2017; Szulc et al. 2017), both genera known elsewhere from Norian (Revueltian) strata. Thus, a parsimonious correlation of the vertebrate fossils from Lipie, using the well-known dicynodont, aetosaur, turtle and amphibian records, studied globally for more than 100 years, indicates the locality is no younger than middle Norian (Revueltian), as this requires no particular stratigraphic range extensions of these taxa. Indeed, other than the dicynodont, the Lipie tetrapod assemblage is dominated by typical early-middle Norian (Revueltian) taxa (Lucas 2015a).

As noted above, Dzik et al. (2008a, p. 737) highlighted an occurrence of advanced (Jurassic-type) elements as an indirect argument for the Rhaetian age of Lipie. The presence of the large 'advanced theropod dinosaur' (*Smok wawelski*) is indeed more probable in the Rhaetian than Norian. But, the taxonomic status of this endemic species still remains unclear, as concluded by Niedźwiedzki et al. (2012), even if it later was again quoted as 'a large basal predatory dinosaur' in Pieńkowski et al. (2014; Figure 3). This taxonomic uncertainty invalidates the correlative significance of the rare (?endemic) species. Indeed, stage-of-evolution arguments as to age are inherently weak. In addition, Brusatte et al. (2010) stressed the fact that Triassic theropods (*Gojirasaurus, Liliensternus*) similar in large size to the Silesian species had already been reported from the Norian of Germany and New Mexico, USA.

The mammaliaform tooth from Lipie assigned to *Hallautherium* (elsewhere known with certainty from Rhaetian strata only) could be used to argue for a younger age, but the stratigraphic ranges of many microvertebrates are certainly not as well established as are those of larger and long-studied taxa because they are profoundly biased by collecting intensity, exemplified by the surprisingly young, Norian record of the diapsid *Palacrodon* recently documented by Kligman et al. (2018). The biostratigraphic significance is also highly uncertain in the case of the other undescribed, mainly reptilian elements of this assemblage (Figure 3).



| Animal in scale | Taxon<br>(l – land; a– aquatic) | Known temporal range in Late Triassic | Bio-chronological potential |
|---|---|---|---|
| 1 m | Dicynodont (l) | Carnian to ?early Norian | Very high |
| | *Smok wawelski*<br>Large predatory dinosaur (l) | Endemic, unclear taxonomy<br>?Norian to Rhaetian | Indefinite |
| | *Cyclotosaurus*<br>Capitosaur (a) | Carnian to middle Norian | High |
| | *Gerrothorax*<br>Plagiosaur (a) | Early to middle Norian | |
| | Small dinosauromorph (l) | Carnian to ?Rhaetian | |
| | Poposaur (l) | Carnian to Norian | |
| | Rhynchosaur (l) | ?Carnian to early Norian | |
| | Pterosaur (l) | ?Norian to Rhaetian | |
| | *Hallautherium*<br>Mammal or mammaliaform (l) | Rhaetian | None<br>(high sampling bias) |

**Figure 3.** Schematic representation of the vertebrate assemblage from Lipie Śląskie (based on fig. 9 in Pieńkowski et al. 2014; some taxa are omitted) to show the contrasting values of particular taxa for age interpretation (in light of Cuvier's approach to the species extinction question). Biochronological potential is thus approximated by a combination of body size and preservation/collection probability.

## Integrative regional arguments for a Norian age

One key argument concerning the dating of the Lisowice bone-bearing level is its position below the Woźniki Limestone Member, a regional marker unit of mid-Norian age, in the revised lithostratigraphic scheme of Szulc et al. (2015b). The correlation of the 8 m thick Lipie section with the regional reference section of Szulc et al. (2015b), based on composite borehole successions, allows establishment of its temporal equivalence with the middle segment of the Patoka Member characterized locally by gray to blackish, sandstone-conglomerate to claystone in graded cyclic deposits, up to 20 m thick, in places with abundant plant debris and sporadically with bones. The Lisowice level is therefore located in the regional stratotype between 100 m and at least 180 m below the assumed Rhaetian mudstone series, marked by light kaolinite clays and siderite-concretionary horizons (Szulc et al. 2015a; fig. 17, 2015b; fig. 10), as well as by an overall absence of carbonate and hematite admixtures (Środoń et al. 2014; Racki 2017). Crucial independent support is provided by the chemostratigraphic analysis by Środoń et al. (2014), based mostly on Cr/Ti and Cr/Nb ratio trends. In this scheme, the Lisowice fossiliferous level was assigned to chemozone II, and therefore to the middle Norian. The very recent U/Pb dating of a single zircon grain from the Lipie Śląskie locality as 211 ± 3 Ma (Kowal-Linka et al. 2018) confirms an overall Norian age, and the mid-Norian position is clear under the 'short Rhaetian' concept (Figure 5(b)).

Thus, the Lisowice bone beds are considered to be middle Norian (Revueltian) in age, refined conclusively as the lower slice of the middle *Classopollis meyeriana* Palynozone (IVb, Fijałkowska-Mader et al. 2015; Figure 1(b); compare Nitsch 2018, Figure 3 therein). This conclusion agrees well with the climatostratigraphic inferences of Środoń et al. (2014) and Szulc et al. (2015a). The Lisowice bone-bearing deposits records a mid-Norian pluvial-tectonic episode in a semi-arid climatic setting, whereas the Rhaetian interval in this part of Europe is characterized by far more intensive wet conditions as the result of a long-term shift toward a humid climate (see the Scania reference succession in Figure 5(a); see also Tanner 2018)).

## Timing of dicynodont extinction

Two principal conceptions are involved in the timing of dicynodont extinction (Figure 4). As highlighted above, due to the conjectural Rhaetian age assigned to the Lipie site, the final disappearance of dicynodonts was causally linked to an increasing volcanic cataclysm of the end-Triassic mass extinction (*sensu lato*), i.e., 'between the middle Rhaetian and earliest Hettangian' (Pieńkowski et al. 2014; p. 282; see also Dzik et al. 2008a, 2008b; Benton et al. 2014; Figure 2 only).

Conversely, in the four editions of the well-known textbook on vertebrate paleontology, Benton (1997; 2014; also Benton 2006) claimed that a faunal turnover at or near the end of the Carnian resulted in the disappearance of all dominant herbivore groups (dicynodonts, most herbivorous cynodonts and the rhynchosaurs), and this niche was taken by rapidly radiating dinosaurs. In fact, Benton had proposed this hypothesis already in the 1980s (Tucker & Benton 1982; Benton 1983), but the exact timing of dicynodont extinction was initially assigned to the middle Norian; in a recent paper (Benton et al. 2014), this turnover is again re-assigned to the early Norian.

As stressed by Irmis (2011), these varying age determinations were forced by a serious uncertainty concerning the position of the Carnian-Norian boundary, paired with

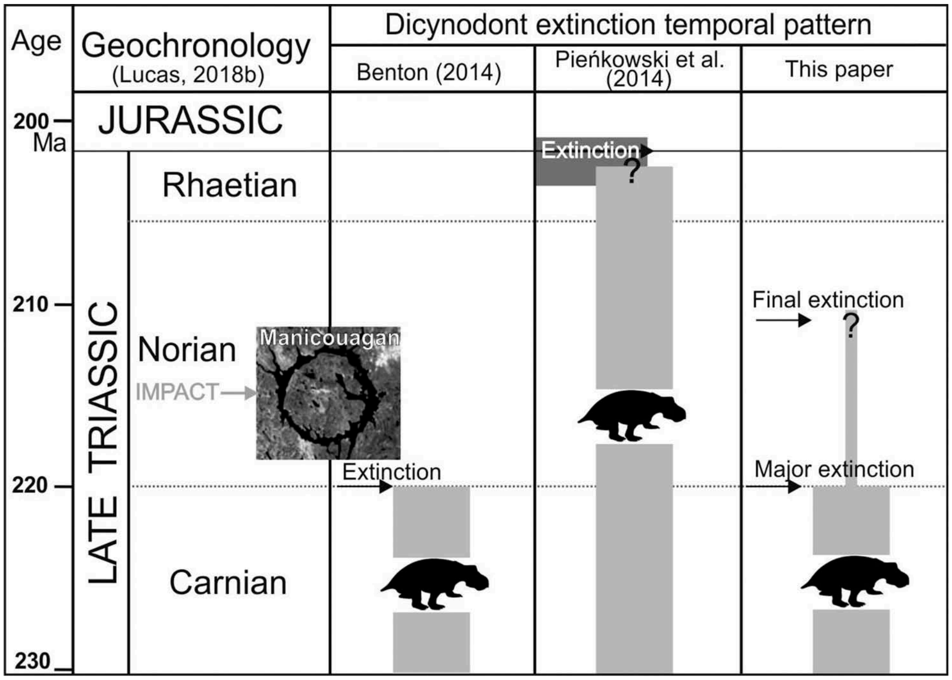


**Figure 4.** Three main alternatives of the timing of dicynodont extinction, as proposed by Benton (2014, fig. 6.13) and Pieńkowski et al. (2014; cf. figs 8 and 9), and the two-step pattern implied by the Cuvier reasoning principle applied to the Lipie fauna (fig. 3), versus a timing of the 85 km diameter Manicouagan impact structure in Quebec (http://www.passc.net/EarthImpactDatabase/manicouagan.html). Note that the end-Triassic extinction was in fact seen as a prolonged multiphase crisis by Pieńkowski et al. (2014; compare Lucas & Tanner 2018), and that Norian ages of the dicynodont extinction were also proposed in Benton's papers (middle Norian: Tucker & Benton 1982, Benton 1983; early Norian: Benton et al. 2014).

transferring some bone-rich formations from the Carnian to Norian. He also concluded that 'there is no evidence either for a Carnian–Norian extinction of rhynchosaurs, dicynodonts and "gomphodont" cynodonts', nor for their evolutionary replacement by herbivorous dinosaurs (Irmis 2011, p. 411). Similar hesitations were expressed in several earlier papers (e.g. Hallam & Wignall, 1997, pp. 145–147; Brusatte et al. 2010; also compare Lucas 1994). However, Lucas and Tanner (2018) and Lucas (2018a) confirmed the real status of a Carnian-Norian boundary extinction event and evolutionary turnover in the terrestrial tetrapod and marine records, followed by two extinction pulses during the Norian, i.e., dicynodont demise succeeded by the decline of rauisuchians, most temnospondyls (including capitosauroids) and cynodonts.

All combined arguments, addressed above, clarify doubts concerning the highest occurrence of dicynodonts and the timing of their extinction (thus, by abandoning the Rhaetian age of the Lipie fauna). Remarkably, the unnamed Lipie dicynodont represents the largest known species, probably just before the total extinction of dicynodonts in the unique Silesian refugium, in accordance with Cope's Rule. Animal lineages tend to evolve toward large size, but such populations are more susceptible to environmental stress (Hone and Benton 2005). Among Late Triassic vertebrates, however, this was an extremely rare case according to the body size analysis by Sookias et al. (2012), which shows a trend of decreasing size in post-Carnian therapsids.

This final demise of dicynodonts took likely place during one of two Norian extinction events in terrestrial vertebrates (Lucas and Tanner 2018; fig. 15.15; Lucas 2018a), well after a major turnover in dicynodonts across the Ladinian-Carnian boundary (Fröbisch 2008) followed by a faunal collapse near the Carnian-Norian boundary (Figure 4). At the regional refugium scale, after thriving during the mid-Norian pluvial interlude (Szulc et al. 2015a), the dicynodont decline was likely promoted by increasing climatic aridity that resulted in shrinking and evolving (toward conifer-dominated) trophic resources, and/or increasing evolutionary competition between herbivorous therapsids and archosauromorphs (see Tucker & Benton 1982; Benton 1983, 2014; pp. 149–150; Irmis 2011; Sookias et al. 2012).

In a wider paleogeographic perspective, the transient tetrapod acme in the Lisowice level was probably at least partly promoted by the rapid wetting of climate in the domains located north of the Tethys during the middle Norian (Alaunian), an effect of the orogenic uplift of the Cimmerian Mountains (Onoue et al. 2018). On the other hand, the above quoted faunal turnovers may have been influenced also by the Norian Manicouagan impact in eastern Canada (Olsen et al., 2011; see summary in Racki 2012; Clutson et al. 2018; Figure 4), as evidenced by the marine plankton (Onoue et al. 2016).

Pieńkowski et al. (2014) designated several other typically Late Triassic (Carnian-Norian) groups, the Plagiosauridae, Rhynchosauria, 'Rauisuchia' and Pseudosuchia, as having also eventually collapsed during a broadly defined end-

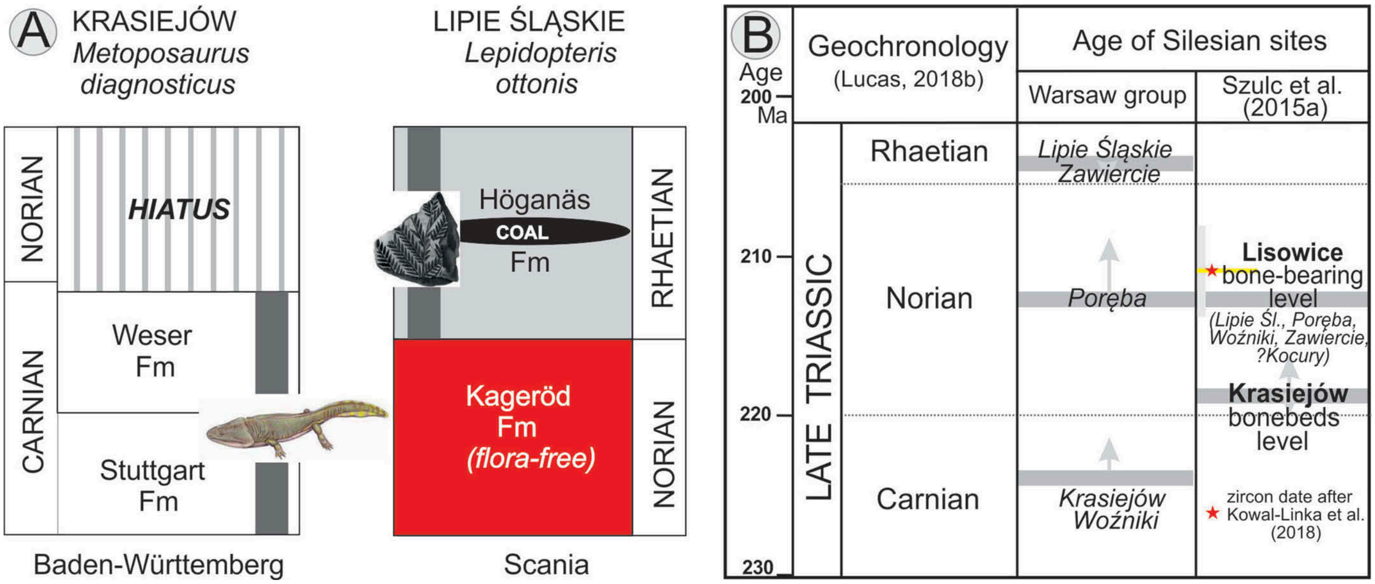


**Figure 5.** A. Inconclusive correlation data for Silesian vertebrate localities due to incomplete fossil succession in the hitherto preferred Keuper reference sections in Germany and Sweden, with emphasis on selected key species (e.g. Dzik and Sulej 2007; Pacyna 2014), across the Carnian-Norian (overlying the major Eo-Cimmerian hiatus) and Norian-Rhaetian boundaries (underlying barren redbeds; see Dobruskina 1994; p. 48; Erlström and Guy-Ohlson 1998; Lucas 2015a, 2018a; Szulc et al. 2015b, 2017). B. Diagram showing the main differences in dating of bone-bearing Keuper deposits in Upper Silesia, in interpretation proposed by the Warsaw author group and by Szulc et al. (2015a; fig. 19 modified after Racki 2017; Lucas 2018b). Uncertainty in the timing of the Upper Triassic stages is marked as gray, broken boundary lines, as well as the extent of timing ambiguity for particular bone-enriched horizons (light gray arrows), shown for both alternative proposals.

Triassic global event. However, as Lucas and Tanner (2018) recently discussed, the amphibian, archosaur and synapsid (and many other lineages) extinctions of the Late Triassic are not a single catastrophic extinction at the Triassic-Jurassic boundary, but instead occur stepwise, beginning in the Norian and extending into the Hettangian.

## Final remarks and conclusions

Porter (1977, p. 158) stressed that 'Cuvier saw fossils within perspective of the entire history of life', thus 'bursting the limits' of both space and time (Rudwick 2005, p. 591). As a matter of fact, the view that fossilized large-bodied vertebrates are the best documents of Earth's past is obviously prejudiced by paleontological knowledge that has dramatically increased since Cuvier's time. As shown conclusively above, however, the simply rational (indeed parsimonious) approach is fruitful to the key question of the dicynodont disappearance datum. The use of only insufficiently documented non-vertebrate data (Figure 5(a)) led previously to a flawed age interpretation of the Lipie succession and thereby an interpretation of dicynodont demise biased toward end-Triassic volcanic cataclysm. This ambiguous claim is in contradiction to the biochronological reasoning presented above, derived directly from the vertebrate record in accordance with Ockham's razor (Figure 3), that clearly indicates support for a middle Norian age assignment to the Lipie locality (as was already proposed by Szulc et al. 2006).

Following Szulc et al. (2015a), we stress that the general and methodological weaknesses of Upper Triassic stratigraphy, starting with a lack of stage stratotypes and discontinuous stratigraphic record (Nitsch 2018), are wholly manifested in the case of variously dated Upper Silesian tetrapod localities (Figure 5(b)). For example, the conchostracan-based zonation is believed to be an efficient alternative tool to palynostratigraphy (Kozur and Weems 2010), but has been based frequently on incomplete taxonomy and uncertain terrestrial-marine correlation (Becker 2015; Scholze and Schneider 2015), and also on single-locality succession data. As claimed aptly by Nitsch (in Szulc et al. 2015a, p. 614), 'biostratigraphy of the Keuper has always been a kind of a quiz game that has lost the answer cards.' In fact, in the greater Germanic Basin we do not know the details of succession across the vaguely-defined Upper Triassic stage boundaries in non-marine settings for tetrapod faunas (owing to a regional tectonic event, the Eo-Cimmerian discordance, which biases the record of the Carnian-Norian transition; Szulc et al. 2017) or for macrofloras (assumed previously to be crucial for identifying the Rhaetian Stage at Lipie; Figure 5(a)).

An appropriate inter-basin documentation of the full stratigraphic ranges of taxa is in an incipient stage of study at this point. In this case, a fundamental constraint of the Polish Triassic has an essential significance for vertebrate evolutionary biochronology, defined by detailed documentation and the plausible understanding of evolutionary lineages and the ranges of chronospecies in the case of phylogenetic correlation and biozonation (phyletic events of Johnson 1979). As claimed by Kligman et al. (2018, p. 125), 'other than the well-developed biostratigraphic zonations of phytosaurs and aetosaurs . . ., the use for Triassic biostratigraphy of taxa known only from specific skeletal elements, including microvertebrate taxa, should be utilized with caution'. Another symptomatic case from evolutionary biochronology of putative tetrapods from the Polish Devonian: without the fortunate finds of age-diagnostic conodonts in the famed Eifelian tetrapod footprint (Niedźwiedzki et al. 2010; or fish nests: Lucas 2015b) locality at Zachełmie, Holy Cross Mts, the purely phylogenetic approach would even result in a serious error (i.e., assignment to the Givetian or Frasnian).

As discussed by Lucas (2015a, 2018a), the Norian age of the Lipie assemblage matches the global zoogeographic pattern well. Therefore, the proposal by the Warsaw group, that the 'Rhaetian' tetrapod fauna from Lipie represents a compositional paradox and was an apparent long-lasting refugium for some groups like dicynodonts, can be definitely abandoned. In summary, the reliable megafaunal argument appears to be conclusive despite the uncertainties of Keuper biochronology, in particular generally supporting the traditional view of the end-Carnian dicynodont demise, even if the last populations persisted diachronously into the Pangean Norian (Irmis 2011), exemplified perfectly by the Silesian faunas (in accordance with Cope's Rule).

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